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Interrelationships and evolution of the east Asian grass lizards, *Takydromus* (Squamata: Lacertidae)

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The east Asian lacertid lizard genus, *Takydromus*, is well-defined but its relationships to other primitive Palaearctic lacertids are still uncertain and, although it has similarities to the lower Miocene *Miolacerta*, *Takydromus* does not appear to be identical with this. The 16 or 17 recognizable species are reviewed and a key provided for their identification; the remaining area of uncertainty about species boundaries is the *Takydromus sexlineatus* group in Assam. A phylogeny for *Takydromus* is estimated using a data set of 35 morphological characters drawn from external features, skeleton and soft-parts. There are two main constituent clades which may be informally recognized as *Takydromus s.s.* and *Platyplacopus*. *Platyplacopus* is subtropical and perhaps relict, whereas *Takydromus* ranges from temperate to tropical areas. The two clades have different ranges of eggs per clutch. In both of them, elongate forms that climb extensively in flimsy vegetation have evolved and have independently acquired similar features that confer performance advantages in this situation. Interestingly, the order of assembly of these features is markedly different.

ADDITIONAL KEY WORDS: — phylogeny – natural history – evolution – character assembly – clutch size – *Miolacerta* – *Platyplacopus*.

CONTENTS

INTRODUCTION

The lacertid genus *Takydromus* consists of 16 or 17 species widely distributed in eastern Asia. In this paper common features of the genus are reviewed as are its

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species and their relationships to each other and the natural history and evolution of the group. Many of the characters referred to here are discussed more fully elsewhere (Arnold, 1989a). Literature dealing with the genus has been usefully listed by Walley (1993).

BMNH - British Museum (Natural History), now the Natural History Museum, London.

Takydromus Daudin

Takydromus Daudin, 1802: 251. Type species: *Takydromus quadrilineatus* (= *T. sexlineatus*).
Tachysaurus Gray, 1845:52. Type species: *Takydromus tachydromoides* (Schlegel, 1838).
Platyplacopus Boulenger, 1917: 231. Type species: *T. keuhnei* Van Denburgh, 1909.
Apeltonotus Boulenger, 1917: 233. Type species: *Takydromus dorsalis* Stejneger, 1904.

Distinctive features of *Takydromus* that are likely to be derived, on the basis of comparison with outgroups to the Lacertidae and restricted distribution within that family, include: tricuspid posterior teeth (posterior cusp sometimes secondarily reduced), no anterior descending processes of frontal bones, palpebral bone with an elongate posteriorly directed process, postorbital and postfrontal bones fused; mid-vertebral neural spines on body of post-pygal caudal vertebrae laterally compressed and bladelike, higher than the posterior neural spine; clavicles and interclavicle usually flanged; temporal scales keeled in most cases, postmental shields reduced to three or four pairs, at least the outermost of the ventral scales keeled and pointed, dorsal scales with single keels that form continuous more or less parasagittal ridges, at least in sacral region, scales on underside of thigh all relatively large (Fig. 10), number of femoral pores on each side reduced to five or fewer; lobes of retracted hemipenis with laterally compressed or triskelial transverse section; at least the dorsal scales with a micro-ornamentation of wavy, anastomosing longitudinal ridges crossed by much finer transverse ones that are the posterior borders of the strap-shaped cells that form the oberhautchen; in forms where pale stripes are present on the dorsum these are absent in juveniles.

Of the above features, the most distinctive among lacertid lizards are tricuspid teeth (shared only with some *Gallotia*, continuous series of dorsal keels (shared with *Poromera*), rows of small scales under thigh reduced (shared with some *Adolfus*), and reduction of femoral pores to five or fewer (rare in *Lacerta vivipara*).

Primitive features of *Takydromus* and ones where both primitive and derived states occur include the following. Nasal opening of skull relatively small with little dorsal exposure of the main nasal cavity, septomaxilla simply convex above with a rounded posterior margin and a narrow anterior shelf without anterior and posterior projections (Arnold, 1989a: fig. 4a), no medial depression on snout, frontal bones separate throughout life, dorsal process of maxilla variable in shape and in its detailed relationship to the frontal bone, frontoparietal suture quite complex, pineal fontanelle present, cranial osteoderms extensively reaching or closely approaching the back of the parietal bone in medial area, contact between squamosal and parietal bones absent or present, squamosal slender or pistol shaped, quadratojugal process of jugal bone distinct, external exposure of jugal without stepped lower margin and small anteriorly, in ventral view inner crest of jugal not clearly visible behind

ectopterygoid bone, temporal scales not ossified, 14 scleral ossicles all possessing a peripheral radial portion.

Medial part of clavicle strongly expanded and consistently forming a continuous loop, interclavicle cruciform, sternal fontanelle relatively large and roughly elliptical, xiphisternal cartilages close together, marked sexual variation in number of presacral vertebrae, usually 25 or 26 (range 24–27) in males and 26 or 27 (range 25–28) in females, long free dorsal ribs more numerous than more posterior short ones, usually 3 pairs of ribs attached directly to sternum and 2 to xiphisternum but this pattern occasionally intraspecifically variable, one pair of post-xiphisternal inscriptional ribs often present and sometimes more, transverse processes on anterior autotomic caudal vertebrae simple.

Rostral scale un-narrowed and reaching nostril or not, one or two postnasal scales, if two then the upper one usually separating the supranasal from the anterior loreal, first upper labial scale reaching nostril, second supraciliary scale sometimes elongate and extended posteriorly beyond the suture between the second and third supraocular scales, lateral border of parietal scale reaching edge of parietal table anteriorly or not, occipital and interparietal scales both usually present, no transparent window in lower eye-lid, no masseteric scale in nearly all cases. Posteriorly directed collar beneath throat nearly always present though sometimes weak, mid-dorsal body scales and lower lateral scales variable in size, ventral scales in six or eight more or less straight longitudinal rows, scales bearing femoral pores more or less flat, no additional lateral scale rows on fingers or toes, subdigital lamellae smooth or tuberculate below, the more basal ones sometimes laterally expanded, no mite pockets, no blue pigment on outer ventral scales.

Tongue colour variable, nasal vestibule short, its lateral postnasal wall thin in horizontal section, kidney clearly extending posterior to level of vent, with less than half its length anterior to the sacrum. Hemipenis more or less symmetrical without a hemipenial sheath (Arnold, 1984) or armature (Arnold, 1973, 1986), cross section of lobes in uneverted hemipenis not complexly folded, lobes relatively thick-walled and long, lobe lips very small or outer ones larger and extending basally as flaps; lobe microornamentation of simple spines or rods sometimes recurved at their tips (Böhme, 1971). No marked voice; male apparently grasps female by flank in copulation (*T. tachydromoides* - Inukei, 1930, *T. dorsalis* personal observation, *T. smaragdinus* - Sengoku, 1979: 31).

Distribution. Japan, extreme southeastern Russia (Maritime Province), China, the Ryukyu archipelago, Taiwan, Vietnam, Laos, Cambodia, Thailand, Burma, Assam, Malaya, Borneo, Natuna islands, Sumatra, Bangka and Java.

Relationships of Takydromus

Takydromus belongs to the perhaps paraphyletic primitive Palaearctic assemblage of lacertids (Arnold, 1989a). It has similarities to *Lacerta vivipara* but the common derived traits are often variable in one or both taxa, so they do not provide unequivocal indications of relationship (Arnold, 1989a). The dentary and posterior lateral teeth of *Takydromus* bear superficial resemblance to those of *Miolacerta* Roček, 1984 which is known from fragments from the lower Miocene of Bohemia. As in *Takydromus*, the dentary of *Miolacerta* is slender with tricuspid posterior lateral teeth.

However, it differs in lacking a coronoid facet, the teeth are less elongate and the longitudinal edge on the roof of Meckel's groove is more elongate posteriorly (see figures in Roček, 1984).

SPECIES OF *TAKYDROMUS*

Where appropriate, modern transliterations of Chinese localities have been inserted in square brackets; these are mainly drawn from Zhao & Adler (1993).

Takydromus kuehnei Van Denburgh
Takydromus kuehnei Van Denburgh, 1909: 50. Type locality: Kanshirei [= Kuantzuling], Formosa [= Taiwan].
Takydromus chinensis Vogt, 1914: 98. Type locality: Northern parts of Kuangtung [Guangdong] Province, South China.
Platyplacopus kuehnei (comb. nov.) Boulenger, 1917: 232.
Platyplacopus kuehnei carinatus Gressitt, 1938: 129. Type locality: Ta Han [= Da'an], 775 m, central part of Hainan Island, S. China.

Range. Taiwan, Hainan and southern mainland China (Guangdong, Guangxi and Guizhou).

Remarks. T. keuhnei is the only species of *Takydromus* characterized by strong transverse expansion of the lamellae beneath its digits. Taiwan and mainland China material is generally similar, but there is minor variation in colouring and the latter may have all the ventral scales pointed and weakly keeled in young animals and males; also the series of supraciliary granules may be incomplete. *Takydromus chinensis* is based on a single male and is identical with mainland *T. kuehnei* material, apart from having only three pairs of chin shields. In fact the leftmost anterior one exhibits a suture partly dividing it into anterior and posterior sections. The male type of *Platyplacopus kuehnei carinatus* from Hainan is like some mainland China material in having all the ventral scales keeled. The discontinuity in the dorsal scale rows mentioned in the original description appears to be an individual anomaly.

Takydromus intermedius (Stejneger)
Platyplacopus intermedius Stejneger, 1924: 120. Type locality: Shin-kai-si [= Xin-kai Si], Mount Omei [Mt Emi], near Kiating [= Leshan Shi], 4400 feet, Szechwan [= Sichuan].

Range. Southwest China: Sichuan (Yachow [Yaan Shi], Mt. Emei, Süchow [= Yibin Shi], Chouchiakou [Zhoujiagou]); Yunnan (Yunnanfu [Kunming Shi]); localities mainly from Pope (1935) and Schmidt (1927b).

Remarks. Differs from *Takydromus kuehnei* in the following features: probably smaller (apparently under 50 mm from snout to vent compared to sometimes over 60 mm in *T. keuhnei*) with a less sharply pointed snout, third scale row beneath the thigh reduced, only two femoral pores on each side and the subdigital lamellae not strongly differentiated into a broad basal series and a narrower distal one; the dorsal process of the maxilla is not strongly developed, as it is in *T. keuhnei*, nor is its tip embraced by the frontal; there are 24 presacral vertebrae in the two males that have been examined compared with the 25 usually found in male *T. keuhnei*.

Takydromus dorsalis Stejneger
Takydromus dorsalis Stejneger, 1904: 294. Type locality: Ishigaki shima, Yayeyama group, Ryukyu archipelago.
Apeltonotus dorsalis (comb. nov.) Boulenger, 1917: 234.

