REASSESSMENT OF THE VALIDITY AND DIAGNOSIS OF THE PITVIPER
TRIMERESURUS VENUSTUS VOGEL, 1991

ANITA MALHOTRA AND ROGER S. THORPE

School of Biological Sciences, University of Wales Bangor, Bangor, UK

Trimeresurus venustus Vogel, 1991 was described from southern Thailand in 1991, and
distinguished from the similar T. kanburiensis primarily by the following characters: 21 scale
rows at midbody rather than 19 and less irregular and indented supraoculars. However, very few
specimens of T. kanburiensis were known at the time of this description, and the name T. venustus
has not been universally accepted. Recently, live specimens from the type locality of T.
kanburiensis in western Thailand have become available, allowing a reassessment of the status
of the southern Thai population. Phylogenetic analysis of two mitochondrial gene regions
indicated that specimens from south Thailand are genetically quite distinct from the specimen
from the type locality, and the former are more closely related to T. macrops than to T.
kanburiensis. We present a multivariate morphometric analysis of the six specimens of T.
kanburiensis from the type locality that are now known and twenty specimens from southern
Thailand. Despite the small sample size, it is clear that some of the diagnostic characteristics used
to define T. venustus are invalid. We conclude that the current evidence indicates that T. venustus
is a valid species, and present new diagnostic characters to separate it from T. kanburiensis.

Key words: Crotalinae, systematics, Thailand, Trimeresurus kanburiensis, Viperidae

INTRODUCTION

The genus Trimeresurus (Serpentes: Viperidae: Crotalinae) contains many taxonomically vexing issues
that are still awaiting resolution (Malhotra & Thorpe, 1997, 2000). Recently, molecular data have promised to
resolve some of these issues. One example is the status of the taxa T. kanburiensis Smith 1943 and T. venustus
Vogel 1991. The holotype of T. kanburiensis (a female) was collected in 1938 from Kanchanaburi (then known as
Kanburi) province in western Thailand (Fig. 1). It was at first identified as T. puniceus and only described
as a new species in 1943 (Smith, 1943). It remained the only specimen available for the species until the late
1980s. In the interim, confusion developed over the identity of this species following specimens of another
species T. purpureomaculatus, that occurs in the same region, being mistakenly labelled T. kanburiensis in
books and by dealers in the captive trade (see Warrell et al., 1992, for details). In the late 1980s, two additional
specimens, also females, were found in Kanchanaburi Province (Warrell et al., 1992). Specimens apparently
referable to the species were also found in southern Thailand, in Nakhon Si Thammarat and Krabi
provinces. Ironically, some of these specimens found their way into the captive trade labelled “T.
purpureomaculatus” (Warrell et al., 1992). Vogel (1991) described this southern population as T.
venustus, citing the following diagnostic characters to separate it from T. kanburiensis: 21 scale rows at mid-body
rather than 19; narrower, less indented and divided, supraoculars; slimmer body and a distinctive
brownish-red banded colour pattern.

However, the name T. venustus has not been widely accepted. Among recent checklists of venomous snakes,
it has been listed by Golay et al. (1993) and David & Ineich (1999) but not by McDaid et al. (1999) or the
EMBL taxonomy database (http://www.embl-heidelberg.de/~uetz/families/Viperidae.html).

Specimens of T. kanburiensis that were available to Vogel for comparison were in poor condition. The
holotype of T. kanburiensis is in two pieces and clearly has a section of body and the tail tip missing (also noted
by Warrell et al., 1992). The head is very distorted and squashed, with torn skin on one side, and any pattern has
entirely faded. One of the two additional specimens available is also almost in three pieces and the colour
pattern has faded considerably in both (Warrell et al., 1992). Warrell et al. (1992) doubted that T. venustus
was a different species to T. kanburiensis, after finding a fourth specimen of T. kanburiensis from Kanchanaburi
province in 1991 (the only male), in which the colour pattern was well preserved and appeared to be identical
to that of the southern population.