Range. Ishigaki Island, in the Yaeyama group, southern Ryukyu Archipelago.

Takydromus sylvaticus Pope.
Takydromus sylvaticus Pope, 1928: Type locality: Ch'ungan Hsien [= Chongan], northwest Fukien [Fujian], southeast China.

Range. Known only from type locality.

Remarks. This species is similar to the allopatric *Takydromus dorsalis.* However, the head is narrower and the limbs shorter, there are more dorsal scales in a transverse row across the mid-body (41–44 compared with 28–35), the collar is less distinct, keeling on the ventral scales is confined to the outer row, whereas it may be more extensive in some *T. dorsalis.* The pale supralabial stripe found only on the head of *T. dorsalis* extends along the neck, over the insertion of the forelimb to the groin. Pope (1928) states that *T. sylvaticus* has more transverse rows of ventral scales but there is overlap in this feature. *T. dorsalis* is singular in usually having only 24 presacral vertebrae in males.

Takydromus toyamai Takeda & Ota, 1996
Takydromus smaragdinus part: Van Denbergh, 1912.
Takydromus toyamai Takeda & Ota, 1996. Type locality: Hirara, Myakojima (24°45'N 125°20'E).

Range. Myako Group, southern Ryukyu Archipelago.

Remarks. Takydromus from Myakojima were included in *Takydromus smaragdinus* by Van Denbergh (1912), who however noted distinct differences from other populations assigned to this species.

Takydromus smaragdinus Boulenger, 1887
Takydromus smaragdinus Boulenger, 1887: 147. Type locality: Loo Choo Islands [Ryukyu archipelago].

Range. Okinawa, Amami and Tokara groups, north and central Ryukyu archipelago.

Remarks. As noted by Van Denburgh (1912) there is considerable inter-island variation in *T. smaragdinus.* This is true even when animals now assigned to *Takydromus toyamai* are excluded. It is likely that the types of *T. smaragdinus* came from the central Ryukyus (Takeda & Ota, 1996).

Takydromus sauteri Van Denburgh
Takydromus sauteri Van Denburgh, 1909: 50. Type locality: Koshun [Hengchun], Formosa [Taiwan].

Range. Taiwan; also Lanyu Island (otherwise known as Lan, Koto Sho and Botel Tobago) east of southern Taiwan (Wang, 1962).

Takydromus amurensis Peters
Takydromus amurensis Peters, 1881: 71. Type locality: Kissakewitsch, Amur.
Takydromus kwangakuensis Doi, 1920: 70. Type locality: Kwyakuskan (near Seoul), Keiki Province, Korea.
Takydromus auroralis Doi, 1929: 17. Type locality: Pukhansan, Kyong-ki-do province, Korea.

Range. Russia (Maritime district), Korea and northeastern China.

Remarks. This generally primitive species has a number of distinctive features: the nasal process of the maxillary bone has no broad frontal contact, the suture between the frontal and the parietal bones does not involve strong interdigitation and forms an oblique angle on the mid-line with its point directed forwards, the number of presacral vertebrae in females varies widely from 25–28, there may be traces of a fifth pair of chin shields and the hemipenis has a series of basally directed flaps on its stem. All these features, except perhaps the traces of a fifth pair of chin shields, are likely to be apomorphic. The status of *T. kwangakuensis* and *T. auroralis* was discussed by Walley (1958a, 1962).

Takydromus wolteri J.G. Fischer
Takydromus wolteri J. G. Fischer, 1885: 82. Type locality: Chemulpo, Korea.
Tachydromus wolteri var. *cupreus* Pavlov, 1932: 9. Type locality: Man Keou.
Tachydromus wolteri var. *mandchuriensis* Pavlov, 1932: 10. Type locality: Soun and Man Keou.

Range. Russia (Maritime district), Korea and China (Jiangsu to Jiangxi westward to Hubei and eastern Sichuan – Zhao & Adler, 1993; also reported from Fujian, Anhui and Manchuria - Pope, 1935).

Remarks. Zhao & Adler (1993) have tentatively placed *T. wolteri* var. *cupreus* and *T. wolteri* var. *mandchuriensis* in the synonymy of *T. amurensis*. The original descriptions of these forms are extremely brief and the types are not available for examination (K. Adler, in litt.), so there can be little certainty about their correct allocation.

Takydromus tachydromoides (Schlegel)
Lacerta tachydromoides Schlegel, 1838: 101. Type locality: Nagasaki.
Tachydromus japonicus Duméril & Bibron, 1838: 161. Type locality: Japan.
Tachydromus holsti Boulenger, 1894a: 733. Type locality: Osen Mt., Shimabara, Japan.
Takydromus tachydromoides oldi. Walley, 1958b: 203. Type locality: Tajon, [Ch'ung-ch'ong, Pukto Province], South Korea.

Range. Japan.

Remarks. Takydromus tachydromoides oldi is known from a single specimen said to be distinguishable from the nominate form by possessing a distinct collar of three to four rows of granular scales, keeled ventrals arranged in a reduced number of transverse rows, the neck slightly narrower than head, a distinct white collar and uniform chocolate brown ground colour. In fact the type comes within the range of Japanese material referred to the nominate form. The collar, neck-shape and number of transverse rows of ventral scales are like those of other *T. tachydromoides* which also sometimes have the ventrals lightly keeled; the apparently distinctive colouring is a

preservation artifact, probably resulting from the use of strong formalin. It is uncertain whether the presence of the type of *T. tachydromoides oldi* in Korea was natural.

Takydromus hsuehshanensis Lin & Cheng
Takydromus hsuehshanensis Lin & Cheng, 1981. Type locality: Mt. Hsiao-hsueh (24°17'N 121°1'E), 2500–2950 m, Taiwan.

Range. Taiwan (Mount Hsiao-hsueh, and probably elsewhere in the Hsueh-shan range – Kano, 1923).

Remarks. This high-altitude form is the only species of *Takydromus* on Taiwan to lack keeled medial ventral scales.

Takydromus formosanus Boulenger
Tachydromus formosanus Boulenger, 1894b: 462. Type locality: Taiwanfoo [= Tainan] and central Formosa [= Taiwan].
Takydromus septentrionalis, part: Stejneger, 1907: 232.

Range. Taiwan.

Remarks. See *Takydromus stejnegeri.* Although widely collected at the end of the nineteenth century, *Takydromus formosanus* is now said to be uncommon (Cheng, 1987b).

Takydromus stejnegeri Van Denburgh
Takydromus stejnegeri Van Denburgh, 1912: 8. Type locality: Taipeh [= Taipei], Formosa [= Taiwan].

Range. Taiwan and Pescadores Islands west of Taiwan.

Remarks. The status of *Takydromus stejnegeri* has often been disputed. Boulenger (1921) regarded it as a synonym of *T. formosanus* and later workers have synonymized it with *T. septentrionalis* of the Chinese mainland (Chen, 1956; Cheng & Lin, 1977, 1978; Lin & Cheng, 1980; Liu Yu, 1970 Wang & Wang, 1956; Zhao & Yaoming, 1977). More recently its separate status has been acknowledged (Chen, 1984, Cheng & Lin, 1987 and Cheng, 1987a,b). *Takydromus stejnegeri* can be separated from *T. septentrionalis* by is often smaller size and normal-shaped head in both sexes, more longitudinal rows of enlarged dorsal scales just behind the level of the axillae, often six or more enlarged dorsal scale rows between the hind legs, a weaker collar, and more acuminate posterior dorsal scales. It usually differs from *T. formosanus* in being browner, with one instead of two pairs of femoral pores. These two broadly sympatric species can usually be distinguished but the points of difference vary from place to place. At Kanshirei [Kuantzuling] *T. formosanus* is smaller, with two femoral pores in most cases, dorsals and enlarged lateral scales less acuminate, more supraciliary granules, a better developed collar, fewer longitudinal dorsal scale-rows just behind level of axillae, less markedly recurved claws and, when a pale dorsolateral stripe is present, this is weaker than the ventrolateral one with poor development of a dark inner band.

Takydromus stejnegeri exhibits geographical variation in various features including number of supraciliary granules, number of longitudinal rows of enlarged dorsal scales at the level of the sacrum and whether pale dorsoventral stripes are present

(based in material in California Academy of Sciences). *Takydromus formosanus* also varies from place to place and it is possible that there is character displacement when it and *T. stejnegeri* are syntopic. *T. formosanus* tends to be smaller and smoother than *T. stejnegeri*, but in material from Keelung [Kiirun-To], where the latter species may be absent, *T. formosanus* is larger and rougher than usual.

Takydromus septentrionalis Günther
Takydromus septentrionalis Günther, 1864: 70. Type locality: Ningpo [Ningbo Shi, Zhejiang province, China].
Tachydromus tachydromoides (part): Boulenger, 1887: 5.
Takydromus septentrionalis, part: Stejneger, 1907: 232.

Range. China north to Jilin and Gansu.

Remarks. This large species (up to about 75 mm from snout to vent) shows strong sexual dimorphism in head size, the head of males being large with a relatively flat pileus and often some depression of the frontal and prefrontal scales. Although the ventral scales are usually keeled, this feature is very weak in a specimen from Shanghai (BMNH 74.1.16.73).

Takydromus sexlineatus Daudin
Takydromus sexlineatus Daudin, 1802: 256. Type locality: not given.
Takydromus quadrilineatus Daudin, 1802: 252. Type locality: not given.

This species has a very large range, occurring in southern China, Laos, Cambodia, Vietnam, Thailand, Burma, Assam, northern Malay peninsula, Borneo, Sumatra and Java. Except in southern China, *T. sexlineatus* is the only species of *Takydromus* found over this whole area. It shows marked geographical variation. Animals from Indonesia, Borneo, the Malay peninsula and Burma often have two femoral pores, a single row of enlarged lateral scales, a smooth dorsal head surface and no ocelli on the flanks or only very small ones. In contrast, animals from northern Malaya, Siam, northern Laos, Vietnam and southern China have single femoral pores, often two or three rows of enlarged lateral scales on each flank, frequently rough heads and usually large ocelli on the sides. These two forms have been called *sexlineatus* and *ocellatus* respectively and are usually regarded as subspecies.

Takydromus sexlineatus sexlineatus Daudin, 1802
Tachydromus sexlineatus var. *aenofuscus*. Peters, 1864: 405. Type locality: Bangkok.
? *Tachydromus sikkimensis* Günther, 1888: 167. Type locality: 'Low valleys of Sikkim'. (Stoliczka, 1872).

Range. Assam?, Burma, perhaps north Malaya, Borneo, Natuna islands, Sumatra, Bangka and Java.

Remarks. T. sikkimensis is based on a description by Stoliczka (1872) of 25 specimens from Sikkim. Some features represented in this sample are typical of *T. haughtonianus* and *T. khasensis* (see p. 275).

Takydromus sexlineatus ocellatus Guérin-Méneville
Takydromus ocellatus Guérin-Méneville 1829:. Type locality: not given (for discussion of the type description and locality see Zhao & Adler, 1993, p. 207).
Tachydromus typus Gray, 1838: 389. Type locality: China.

Tachydromus meridionalis Günther, 1864: 70. Type locality: "Southern China and probably also Cochinchina".
Takydromus kwangsiensis Ahl, 1930: 327. Type locality: Yaoshan [Dayao Shan], Kwangsi [Guangxi].
Takydromus sexlineatus ocellatus M. Smith, 1935: 368.

Range. North Malaya, Thailand, eastern Burma, Laos (?), Cambodia (?), Vietnam and South China (Hainan, Hong Kong and westward to Yunnan).

Takydromus khasiensis Boulenger
Tachydromus sexlineatus, part: Boulenger, 1887: 4.
Tachydromus khasiensis Boulenger, 1917: 221. Type locality: Khasi hills, near Assam.

Range. Khasi Hills near Assam; and perhaps north of Imphal, Assam.

Remarks. This form is similar to the widespread and variable *T. sexlineatus* and Smith (1935) regarded it as a subspecies of this form, suggesting that intermediates occurred to the south. However, the types of *T. khasiensis* have a distinctive hemipenis with a clear outer sulcal lip in each lobe which extends backward as a basally directed flap, similar to that found in members of the *Platyplacopus* clade. The animals are also particularly short-headed compared with *T. sexlineatus*; in this they resemble a female *Takydromus* from Kohuma, north of Imphal in Assam but differ from the only specimen from Cachar, Assam available to me which is also female but very long-headed.

Takydromus haughtonianus Jerdon, 1870
Tachydromus haughtonianus Jerdon, 1870: 72. Type locality: Goalpora, Assam.

Range. Known only from the type locality.

Remarks. Takydromus haughtonianus is only known from the single type specimen which it was not possible to examine during the course of this study. This form reputedly differs from *T. sexlineatus* in the following features: no posteriorly directed ventral collar on the neck, rather more elongate head, shorter tail, six rows of enlarged dorsal scales, 30 transverse series of ventral scales and four pairs of postmental scales. In fact the scale features all occur as minority conditions in *T. sexlineatus*. The status of *T. haughtonianus* and its relationships to *T. khasiensis* and *T. sexlineatus* will only become apparent when more material from Assam is available.

PHYLOGENY OF *TAKYDROMUS*

External characters and skeletal features accessible by radiography were checked on at least 15 individuals of each species, except the following where only smaller numbers were available (given in parentheses): *T. hsueshanensis* (3), *T. khasiensis* (7), *T. intermedius* (2), *T. sylvaticus* (2), *T. toyamai* (2). Cranial and hemipenial features were checked on at least three specimens of each species where possible, but fewer in the case of rare species; in one or two species some cranial and hemipenial features could not be investigated (see Table 1).

Characters used to estimate phylogeny

The distribution of these characters among species is shown in Table 1.

Skeleton

1. *Palatal processes of premaxilla slender and narrow and set at a fairly narrow angle to each other* (Fig. 1). No (0); yes (1).
2. *Premaxillary nasal process* (Fig. 2). Narrow (0); broad (1).
3. *Nasal process of maxilla narrow and extended* (Fig. 2). No (0); yes (1).
4. *Tip of nasal process of maxilla embraced by frontal* (Fig. 2). No (0); yes (1).
5. *Head distinctly depressed.* Yes (0); no (1).
6. *Squamosal bone contacting parietal* (Arnold, 1989a, fig. 5). No (0); yes (1).
7. *Posteroventral border of external exposure of coronoid bone forming an acute angle* (Fig. 3). No (0); yes (1).
8. *Posterior lateral teeth* (Fig. 3). Third cusp often very small (0); strongly tricuspid (1).
9. *Usually 26 or more presacral vertebrae in males.* Yes (0); no (1).

External features

10. *Snout elongate.* No (0); yes (1).
11. *Postnasal scales* (Fig. 4). One (0); sometimes two, the upper usually separating the supranasal scale from the first loreal (1).
12. *First supraocular scale* (Fig. 5). Usually present (0); usually absent, with the second supraocular contacting the loreal (1).
13. *A series of supraciliary granules usually present* (Fig. 5). Yes (0); no (1).
14. *Number of supraciliary scales* (Fig. 5). Usually more than three (0); three (1).
15. *Number of pairs of chin shields* (Fig. 6). Four (0); three (1).
16. *Keeling on median gular scales extends anterior to line joining ears* (Fig. 6). No (0); yes (1).
17. *Dorsal scales on forebody* (Fig. 7). All small, not in obvious longitudinal rows (0);

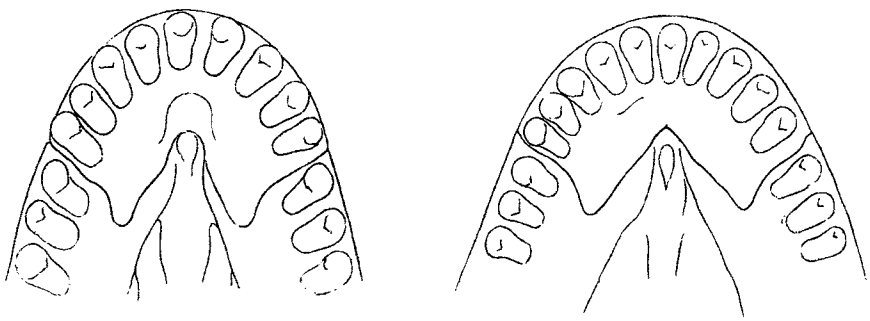

Figure 1. Ventral views of anterior skulls, showing differences in shape of the palatal processes of premaxilla and in their angle to each other. *Left. Takydromus smaragdinus*, processes slender, set at a narrow angle. *Right. Takydromus tachydromoides*, processes broader, set at a wider angle. Scale bar 1mm.

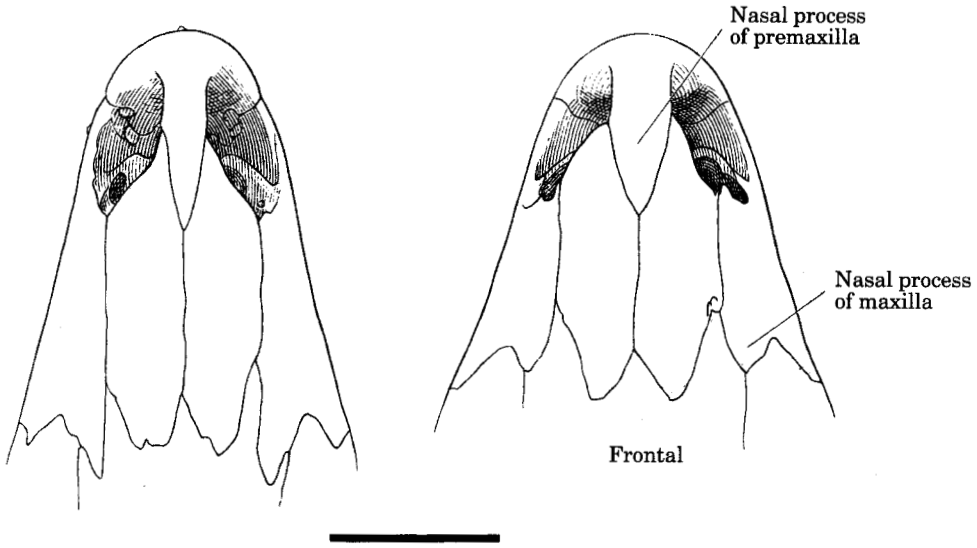

Figure 2. Dorsal views of anterior skulls, showing nasal processes of premaxilla and maxilla. *Left. Takydromus smaragdinus*, premaxillary process narrow, maxillary process narrow and embraced by frontal. *Right. Takydromus tachydromoides*, premaxillary process broad, maxillary process broad and unembraced by frontal bone. Scale bar 2mm.

more posterior scales large and in longitudinal rows but not those anterior to forelimbs (1); dorsal scales large and in longitudinal rows extending beyond forelimbs on to neck (2).

18. *Longitudinal rows of large dorsal scales between hind legs.* Eight to ten (0); six (1); four (2).

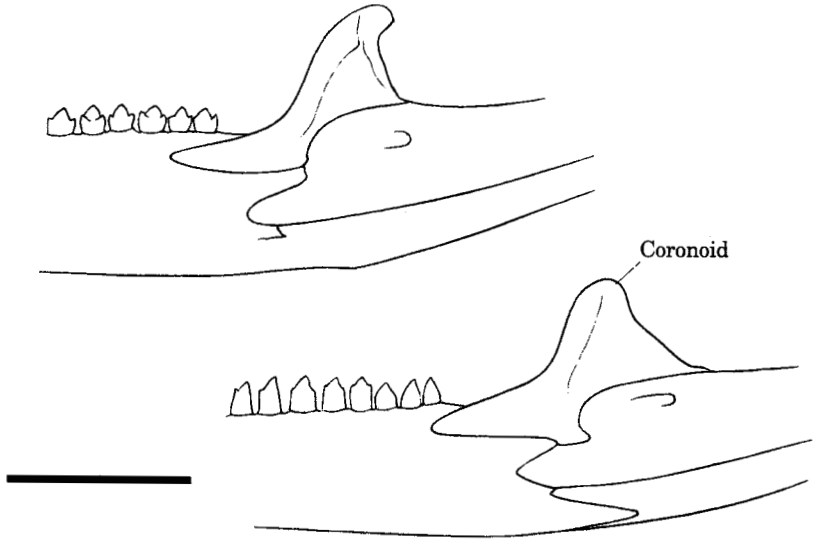

Figure 3. Outer surfaces of mandibles showing differences in the shape of the postero-ventral border of the coronoid bone and of the lateral teeth. *Above. Takydromus septentrionalis*, coronoid border obtuse, lateral teeth tricuspid. *Below. Takydromus sauteri*, coronoid border acute, posterior cusp of lateral teeth usually reduced. Scale bar 2mm.