Further doubt was cast on the validity of T. venustus when, during fieldwork in Thailand in the 1990s, we
found several specimens in the vicinity of the Khao Luang massif, near Nakhon Si Thammarat (Fig. 1), that
also had 19 scale rows at mid-body. One of these, a roadkill, has since been presented to the Natural History
Museum, London (BMNH 2002.52). A specimen from Surat Thani with the same character state was also seen
by the senior author at the Queen Savoah Memorial Institute. Therefore, the status of T. venustus required
further verification (Malhotra quoted in Gumprecht, 2002a). Recently, a number of live specimens of T.
kanburiensis have become available from the type locality. One of these (a female) was sent to the authors by the

Correspondence: A. Malhotra, School of Biological
Sciences, University of Wales, Bangor, Gwynedd, LL 57
2UW UK. E-mail: A.Malhotra@bangor.ac.uk
or muscle tissue preserved in 80% ethanol, using standard protocols (Sambrook et al., 1989). Cytochrome b (cyt b) sequences were obtained as described in Malhotra & Thorpe (2000), NADH dehydrogenase (ND4) as described in Parkinson et al. (2000) and 12S small subunit ribosomal RNA (12S) as described in Knight & Mindell (1993). Unincorporated nucleotides and primers were removed using a variety of commercially available kits (e.g. Prep-a-gene [BioRad], Wizard minicolumns [Promega], or QIAquick columns [QIAGen]). The double-stranded product was sequenced using dye-labelled terminators (ABI Prism™ BigDye™ Terminator Cycle Sequencing Ready Reaction Kit), and subsequently run on an ABI Prism 377 automated DNA sequencer.

**Phylogenetic Analysis**

Malhotra & Thorpe (2000) presented a phylogeny of 21 species of *Trimeresurus* (*sensu lato*) based on cyt b sequences, and evaluated the taxonomic value of certain morphological characteristics against this tree. On this basis, four species groups were defined within *Trimeresurus* *sensu stricto*, which are diagnosed by a combination of the condition of the first upper labial and nasal scale (fused or separate) and the hemipenal structure. By these criteria, the *T. kanburiensis/T. venustus* complex is a part of the *albolabris* species group, although it is quite genetically divergent and apparently diverged early in the history of the species group. We therefore analyse a number of species from the *albolabris* species group, as well as representatives of the other three species groups, together with one specimen of *T. kanburiensis*, and four specimens of *T. venustus*, including all three specimens from the Khao Luang area with 19 scale rows at mid-body. A full list of sequences included and their origins is listed in Table 1.

The coding sequences were first translated into amino acid sequences using MEGA version 2.1 (Kumar et al., 2001) to check for the unexpected occurrence of stop codons which might indicate amplification of pseudogenes. The possibility of non-neutral evolution was tested using a variety of tests implemented in the program DnaSP 3.51 (Rozas & Rozas, 1999), including McDonald and Kreitman’s (1991) test, Fu and Li’s D* and F*, and their modifications for use with an outgroup sequence (Fu & Li 1993), and Tajima’s D (Tajima, 1989).

We used both unweighted parsimony and Bayesian Markov Chain Monte Carlo (MCMC) approaches to reconstruct phylogenies, using PAUP* 4.0b8 (Swofford, 2001) and MrBayes (Huelsenbeck & Ronquist, 2001) respectively. We first checked the dataset for homogeneity of base composition among taxa, to detect problems with the assumption of a similar underlying substitutional model. Parsimony searches were heuristic, with starting trees obtained by random addition with 100 replications, and tree-bisection-reconnection (TBR) branch swapping. Confidence in the inferred branches of the optimal trees was obtained by bootstrapping (1000 replication) with the search strat-
<table>
<thead>
<tr>
<th>Species</th>
<th>Cat.</th>
<th>Location</th>
<th>GenBank accession nos. (cyt b, ND4, 12S)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trimeresurus venustus</em></td>
<td>A74</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Khao Luang)</td>
<td>AY289224, AY289230, AY289218</td>
</tr>
<tr>
<td>T. venustus</td>
<td>A75</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Khao Luang)</td>
<td>AY289223, AY289229, AY289217</td>
</tr>
<tr>
<td>T. venustus</td>
<td>A249</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Khao Luang)</td>
<td>AY289224, AY289233, AY289235</td>
</tr>
<tr>
<td>T. venustus</td>
<td>A237</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Thung Song)</td>
<td>AY289222, AY289228, AY289216</td>
</tr>
<tr>
<td>T. kanburiensis</td>
<td>B522</td>
<td>Kanchanaburi Province</td>
<td>AF171914, to come</td>
</tr>
<tr>
<td>T. flavomaculatus</td>
<td>B7</td>
<td>Bangkok</td>
<td>AF171914, AY289231, AY289219</td>
</tr>
<tr>
<td>T. macrops</td>
<td>B27</td>
<td>Champassak Prov., S Laos</td>
<td>AF517184, AF517219, AF517163</td>
</tr>
<tr>
<td>T. stejnegeri</td>
<td>A164</td>
<td>NE Thailand, Loei Province</td>
<td>AY289221, AY289227, AY289215</td>
</tr>
<tr>
<td>T. gumprechtii</td>
<td>B97</td>
<td>NE Thailand, Nakhon Ratbiasima Pr.</td>
<td>AF171896, AY059593, AY059539</td>
</tr>
<tr>
<td>T. vogeli</td>
<td>A160</td>
<td>Taiwan, Taipei county</td>
<td>AF171898, AF157224, AF517168</td>
</tr>
<tr>
<td>T. venustus</td>
<td>A241</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Thung Song)</td>
<td>AY059574, AY059596, AY059546</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>B33</td>
<td>Thailand, Songkhla Province</td>
<td>AF171916, AY059584, AY059535</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>B6</td>
<td>Indonesia, W Java</td>
<td>AY059567, AY059585, AY059536</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>B22</td>
<td>Nonthaburi, C Thailand</td>
<td>AF517186, AF517213, AF517158</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>B47</td>
<td>Phethuri Province, W Thailand</td>
<td>AF171819, AF517221, AF517165</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>A229</td>
<td>N Thailand, Pha Yao Province</td>
<td>AF517187, AF517216, AF517160</td>
</tr>
<tr>
<td>T. purpureomaculatus</td>
<td>A83</td>
<td>Satun province, S Thailand</td>
<td>AY059566, AY059583, AY059544</td>
</tr>
<tr>
<td>T. septentrionalis</td>
<td>A100</td>
<td>Nepal, Mahattari District</td>
<td>AF517188, AF517218, AF517162</td>
</tr>
<tr>
<td>T. insularis</td>
<td>B7</td>
<td>Indonesia, West Timor</td>
<td>AF171909, AY059592, AY059543</td>
</tr>
<tr>
<td>T. popeiorum</td>
<td>A203</td>
<td>S Thailand, Nakhon Si Thammarat Pr.</td>
<td>AY059568, AY059586, AY059534</td>
</tr>
<tr>
<td>T. malabaricus</td>
<td>A218</td>
<td>S India, Tamil Nadu State</td>
<td>AF171904, AY059588, AY059537</td>
</tr>
<tr>
<td>T. trigonocephalus</td>
<td>A58</td>
<td>SW Sri Lanka</td>
<td>AY059569, AY059587, AY059548</td>
</tr>
<tr>
<td>Tropidolaemaus wagleri</td>
<td>B132</td>
<td>W Malaysia, Perak</td>
<td>AF171800, AY059597, AY059549</td>
</tr>
<tr>
<td>Protobothrops</td>
<td>B165</td>
<td>N Vietnam, Nghe An province</td>
<td>AF171791, AF517223, AF517167</td>
</tr>
<tr>
<td><em>Trimeresurus venustus</em></td>
<td>A74</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Khao Luang)</td>