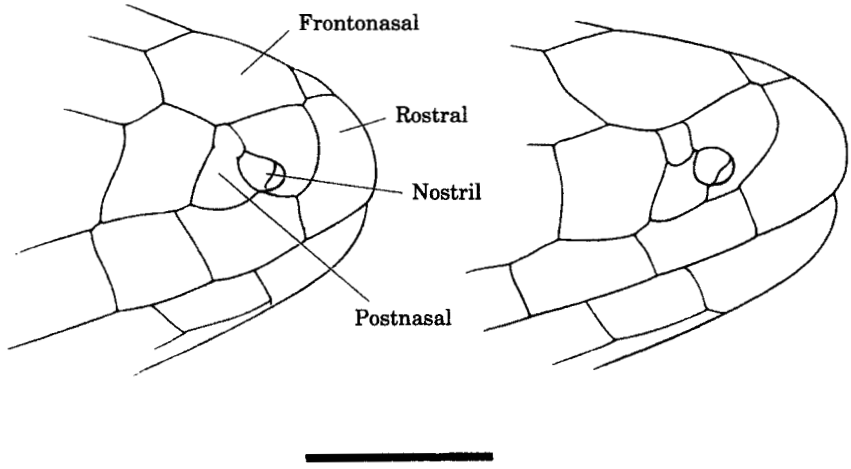

Figure 4. Snouts showing frontonasal, rostral and postnasal scales. *Left Takydromus amurensis*, frontonasal and rostral scales in contact, one postnasal. *Right. Takydromus kuehnei*, frontonasal separated from rostral scale, two superposed postnasals. Scale bar 2mm.

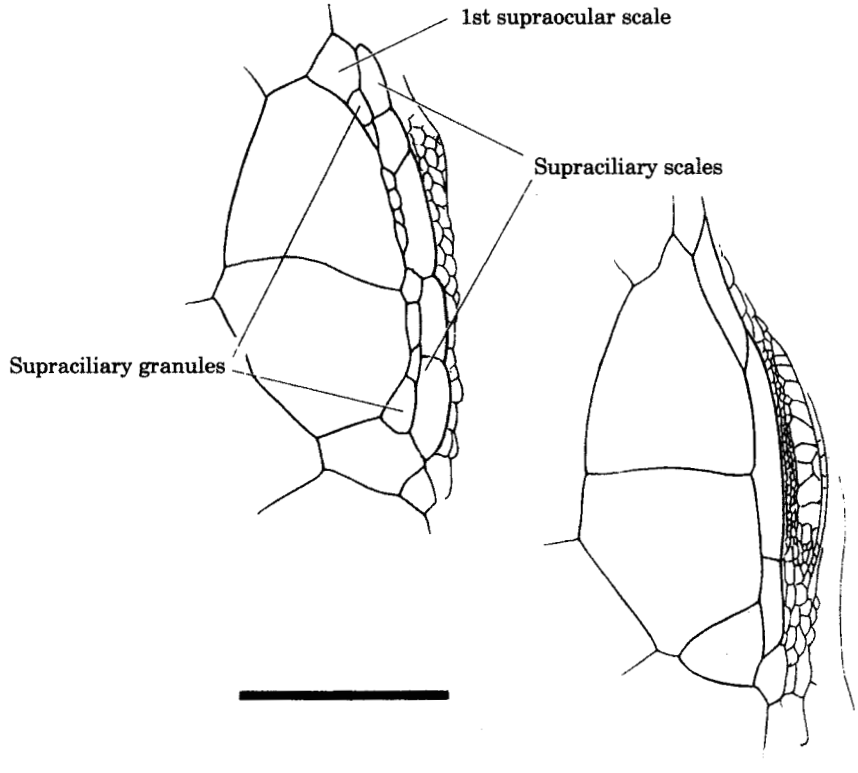

Figure 5. Area above right eye. *Left. T. amurensis*, first supraocular scale and supraciliary granules present, supraciliary scales more than three. *Right. Takydromus sexlineatus*, first supraocular scale and supraciliary granules absent, supraciliary scales three. Scale bar 2mm.

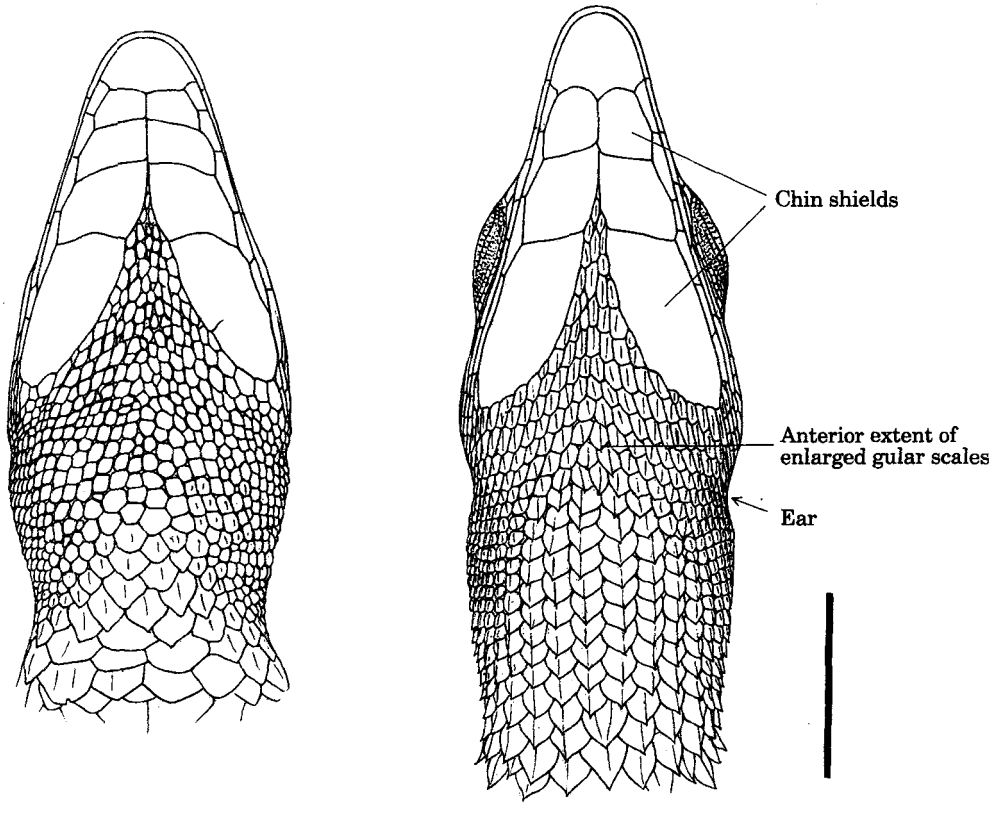

Figure 6. Underside of head and neck. *Left. Takydromus amurensis*, four pairs of chin shields, enlarged keeled median gular scales not extending anteriorly to level of ears. *Right. Takydromus sexlineatus*, three pairs of chin shields, enlarged keeled median gular scales extending anteriorly to level of ears. Scale bar 5mm.

19. *Longitudinal series of dorsal scales bordering the mid-line of tail.* Not extending on to body (0); extending on to body but diverging (1); extending as far as nape without diverging (2).
20. *Second longitudinal row of ventral scales on posterior belly usually broader than those bordering it* (Fig. 8). Yes (0); no (1).
21. *Number of longitudinal ventral scale rows.* Eight (0); six (1).

In lacertids with large lateral scales, it is often difficult to decide where these end and the equally large ventral scales begin. But in forms with small dorsal scaling easily distinguished from the ventrals, the lateral margin of the latter corresponds closely to that of the rectus abdominis lateralis muscle (Arnold, 1973). In species with large lateral scales like some *Takydromus*, this muscle can consequently be used to define the ventrals among which any scale at least partly overlying the muscle will be included.

22. *Enlarged lateral scales present* (Fig. 9). No (0); yes (1). These are lateral body-scales adjoining the ventrals in the mid-body region. They are distinctly bigger than the scales immediately above them and those in the post-axillary area.
23. *Enlarged lateral scales adjoining ventral ones as long as these* (Fig. 9). No (0); yes (1).

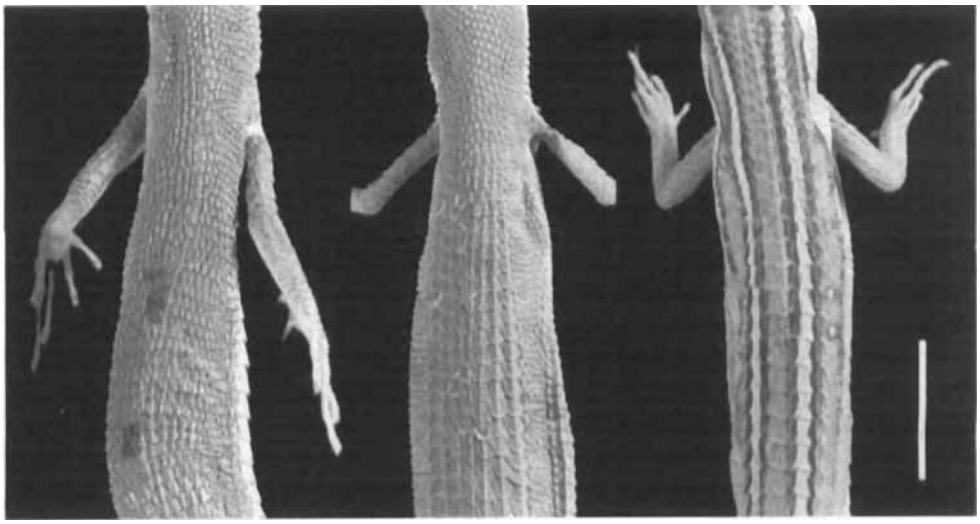

Figure 7. Dorsal scales on forebody. *Left. Takydromus dorsalis*, all scales small. *Centre. Takydromus sauteri*, more posterior scales large and in longitudinal rows but not anterior to forelimbs. *Right. Takydromus sexlineatus*, dorsal scales large and in longitudinal rows extending beyond forelimbs on to neck. Scale bar 10mm.

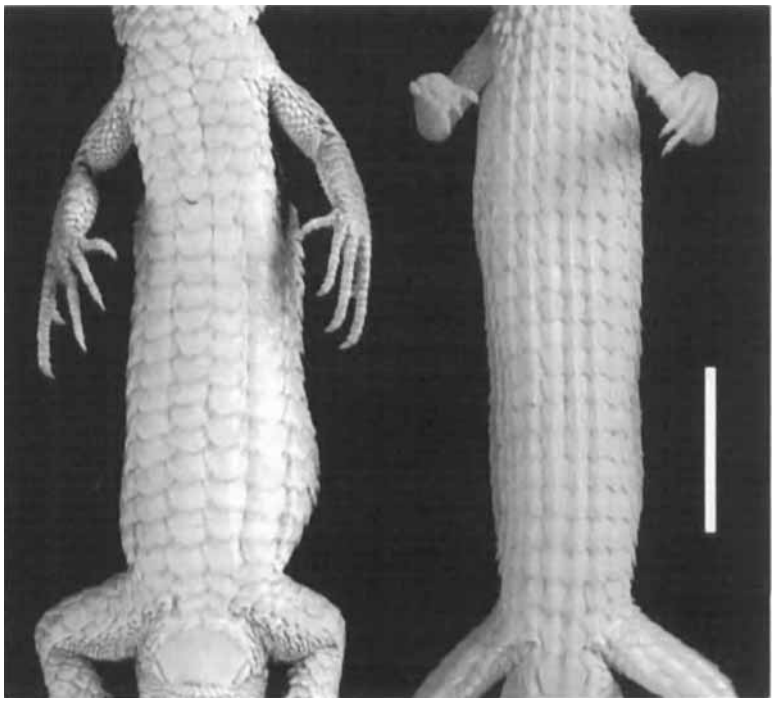

Figure 8. Ventral scales. *Left. Takydromus amurensis*, eight longitudinal rows of ventral scales, the second from the mid-line being widest and none keeled. *Right. Takydromus sexlineatus*, eight longitudinal rows of ventral scales, all keeled. Scale bar 10mm.