<td>AY289224, AY289230, AY289218</td>
</tr>
<tr>
<td>T. venustus</td>
<td>A75</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Khao Luang)</td>
<td>AY289223, AY289229, AY289217</td>
</tr>
<tr>
<td>T. venustus</td>
<td>A249</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Khao Luang)</td>
<td>AY289224, AY289233, AY289235</td>
</tr>
<tr>
<td>T. venustus</td>
<td>A237</td>
<td>S Thailand, Nakhon Si Thammarat Pr. (Thung Song)</td>
<td>AY289222, AY289228, AY289216</td>
</tr>
<tr>
<td>T. kanburiensis</td>
<td>B522</td>
<td>Kanchanaburi Province</td>
<td>AF171914, to come</td>
</tr>
<tr>
<td>T. flavomaculatus</td>
<td>B7</td>
<td>Bangkok</td>
<td>AF171914, AY289231, AY289219</td>
</tr>
<tr>
<td>T. macrops</td>
<td>B27</td>
<td>Champassak Prov., S Laos</td>
<td>AF517184, AF517219, AF517163</td>
</tr>
<tr>
<td>T. stejnegeri</td>
<td>A164</td>
<td>NE Thailand, Loei Province</td>
<td>AY289221, AY289227, AY289215</td>
</tr>
<tr>
<td>T. gumprechtii</td>
<td>B97</td>
<td>NE Thailand, Nakhon Ratbiasima Pr.</td>
<td>AF171896, AY059593, AY059539</td>
</tr>
<tr>
<td>T. vogeli</td>
<td>A160</td>
<td>Taiwan, Taipei county</td>
<td>AF171898, AF157224, AF517168</td>
</tr>
<tr>
<td>T. flavomaculatus</td>
<td>B3</td>
<td>Thailand, Songkhla Province</td>
<td>AF171916, AY059584, AY059535</td>
</tr>
<tr>
<td>T. hageni</td>
<td>B33</td>
<td>Thailand, Songkhla Province</td>
<td>AY059567, AY059585, AY059536</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>B6</td>
<td>Indonesia, W Java</td>
<td>AF517186, AF517213, AF517158</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>B22</td>
<td>Nonthaburi, C Thailand</td>
<td>AF517189, AF517221, AF517165</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>B47</td>
<td>Phethuri Province, W Thailand</td>
<td>AF517187, AF517216, AF517160</td>
</tr>
<tr>
<td>T. albolabris</td>
<td>A229</td>
<td>N Thailand, Pha Yao Province</td>
<td>AY059566, AY059583, AY059544</td>
</tr>
<tr>
<td>T. purpureomaculatus</td>
<td>A83</td>
<td>Satun province, S Thailand</td>
<td>AF517188, AF517218, AF517162</td>
</tr>
<tr>
<td>T. septentrionalis</td>
<td>A100</td>
<td>Nepal, Mahattari District</td>
<td>AF517190, AY059592, AY059543</td>
</tr>
<tr>
<td>T. insularis</td>
<td>B7</td>
<td>Indonesia, West Timor</td>
<td>AY059568, AY059586, AY059534</td>
</tr>
<tr>
<td>T. popeiorum</td>
<td>A203</td>
<td>S Thailand, Nakhon Si Thammarat Pr.</td>
<td>AF171904, AY059588, AY059537</td>
</tr>
<tr>
<td>T. malabaricus</td>
<td>A218</td>
<td>S India, Tamil Nadu State</td>
<td>AY059569, AY059587, AY059548</td>
</tr>
<tr>
<td>T. trigonocephalus</td>
<td>A58</td>
<td>SW Sri Lanka</td>
<td>AF171800, AY059597, AY059549</td>
</tr>
<tr>
<td>Tropidolaemaus wagleri</td>
<td>B132</td>
<td>W Malaysia, Perak</td>
<td>AF171791, AF517223, AF517167</td>
</tr>
<tr>
<td>Protobothrops</td>
<td>B165</td>
<td>N Vietnam, Nghe An province</td>
<td>AY289226, AY289232, AY289220</td>
</tr>
</tbody>
</table>
A principal component analysis (PCA) was then carried out on the characters showing significant between-group differences, excluding those that showed sexual dimorphism in the case of joint analyses of both sexes. Although having less discriminatory power than methods that define a priori groups such as canonical variate analysis (CVA), PCA is to be preferred in this case since we do not wish to prejudice the distinctness of the groups. However, PCA does not take between-character correlations into account, so all size-related characters were first adjusted to a common size using the pooled within-group slope, with either snout-vent length (SVL) or head length (LHEAD) as the covariate. Included characters were screened for high correlations with each other \((r > 0.7)\), which would indicate that they do not provide independent information. In CVA, these correlations are taken into account, but in PCA they may result in over-emphasis of the correlated variables (Thorpe, 1983). If this was found, only one of the characters from the correlated character sets was used in PCA.

Adding internal characters can substantially improve the resolution of taxa (Thorpe, 1979, 1989). However, internal characters are not particularly useful for identification in many situations and also substantially reduce the sample size, as internal data were not available for many specimens. Given the generally poor condition of many of the specimens from Kanchanaburi, many head-shape characters are also missing in this group. Therefore, two sets of analyses were carried out, the first included scalation and colour pattern characters only, and the second included all types of characters. If the PCA indicated that the groups were distinct, a discriminant function analysis was carried out, using the same subsets of data as in the PCA, in order to find the characters most useful at distinguishing them.

**RESULTS**

**Phylogenetic Analysis**

The final data set consisted of 26 taxa and 1612 base pairs of sequence data (587 bp from cyt b, 600 bp from ND4, and 425 bp from 12S). The coding sequences translated into amino acid sequence without the occurrence of stop codons, and were easily aligned by eye. The chi-square test for the homogeneity of base frequencies showed that base composition was not significantly different in all taxa included \((P = 0.99)\). None of the neutrality tests showed a significant departure from neutrality. The mean likelihood score was -9419.258.

The mean values for the parameters of the model, estimated by the program, were: base frequencies \((A: 0.33704, C: 0.32727, G: 0.11341, T: 0.22228)\), alpha = 0.214011.

Most branches in the group of interest were highly supported. These show that while all specimens from south Thailand are closely related, regardless of whether they have 19 or 21 scale rows at mid-body, they are very distinct from the specimen from Kanchanaburi Province and indeed are more closely related to *T. macrops* (Fig. 1).
**VALIDITY OF TRIMERESURUS VENUSTUS**

2). *Trimeresurus venustus* is supported as a distinct species by this analysis. The relationships of these three species with the other species groups is unresolved in this analysis, however, and is addressed in a larger analysis of *Trimeresurus s.s.* that includes more species (Malhotra & Thorpe, 2004).

**MULTIVARIATE MORPHOMETRICS**

ANOVA and ANCOVA showed that only a few characters that were significantly different between localities were also significantly sexually dimorphic. These included SCS, TAIL, CLOPOST, VS19 to 17, HTANT, and HTPOST. Therefore, to maximise sample size, both sexes were analysed together excluding these characters. To check the effect that these characters had on the discrimination, a parallel analysis on just females, and analyses are not discussed further. The final scaling and colour pattern character set for PCA included VS21 to 19, DV17 to 15, BTWSUP2, LAB3, ROST, GENERAL, VENTEDGE, and SCR1. Unfortunately, one of the Khao Luang specimens (BMNH 2002.52) had some damage to the rostral scale and could not be included with this dataset. Since the position of these specimens is important, the analysis was repeated with ROST removed, so that both specimens could be included. This had the effect of slightly reducing the separation between the groups, but otherwise the difference was negligible. While the resulting discrimination clearly separated the western and southern population with 21 scale rows, the intermediate position of the specimens from the south with 19 scale rows cast doubt on their distinctness (Fig. 3a). Since the number of scales at mid-body was influential in the ordination, we investigated whether the Khao Luang specimens most resembled *T. kanburiensis* or *T. venustus* in other characteristics. This was done by repeating the analysis with this character (VS21 to 19, which actually measures the position along the body where the reduction from 21 to 19 scale rows occurs) removed. The only marked effect on the discrimination was to shift the two Khao Luang specimens towards the other southern specimens (Fig. 3b), thus clearly indicating that in other respects they were clearly identifiable as *T. venustus*. Removal of VS19 to 17 also has a marked effect on the CVA, with the Khao Luang specimens grouping with the specimens from western Thailand when it was included, but with the other southern specimens when it was included. Finally, inclusion of internal characters (DENT, RKPOST, LKPOST) substantially improved the discrimination of the two species in the PCA (Fig. 3c) and CVA (not illustrated). In all analyses, the two specimens from an unknown locality clearly grouped with other *T. venustus* specimens as might be expected from their mid-body scale counts. These were therefore included within the southern Thailand population for the CVA.

The CVA allowed us to assess which characters contribute to the discrimination of *T. venustus* and *T. kanburiensis*, as well as their mean value, and range. Since the use of internal characters substantially reduces sample size, the results of the analysis of external characters are used in preference. However, internal characters that are important in the discrimination when all characters are used are also listed. It can be seen that the difference in any single character is subtle, with largely overlapping ranges (Table 2).