There are often two transverse rows of enlarged lateral scales bordering each transverse row of ventrals but, in some cases, at least the lowest lateral scales are as long as the adjoining ventrals.

24. *Ventral scales with longitudinal keels* (Fig. 8). None or outermost row of ventral scales only (0); all ventral scales (1).
25. *Series of smaller scales surrounding the preanal scale* (Fig. 10). Continuous (0); interrupted medially (1).
26. *Preanal scale divided by a longitudinal suture* (Fig. 10). No (0); yes (1).
27. *Number of femoral pores on each side* (Fig. 10). Three to five (0); two (1); one (2).

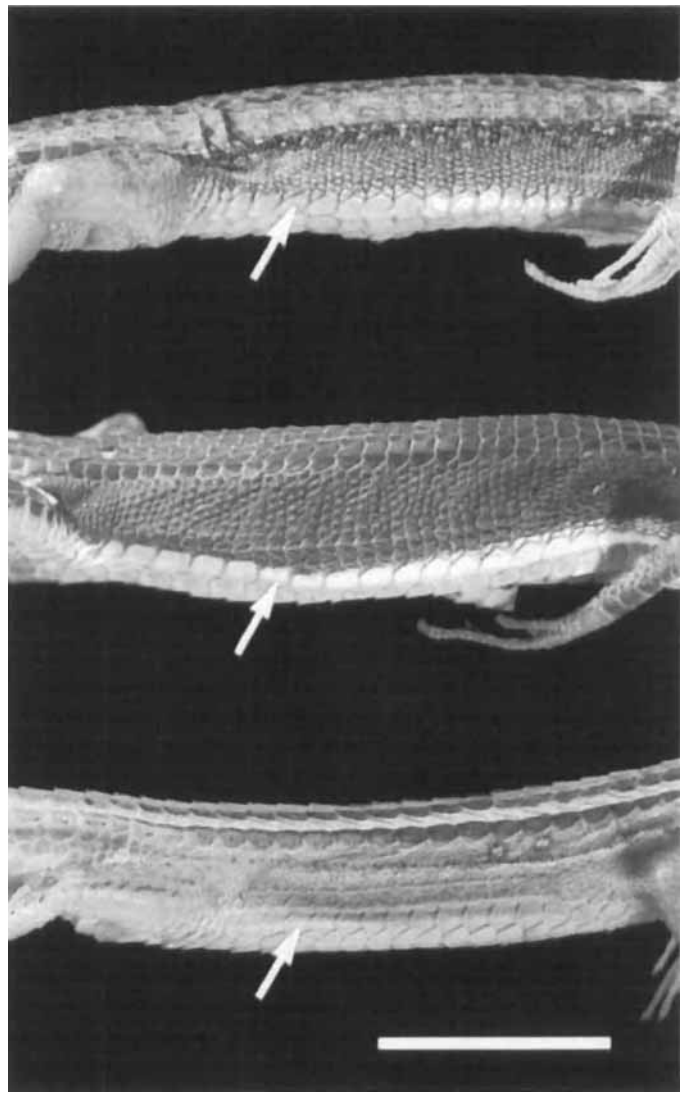

Figure 9. Lateral view of body (outermost row of ventrals arrowed). *Top. Takydromus keuhnei*, no enlarged lateral scales. *Centre. Takydromus sauteri*, enlarged lateral scales present but shorter than ventrals. *Bottom. T. sexlineatus*, enlarged lateral scales present and as long as ventrals. Scale bar 10mm.

28. *Number of rows of large scales running along underside of each thigh* (Fig. 10). Three plus traces of fourth (0); three well developed (1); three with third reduced (2); two (3).
29. *Distal part of second row of large scales beneath thigh and main subtibial scale row with keels.* No (0); yes (0).
30. *Internal tibial scale row usually with keels.* No (0); yes (1).
31. *Pale dorsolateral stripes often present on body.* No (0); yes (1).
32. *Dorsum distinctly green.* No (0); yes (1).

Hemipenis

For general structure, see Arnold (1986).

33. *Outer lips of lobe sulci produced into basally directed flaps.* No (0); yes (1).

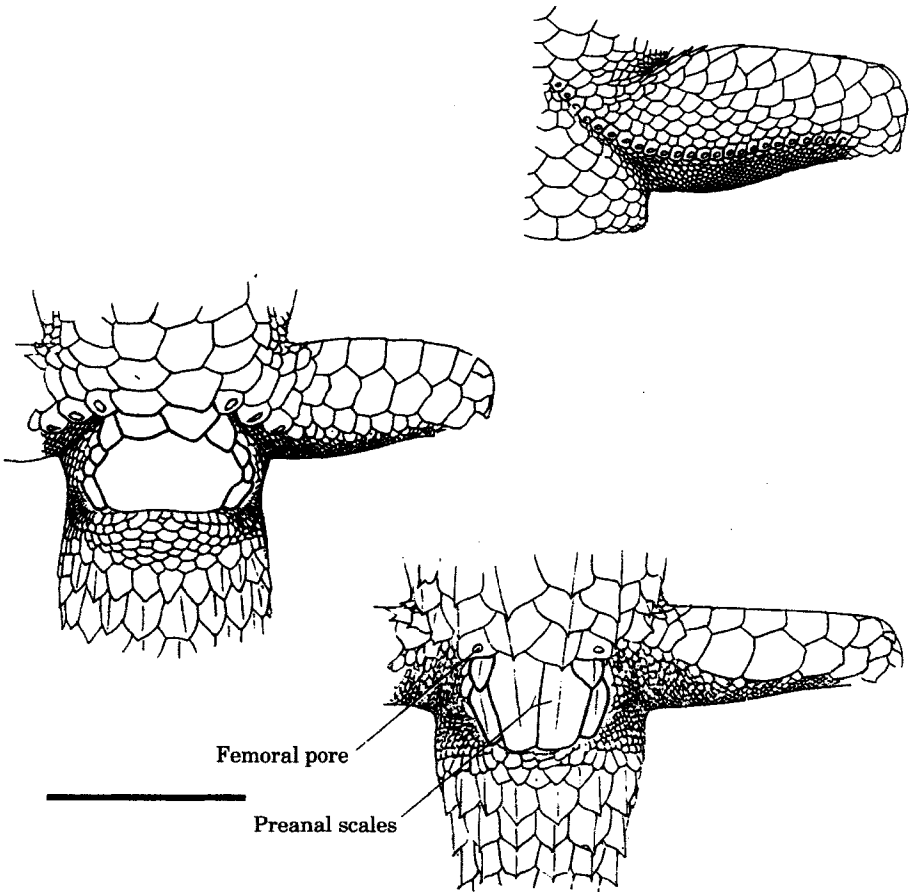

Figure 10. Vent region and underside of left thigh. *Upper right. Acanthodactylus schmidti*, showing long series of femoral pores and relatively small scales beneath thigh typical of most lacertid lizards. *Left. Takydromus amurensis*, continuous series of smaller scales surrounding preanal scale, femoral pores reduced but more than two on each side, and three rows of large scales running beneath thigh with traces of a fourth. *Lower right. Takydromus sauteri*, series of small scales around preanal scales interrupted medially, a single femoral pore on each side, and reduction in the number of rows of large scales beneath thigh to two. Scale bar 10mm.

34. Hemipenis with sulci extending into lobes. No (0); yes (1).
35. Transverse section of hemipenial lobe triskelial. No (0); yes (1).

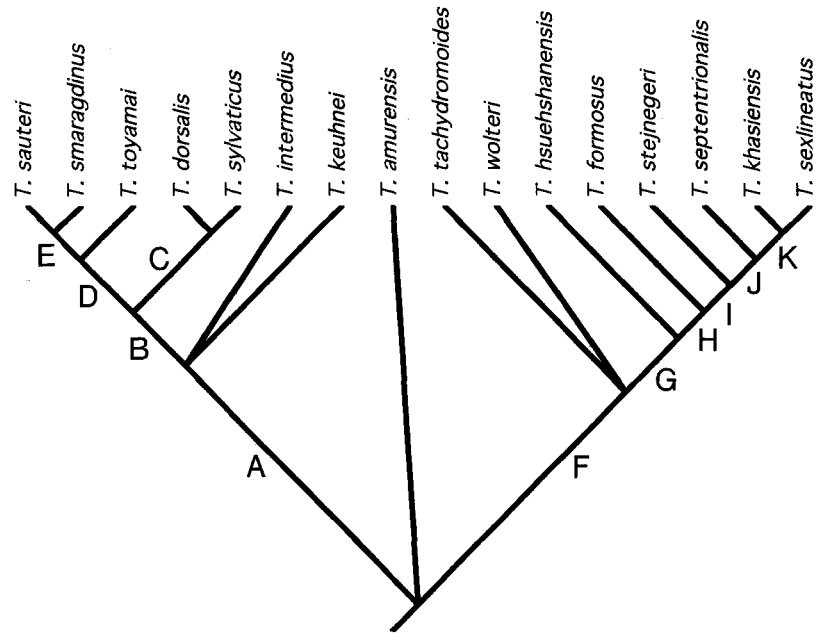

Figure 11. Estimate of the phylogeny of the species of *Takydromus* (excluding *T. haughtonianus*) based on data set in Table 1; a Nelson consensus of six unweighted Wagner trees. Characters giving simple support to component relationships are given below. V - character variable in some species; R - reversal; ↑ - character subsequently reverses; // - character develops in parallel elsewhere in phylogeny.
Node A: 1 - palatal processes of premaxilla slender, 11 ↑ - sometimes two postnasal scales, 21 ↑ - six longitudinal rows of ventral scales, 33 - outer lips of hemipenial lobe sulci produced into ventrally directed flaps, 34// - hemipenis with sulci extending on to lobes (28// - only three complete rows of large scales running beneath thigh, not *T. keuhnei*; 10 - snout elongate, 29// - distal part of second row of large scales beneath thigh and main subtibial scales with keels, not *T. intermedius*). Node B: 32 - dorsum distinctly green. Node C: 17R - Dorsal scales all small, 18R - eight to ten longitudinal rows of large dorsal scales between hind legs. Node D: 8R third cusp on posterior lateral teeth often very small, 22// - enlarged lateral scales present, 24// - all ventral scales with keels, 26V - preanal scale divided by a longitudinal suture, 30// - internal tibial scale row usually with keels. Node E: 7 - external exposure of coronoid bone forming an acute angle, 25V// - Series of smaller scales surrounding preanal scale sometimes interrupted, 28.3 - only two rows of large scales beneath thigh. Node F: 5 - head not distinctly depressed, 22// - enlarged lateral scales present, 30 ↑ // - internal subtibial scale row usually with keels. Node G - 15// - usually three pairs of chin shields, 23 ↑ - enlarged lateral scales as long as adjoining ventral ones, 28// - only three rows of large scales beneath thigh. Node H. 24// - all ventral scales with keels, 29// - distal part of second row of large scales beneath thigh and main subtibial scales with keels. Node I: 18.2V - longitudinal rows of large dorsal scales between hind legs often reduced to four, 31 - pale dorsolateral stripes often present on body; Node J: 16// - keeling on median gular scales extends anterior to a line joining ears, 18.2 - longitudinal rows of large dorsal scales between hind legs nearly always reduced to four; Node K: 3// - nasal process of maxilla narrow and extended, 6// - squamosal bone contacting parietal, 10// - snout elongate, 12 - first supraocular scale usually absent, with the second supraocular scale contacting the loreal, 13 - series of supraciliary granules absent, 14// - only three supraciliary scales, 34// - hemipenis with sulci extending into the lobes, 35 - transverse section of hemipenial lobe triskelial.

TABLE 1. Data set used for phylogenetic analysis of *Takydromus*. Dashes indicate no data available or, in the case of ancestral conditions, that polarity is uncertain

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Ancestor	0	0	0	0	–	0	0	0	0	0	–	0	0	0	0	0	0	0
T. keuhnei	1	0	1	1	0	0	0	1	1	1	1	0	0	0	0	0	1	1
T. intermedius	–	0	0	0	–	–	–	1	1	0	1	0	0	0	0	0	2	1
T. dorsalis	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0
T. sylvaticus	1	0	0	1	0	–	–	1	1	1	1	0	0	0	0	0	0	0
T. toyamai	1	0	0	0	–	0	0	0	1	1	1	0	0	0	1	1	2	2
T. smaragdinus	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0,1	0	1	1
T. sauteri	1	0	0	0	0	0	1	0	0	1	1	0	0	0,1	0	0	1	1
T. amurensis	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	2	1
T. tachydromoides	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	2	1
T. wolteri	0	1	0	0	1	0	0	0	0	0	0	0	0	0,1	0	0	2	0,1
T. hsuehshanensis	0	1	0	0	–	0	0	1	1	0	0	0	0	0	1	0	2	1
T. formosanus	0	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	2	1
T. stejnegeri	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	2	1,2
T. septentrionalis	0	1	0	0	1	0	0	1	1	0	0	0	0	0	1	1	2	2
T. khasiensis	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	2	2
T. sexlineatus	0	1	1	0	1	1	0	1	1	1	0	1	1	1	1	1	2	2

Character	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
Ancestor	0	–	–	0	0	0	0	0	0	0	0	0	–	0	0	0	0
T. keuhnei	2	0	1	0	–	0,1	0	0	0	0	1	0	0	0	1	1	0
T. intermedius	2	0	1	0	–	0	0	0	1	2	0	0	0	0	1	1	0
T. dorsalis	0	0	1	0	–	0	0	0	0	2	1	0	0	1	1	1	0
T. sylvaticus	0	0	1	0	–	0	0	0	0,1	2	1	0	0	1	–	–	0
T. toyamai	1	0	0	1	0	1	0	1	2	1	1	1	0	1	–	–	–
T. smaragdinus	1	0	1	1	0	1	0,1	0,1	2	2,3	1	1	0	1	1	1	0
T. sauteri	0	0	1	1	0	1	0,1	0,1	2	3	1	1	0	1	–	–	0
T. amurensis	2	0	0	0,1	–	0	0	0	0	0	0	0	0	0	0	0	0
T. tachydromoides	2	0	0	1	0	0,1	0	0	1	0	0,1	1	0	0	0	0	0
T. wolteri	2	1	0	1	0	0	0	0	2	0	0,1	1	0	0	0	0	0
T. hsuehshanensis	2	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0
T. formosanus	2	1	0	1	1	1	0	0	1	1	1	1	0	0	0	0	0
T. stejnegeri	2	1	0	1	1	1	0	0	2	1	1	1	1	0	0	0	0
T. septentrionalis	2	1	0	1	0	1	0,1	0	2	1	1	1	1	0	0	0	0
T. khasiensis	2	1	0	1	1	1	0	0	1,2	1	1	1	1	0	1	1	1
T. sexlineatus	2	1	0	1	1	1	1	0	2,3	1	1	1	1	0	0	1	1

Phylogenetic analysis

The phylogeny of *Takydromus*, except for the poorly known *T. haughtonianus*, was estimated using the 35 characters listed above, four of which had two derived states and one three. The distributions of character states among taxa are shown in Table 1. They were polarized using the remainder of the Lacertidae and the Teiidae plus Gymnophthalmidae as successive outgroups. Because the relationship of *Takydromus* to other lacertids is unclear, it is possible that the latter really represent more than one outgroup. Primitive status (0) was assigned to conditions that are widespread in the outgroup taxa. This was so even when they are not universal, especially if they

are present in primitive members of the outgroups concerned. Where more than one condition of a character is widely present in outgroups, polarity was not assigned.

The data set was analysed using the Hennig86 (version 1.5) phylogenetic inference programme (Farris, 1988) which produces unweighted Wagner trees. A root was provided by including a hypothetical ancestor in which the primitive state of each character was inserted, if this could be estimated. Multistate characters were treated additively. Where more than one state exists for particular characters in some species, this situation was entered in the data set as if no information were available. This approach produced six trees of 79 steps with a consistency index (CI) of 0.51 and an RI of 0.74. The strict consensus of these trees is shown in Figure 11. When the successive weighting option of Hennig86 is applied to the initial results, more differentiation is achieved: *T. keuhnei* is basal to *T. intermedius, T. tachydromoides* is basal to *T. wolteri* and *T. amurensis* becomes the most basal taxon on the right hand branch of the phylogeny (Fig. 12). If characters where more than one state is present in some species are treated by entering just the more derived state in the data set, three trees of 88 steps with a CI of 47 and an RI of 70 are produced. The strict consensus of these longer trees is somewhat different from that shown in Figure 11 but application of successive weighting produces the same result as in the initial treatment.

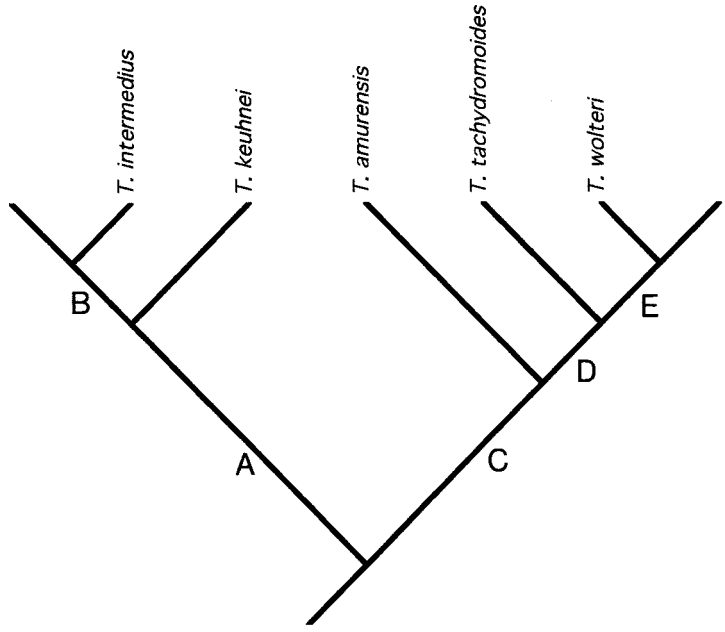

Figure 12. Effect of successive weighting on unweighted Wagner trees. Node A: 1 - palatal processes of premaxilla slender, 11 ↑ - sometimes two postnasal scales, 21 ↑ - six longitudinal rows of ventral scales, 33 - outer lips of hemipenial lobe sulci produced into ventrally directed flaps, 34// - hemipenis with sulci extending on to lobes distal part of second row of large scales beneath thigh and main tibial scales with keels, not *T. intermedius*. Node B: 28// - only three complete rows of large scales running beneath thigh. Node C: 2 - premaxillary nasal process broad, 22V - enlarged lateral scales often present. Node D: 5 - head not distinctly depressed, 22// - enlarged scales present; Node E: 20 - second longitudinal row of ventral scales on posterior belly not broader than those bordering it.

GENERIC AND SUBGENERIC ALLOCATION

Two other generic names have been proposed for species of *Takydromus: Apeltonotus* Boulenger, 1917 for *T. dorsalis*, and *Platyplacopus* Boulenger, 1917 for *T. keuhnei*. *Apeltonotus* was distinguished from *Takydromus* by its small dorsal scales and a second species with this feature, *A. sylvaticus* was subsequently assigned to it. *Platyplacopus* was separated on the basis of the distinctive toes of *T. keuhnei* which have lamellae beneath that are strongly expanded transversely, but not distally where the digit is laterally compressed. (The angling of the digits mentioned by Boulenger in his definition of *Platyplacopus* is no greater than that in other *Takydromus* with compressed toes.) Later, *Takydromus intermedius* and both species of *Apeltonotus* were transferred to *Platyplacopus* by Pope (1935), because the toes of *A. dorsalis* are differentiated in a similar way to those of *T. keuhnei*, although to a far lesser degree, and traces of this condition are also found in *A. sylvaticus* and *T. intermedius*. However, there is a complete gradation among the species assigned by Pope to *Platyplacopus* from the condition of digits found in *P. keuhnei* to that occurring in typical *Takydromus*. Furthermore, *Platyplacopus*, as delineated by Pope, turns out to be a paraphyletic group which, if recognized, divides *Takydromus*, as understood in this context, into two separate phylogenetic entities. Recognition of *Platyplacopus* as a formal genus with this content is consequently inappropriate (Arnold, 1989a). *Platyplacopus* could be retained for the total left-hand clade in Figure 11, but this would create three new combinations and there is no guarantee that *Takydromus* would be holophyletic, as the precise position of *T. amurensis* is still not strongly supported. In the interests of stability, generic status should be assigned to the one assemblage that is almost certainly a clade, *Takydromus* in its wide sense including *Platyplacopus* and *Apeltonotus*. Within this, *Platyplacopus* and *Takydromus s.s.* can be used as subgenera for the two main clades within *Takydromus s.l.*, with *T. amurensis* tentatively assigned to *Takydromus s.s.*.

NATURAL HISTORY OF *TAKYDROMUS*

Takydromus s.l. has a very large range, extending from about 12°S to 46°N and from 91° to 142°E. It extends over a variety of climates from continental temperate conditions to moist tropical ones. Its members feed on arthropods and hunt actively (*T. dorsalis, T. smaragdinus* and *T. sexlineatus* – personal observations on captive animals; *T. stejnegeri* – Cheng, 1987b). They are also heliothermic (*T. dorsalis, T. smaragdinus, T. septentrionalis* and *T. sexlineatus* – personal observations on captive animals; *T. hsuehshanensis* – Lin & Cheng, 1981; *T. smaragdinus* – Takeda & Ota, 1996). The genus is associated with vegetation and occurs both in forest (*T. amurensis* on occasion – Terent'ev & Chernov, 1949; *T. sylvaticus* – Pope, 1928) and more open, often grassy habitats (e.g. *Takydromus smaragdinus* and *Takydromus toyamai* – Takeda & Ota, 1996, *T. stejnegeri* – Liang & Wang, 1976; *T. septentrionalis* – Pope, 1928; Liu, 1939 and *T. sexlineatus* – Pope, 1928). All species are oviparous, although the embryo may show substantial development at oviposition (*T. tachydromoides* – Inukei, 1930); there is some variation in clutch-size (Table 2).

Structural niche varies between species. Some forms, like *T. amurensis* and *T. sylvaticus* (Pope, 1928) are largely ground dwelling while others climb readily in flimsy often grassy vegetation (e.g. *T. dorsalis* – personal observation, *T. septentrionalis* – Pope,

1928; *T. sexlineatus* – De Rooij, 1915; Pope, 1928, personal observation; *T. smaragdinus* – personal observation). These latter species at least are very agile and frequently exhibit a variety of acrobatic skills involving the often very elongate and sometimes relatively robust tail. For instance, in *Takydromus sexlineatus ocellatus* walking or running on the ground, the tail follows the path of the body closely and passively but it is used actively at other times. Climbing *T. sexlineatus* readily twist their tails helically around slender twigs, as other lacertids like *Podarcis muralis* are able to do to some extent; in *T. sexlineatus* this may involve much of the organ or just its tip, which may be wound in a tight spiral of low pitch. Animals descending out of grassy vegetation may leave the tail draped over a projection and use it to control rate and mode of descent. If about half the distal tail hangs behind the projection, the lizard can turn and climb back up the basal part. When the tail is extended posteriorly, it may be used as a counterbalance and the head and body of the lizard may be projected stiffly forwards without support, the fore-limbs being laid back along the flanks. Animals placed on a slender twig will run up it using their distinctly prehensile digits and perch at the top; if the twig is inverted, they readily reverse their position and run to the other end. The tail is also used to spread weight when running over the surface of flimsy vegetation but it is not clear that it actually produces significant forward propulsion by lateral serpentine movements; instead the lizard uses its limbs extensively, grasping stems and narrow leaves with its hands and feet.

Takydromus sexlineatus may also react to flying prey by standing upright, penguin-like, with its forelimbs to its sides and then lunging at the potential food item as it passes; in this manoeuvre the weight of long tail appears to allow the lizard to stand up and the organ is flicked in the opposite direction to that of the body as the lizard makes repeated lunges. Much of the behaviour found in *Takydromus sexlineatus* also occurs in other *Takydromus s.l.* species, including *T. dorsalis, T. smaragdinus* and *T. septentrionalis.* As the first two belong to a different subclade from the latter and *T. sexlineatus*, such agility may be characteristic of the genus as a whole. There are, however, specific differences: climbing *T. smaragdinus* more readily leaps to the ground than *T. sexlineatus*, a trend even more apparent in *T. dorsalis* which, like *T. sexlineatus*, can stand upright, as can *T. septentrionalis.*

There is marked a shift in morphology between the mainly ground-dwelling species of *Takydromus s.l.* and the more specialized climbing forms like *Takydromus sexlineatus* and *Takydromus toyamai*, and the derived features found in these may well confer performance advantage in their mode of life. In fact the head and body are not much modified in general shape: they are slender but not markedly elongated, the presacral vertebrae neither being individually extended anteroposteriorly nor increased in number. However, the tail may be very long with many vertebrae and is up to five times the length of the head and body. This may alter balancing capacity considerably compared with most other lacertids. For example, in a *Takydromus sexlineatus* 50 mm from snout to vent, the tail was 3.8 times this length and the centre of gravity when the lizard was completely straight lay 0.8 of the snout-vent distance behind the vent. This backward shift facilitates many aspects of advanced *Takydromus s.l.* behaviour, such as projecting the unsupported body forwards and standing up. Development of rows of large scales above and below the body, each with a continuous series of keels may help increase stiffness in the body when it is extended by allowing it act like a structural girder with an I-shaped cross section. The blade-like anterior caudal neural spines may also enhance postural control and strengthen the action of the tail by increasing the areas of muscle attachment. The flange-like

extension of the flat clavicles and interclavicles may make them more resistant to the pull of the ventral neck and thorax muscles, which is likely to be important in maintaining posture when the body is stiffly extended.

Maintaining position on the surfaces of relatively smooth vegetation is enhanced by the keeled, tectate belly scales. Although the role of the keels themselves is often emphasized, they may be most important as part of a structural arrangement that produces an effective point at the posterior margin of each scale that is directed obliquely downwards and backwards, so that it can engage the surface on which the lizard is placed. The rigidity of such points comes partly from the thickened keel of which each forms the termination. Stiffness also comes from the way the scale is abruptly bent along the line of the keel so that its two sides are angled upwards relative to each other (see Fig. 8, right). The way such angling produces stiffness in a laminar structure can easily be demonstrated by folding a piece of card shaped like ventral scale. Each point contributes individually to an array that often involves many dozens of such spines. The efficacy of this mechanism in engaging the surface on which the lizard sits can be felt by running the belly of a *Takydromus* with sharply keeled ventral scales across an area of sensitive skin, such as the lip.

It might be thought that the rough microscopic striations on the scales of *Takydromus* also increase frictional contact, for instance with grass hairs, but they are too fine to be effective in this context. However, the structure also has the effect of reducing reflectivity so the scale surface is relatively matt. This contributes to camouflage in many kinds of vegetation, especially when combined with the brown or green colouring typical of *Takydromus*.

EVOLUTION OF *TAKYDROMUS*

One of the two main lineages within *Takydromus s.l.*, the subgenus *Platyplacopus*, is essentially tropical and subtropical, with a relatively small range in southern China and on islands lying off its shore, particularly Taiwan and the Ryukyu archipelago. This may well be a relict distribution. In contrast, the *Takydromus s.s.* clade has a much wider range and occurs in Japan, on a large area of the eastern Asian mainland and on a range of often large East Indian islands that were originally connected to the continent. Its primitive species are essentially temperate, as is *T. amurensis* which may possibly belong to this clade. In contrast, the more derived species are southern and at least sub-tropical with the most derived taxon, *T. sexlineatus*, having a huge largely exclusive range extending southwards from southern China.

Although there is no evidence as to whether *Takydromus s.l.* was initially temperate or tropical, it seems likely from species origins on the phylogeny that *Takydromus s.s.* was originally temperate and only later invaded warmer areas, something that is also suggested by the clutch sizes of its more southerly members (Table 2). Possibly it was the spread of *Takydromus s.s.* that resulted in the apparently relict distribution of *Platyplacopus*. In *Takydromus s.l.*, the importance of off-shore islands in preserving taxa that might have become extinct on the mainland is underlined. Thus, four of the seven species of the subgenus *Platyplacopus* are known only from such islands and a sequence of three species on the *Takydromus s.s.* lineage is also preserved exclusively on Taiwan.

In both component clades of *Takydromus s.l.*, there is a shift from more ground-dwelling primitive forms to ones that are known to climb extensively, or are likely to

TABLE 2. Information on clutch size in *Takydromus*

	Range	Detailed data and sources
T. dorsalis	1–2	2 (*n*=2, personal observation); 1–2 (x=1.4, *n*=5, Takenaka, 1989)
T. toyamai	2	2 (*n*=4, Takeda & Ota, 1996)
T. smaragdinus	2	2 (Takenaka, 1989); 2 (*n*=several, Nakamoto, 1993)
T. sauteri	2	2 (*n*=9, personal observation)
T. amurensis	1–8	3–5 (x=4.3, *n*=3, personal observation); 2–8 (Bannikov *et al.*, 1977; 7 (*n*=1, Terent'ev & Chernov, 1949); 6 (*n*=2, Ji *et al.*, 1987); x=5.1 (*n*=5,Takenaka, 1989)
T. wolteri	4–9	4–9 (x =5.45, Ji *et al.* 1987)
T. tachydromoides	1–9	1–9 (x=4.9, *n*=320, Inukai, 1930); 1–8 (x=3.6, *n*=275, Ishihara, 1964); 1–7 (x=3.4, *n*=332, Telford, 1969)
T. hsuehshanensis	2	2 (*n*=2, Lin & Cheng, 1981)
T. formosanus	2–3	2–3 (*n*=3, personal observation); 2–3 (Liang & Wang, 1976)
T. stejnegeri	1–4	2–3 (*n*=4, personal observation); 1–4 (x=2.2, Cheng, 1987b); 2–3 (Liang & Wang, 1976)
T. septentrionalis	1–6	2–4 (x=2.6, *n*=7, personal observation); 1–6 (x=3.2, *n*=23, Pope, 1929); 2–6 (Wang, 1966); x=3.5 (*n*=23, Liu, 1939)
T. khasiensis	2	2 (*n*=1, personal observation)
T. sexlineatus	2–5	3 (*n*=2, personal observation); 2–3 (*n*=3, Pope, 1929); 5 (*n*=1, Schmidt, 1927b); 2–3 (x=2.3, *n*=3, Java, Kopstein, 1930); 2–3 (x=2.2, *n*=6, Kopstein, 1938); 2–4 (Taylor, 1963)

do so. This has been accompanied by the development of a number of non-ancestral resemblances. Thus, if the independent lineages leading to *Takydromus toyamai* and *Takydromus sexlineatus* are compared, the following features have been developed in parallel: snout narrow and elongate (A), chin shields reduced to three pairs (B), all ventral scales keeled (C), femoral pores reduced to one on each side (D), and inner crural scales keeled (E), longitudinal dorsal scale rows between hind legs reduced to four (F), large keeled gulars extend forwards to level of ears (G), eight longitudinal ventral scale rows (H), the ring of smaller scales around the preanal is not interrupted (I) in *Takydromus toyamai* but it is often so in two other members of the subgenus *Platyplacopus*, *T. smaragdinus* and *T. sauteri*, so its order of origin relative to traits that have developed on the common lineage of the three species can be recognized. The sequence in which ecological analogues, such as advanced members of the two main clades within *Takydromus s.l.* assemble their common characters can often be at least partly reconstructed from phylogenies (Arnold, 1994). In such instances it is often found that the sequence in which the features develop is similar but not precisely the same and this is the case in *Takydromus s.l.* (Fig. 13).

Takydromus s.l. shows a number of parallels with the distantly related (Arnold, 1989a) lacertid, *Poromera fordi*, of Cameroon and Gabon, especially the more

Takydromus toyamai A; B C D E; [I]; F G H
Takydromus sexlineatus E H; B; C; F; D; G; A; I

Figure 13. Order of assembly of suite of common characters found in advanced members of the two main clades within *Takydromus*. The sequence of origin of the common characters is traced in the *Platyplacopus* clade on the lineage of *Takydromus toyamai* Takeda and Ota, and in the *Takydromus s.s.* clade on the lineage of *Takydromus sexlineatus*. Letters refer to particular characters and are explained in the text. Semicolons indicate branch-points on the lineages that delineate internal branches where traits appear; when two or more traits appear on an internal branch it is impossible to order them relative to each other.

advanced members of *Takydromus s.s.*, such as *T. septentrionalis* (Arnold, 1989b). Parallels include flanged interclavicle, post-pygal caudal vertebrae with blade like anterior spines and low posterior ones; chin shields reduced in number, collar weak, dorsal scales large with keels that form continuous ridges, ventral scales keeled and pointed, enlarged keeled lateral scales present that are similar to the ventrals, series of femoral pores reduced, scale ornamentation similar, relatively broad pale supraciliary stripes present on body. As noted, many of these features are associated with life mode in *Takydromus s.l.* and it is not surprising to find that *Poromera* is also similar in this respect, occurring at least sometimes in tall grass (Perret & Mertens, 1957). Unfortunately, it is not possible to examine order of trait assembly in *Poromera*, as it is a monotypic genus with relatively unmodified relatives.

Clutch size (Table 2) correlates with phylogeny in *Takydromus s.l.*. In the four members of the subgenus *Platyplacopus* for which information is available, no more than two eggs are produced at once, as is usual in many tropical lizards. In contrast, like many temperate lizard taxa, *T. amurensis* and members of the *Takydromus s.s.* clade frequently have clutches that exceed these numbers. However this trait has persisted in *T. sexlineatus*, which has invaded tropical areas.

As noted, the more basal members of *Takydromus s.l.* tend to be substantially ground-dwelling and it is tempting to think that there was a simple parallel temporal sequence in the two main clades in the genus from primitive largely terrestrial forms to advanced ones that climb extensively. However, there are factors that suggest alternative scenarios. The fact that derived members of both main clades in *Takydromus s.l.* have a similar complex repertoire of acrobatic behaviour suggests it, or the capacity to produce it, may be primitive for the genus. Secondly, even the supposedly largely terrestrial forms of *Takydromus s.l.* have derived morphological features found in other specialized lacertid climbers in vegetation; these include keeled outer ventral scales (also present in *Adolfus africanus, Gastropholis* and *Poromera* – Arnold, 1989a,b) enlarged dorsal scales in regular rows, their keels forming continuous lines (present in *Poromera*) and blade-like anterior neural spines on the post pygal caudal vertebrae (present in *Adolfus, Gastropholis, Philochortus*). All these features are absent from reasonably adept but occasional climbers in vegetation, such as *Podarcis muralis*.

This raises various possibilities. Primitive forms may in fact climb more skillfully and frequently than has been suspected. Alternatively, *Takydromus s.l.* may have originally been specialized climbers which became largely ground-dwelling before reverting to climbing. Finally, *Takydromus s.l.* may have always been essentially climbing but there were a restricted number of individual and independent shifts to ground-dwelling in its existing basal members. Careful examination of the climbing propensities of a wide range of *Takydromus s.l.* species and plotting these on the phylogeny of the genus may allow a choice to be made between these alternatives.

A KEY TO THE SPECIES OF *TAKYDROMUS*

P.-subgenus *Platyplacopus*; *T.*-subgenus *Takydromus*

1. Six longitudinal rows of ventral scales 2

Eight or more longitudinal rows of ventral scales and sometimes also additional rows of similar lateral scales 7

2. Dorsal scales relatively small, a total of 28 or more across mid-body 3
Mid-dorsal scales very large in 4–10 longitudinal rows at mid-body with smaller scales on flanks 4

3. Hind limb reaches axilla; 28–35 dorsal scales across mid-body; no pale ventrolateral stripe running between the insertions of fore and hind limbs. Ryukyu archipelago ..... *Takydromus (P.) dorsalis*
Hind limb does not reach axilla; 41–44 dorsal scales across mid-body; a pale ventrolateral stripe running between the insertions of fore and hind limbs. Southern mainland China ..... *Takydromus (P.) sylvaticus*

4. Not obviously green; paired vertebral series of large scales on tail extend to nape, often no keels on central ventrals, preanal scale intact and surrounded by continuous series of smaller scales, 2–5 femoral pores on each side, 3 rows of large scales discernible beneath thigh, internal tibial scales unkeeled. Southern China, Hainan and Taiwan 5
Bright green or at least greenish; paired vertebral series of large scales on tail not extending to nape, all ventral scales keeled, preanal scale often divided longitudinally with the series of smaller scales bordering it interrupted anteriorly, 1 femoral pore on each side, often only 2 rows of large scales discernible beneath thigh, internal tibial scales keeled. North and central Ryukyu archipelago, Taiwan, Lanyu island 6

5. Toes without very strongly enlarged lamellae beneath, body-size small (often under 50 mm from snout to vent), third row of large scales beneath thigh reduced, 2 femoral pores on each side ..... *T. (P.) intermedius*
Toes with broad basal lamellae beneath, body size moderate (sometimes over 60 mm from snout to vent), third row of large scales beneath thigh not reduced, 3–5 femoral pores on each side ..... *T. (P.) keuhnei*

6. Head narrow, body slender, tail 3.5–4 times snout-vent distance in adults, usually 4 pairs of chin shields, paired vertebral series of large scales on tail do not extend on to body. Taiwan ..... *T. (P.) sauteri*
Head short, tail about 3 times snout-vent distance in adults, sometimes 3 pairs of chin shields, paired vertebral series of large scales on tail extend on to hind body. North and central Ryukyu archipelago ..... *T. (P.) smaragdinus*

7. Eight longitudinal rows of ventral scales the more median ones unkeeled or keeled 8
Ten or more longitudinal rows of ventral scales and large laterals, all keeled 11

8. Bright green, sometimes 2 postnasal scales, 3 pairs of chin shields, 4 large dorsal scales between hind legs, paired vertebral series of large scales on tail do not extend to nape, all ventral scales strongly keeled, preanal scale may be divided,

keels present on large scales beneath distal thigh and beneath tibia. Myako group of Ryukyu Archipelago ..... *T. (P.). toyamai*

Brown, a single postnasal scale, 3 or 4 pairs of chin shields, about six large scales between hind legs or fewer, paired vertebral series of large scales on tail usually extend to nape, median ventral scales unkeeled or only lightly so, preanal scale not divided, keels on large scales beneath distal thigh and beneath tibia often absent. East Asian mainland, Taiwan 9

9. Three pairs of chin shields, enlarged lateral scales similar to ventrals so that there are 10 rows of large scales across the belly, 2 femoral pores on each side. Taiwan ..... *T. (T.) hsuehshanensis*

Four pairs of chin shields, lateral scales absent or shorter than adjoining ventrals, so that there are only 8 rows of large scales across the belly, 1–5 femoral pores on each side. Japan and Asian mainland. 10

10. 3–5 femoral pores on each side, rostral scale contacts frontonasal (Fig. 4), 6 large dorsal scales between hind legs. Asian mainland ..... *T. (T.?) amurensis*

1 femoral pore on each side, rostral scale separated from frontonasal by nasals, 6(8), large dorsal scales between hindlegs. Asian mainland ..... *T. (T.) wolteri*

Two (rarely 3) femoral pores on each side, rostral scale usually contacts frontonasal, usually 4 large dorsal scales between hindlegs. Japan ..... *T. (T.) tachydromoides*

11. First supraocular scale and supraciliary granules usually present, more than three supraciliary scales (Fig. 5) 12

First supraocular scale absent, no supraciliary granules, 3 supraciliary scales 14

12. Usually under 55 mm from snout to vent, keeling on medial gular scales not extending anterior to a line joining ears, 4 or 6 large dorsal scales between hind legs, 1 or 2 femoral pores on each side, head of males not markedly enlarged or with depressed frontal-prefrontal area. Taiwan 13

Up to 75 mm from snout to vent, keeling on medial gular scales extending anterior to a line joining ears, 4 rows of large dorsal scales between hind legs, 1 femoral pore on each side, head of males large often with median frontal-prefrontal area somewhat depressed. Chinese mainland .... *T. (T.) septentrionalis*

13. Usually 2 femoral pores on each side and 6 rows of dorsal scales between the hind legs ..... *T. (T.) formosanus*

Usually 1 femoral pore on each side and 4 or 6 rows of dorsal scales between the hind legs ..... *T. (T.) stejnegeri*

14. No collar, chin shields in 4 pairs, 6 longitudinal rows of large dorsal scales on body. Assam only ..... *T. (T.) haughtonianus*

Collar present, chin shields often in 3 pairs, usually 4 longitudinal rows of large dorsal scales on body 15

15. Head short, series of smaller scales around preanal not interrupted medially, outer lip of sulcus on hemipenial lobes produced into a backwardly directed flap. Assam only ..... *T. (T.) khasensis*
    Head longer, scales around preanal plate often interrupted medially, no backwardly directed flaps on hemipenis. Much of southeast Asia ..... *T. (T.) sexlineatus*, 16

16. Usually with the following features: 2 femoral pores on each side, 4 rows of dorsal scales at level of forelimbs, 1 row of enlarged lateral scales making a total of 10 rows of large scales across the belly, top of head smooth, no ocelli on the flanks or only very small ones. Assam?, Burma, perhaps north Malaya, Borneo, Natuna islands, Sumatra, Bangka and Java ..... *T. (T.) sexlineatus sexlineatus*
    Usually with the following features: often 1 femoral pore on each side, 6 rows of dorsal scales at level of forelimbs, 2 or 3 three rows of enlarged lateral scales on each flank making a total of up to 14 rows of large scales across the belly, top of head frequently rough, usually large ocelli on the sides. North Malaya, Thailand, eastern Burma, Laos (?), Cambodia (?), Vietnam and South China (Hainan, Hong Kong and westward to Yunnan). ..... *T. (T.) sexlineatus ocellatus*

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