*T. venustus* is distinguished from *T. kanburiensis* in both sexes by a scale reduction from 17 to 15 scale rows (DV17 to 15) that involves scale rows higher on the body in *T. kanburiensis* than in *T. venustus* (Table 2), a smaller light blotch on the first dorsal scale row in *T. kanburiensis* than in *T. venustus* (SCR1), a rostral scale with a higher ratio (a squarer shape) in *T. venustus* than in *T. kanburiensis* (ROST). There also tends to be a higher number of gulars (GULAR), fewer scales between the rear edges of the supracoculars (BTWSUP2), and at least one scale separating the third supraorbital and the subocular (LAB3) is more likely to be present in *T. kanburiensis* than in *T. venustus*. Of the internal and head dimension characters, only the length of the head (LHEAD) serves to separate the two species, with *T. kanburiensis* having a relatively longer head than *T. venustus*. Of the sexually dimorphic characters that are also significantly different between groups, only the

---

**FIG. 2.** Bayesian evolutionary hypothesis of the relationships between *T. kanburiensis*, *T. venustus* and *T. macrops*. Despite the close morphological similarity between the former two species, *T. venustus* is actually most closely related to *T. macrops*. Branch lengths are proportional to amount of evolution, and are averaged over all trees. Figures at nodes indicate posterior probabilities (first) of the clades from the Bayesian analysis, followed by parsimony bootstrap support values.
number of subcaudal scales is important, and tends to be higher in *T. venustus*.

Of the characters that help to distinguish between the sexes of both species (Table 3), the most important is relative tail length (TAIL), which is longer in males than females. The number of teeth on the pterygoid bone (PTERY) is also sexually dimorphic with higher numbers in males than females. The scale reduction from 8 to 6 rows on the tail (SC8to6) occurs further down the tail in males than females, which is associated with the length of the tail, the ventral surface tends to be more heavily blotched and speckled in males than females, and the position of the front and rear edges of the liver (LVANT, LVPOST) occur more posteriorly in males than females, as does the anterior edge of the left kidney (LKANT).

**DISCUSSION**

**Evaluation of Diagnostic Characters.**

Of the characters stated in the description (Vogel, 1991) to distinguish *T. venustus* from *T. kanburiensis*, we have shown that the number of scale rows at midbody is not diagnostic. It is also stated to be slighter in body shape than *T. kanburiensis*. The analysis shows that this is only discernible in the slightly longer head of *T. kanburiensis*, which in practise may not be a very useful diagnostic character. Vogel (1991) also states that *T. venustus* lacks the indented, divided and very broad supraoculars found in *T. kanburiensis*. However, in none of the specimens analysed were the supraoculars actually divided. The width (and length) of the supraoculars was also not significantly different between the two species. The irregularity of the inner edge of the supraoculars was not included in the analysis because it is difficult to measure in an objective manner. While it does appear to be more irregular in the specimens of *T. kanburiensis* examined than in *T. venustus*, this is not always true. For example, the *T. kanburiensis* specimen BMNH 1987.943 has broad supraoculars with a smooth margin, while *T. kanburiensis* specimens BMNH 1988.385 and BMNH 2002.51 have only slightly indented supraoculars on one side. Many of the *T. venustus* specimens examined had at least slightly indented and irregular inner edges to the supraoculars, and so this character may only be useful when expressed in its extreme form in each species. Finally, the species were said to differ in colour pattern, in the presence of bands and in the ventral surface being more blotched in *T. venustus*, whereas *T. kanburiensis* was unbanded and had a plain or speckled ventral surface. However, these aspects of colour pattern can now be shown to be an artefact of small sample size. All the specimens of *T. kanburiensis* from which Vogel obtained this information have a very faded colour pattern and are females. The new specimens indicate that banding is the norm in *T. kanburiensis* as well, and although pictures of the live specimens suggest that the colour of the bands may be slightly different in the two species, this cannot be confirmed by analysis at present. The difference in ventral

---

**FIG. 3.** Plot of first two principal components for both sexes. a) external characters only, including VS21to19; b) external characters excluding VS21to19; c) external and internal characters. Circles: *T. venustus* (with 21 scale rows at midbody); triangles: southern specimens with 19 scale rows; squares: *T. kanburiensis*. Empty symbols indicate females and filled symbols indicate males. The two specimens of unknown locality are indicated by arrows in 3a and are clearly assignable to *T. venustus*. They are therefore not highlighted in the remaining figures.
TABLE 2. Mean values and range of morphological characters important in multivariate discrimination between T. venustus and T. kanburiensis. Size-related characters are adjusted to a common size of SVL (47.0 cm). Characters are listed in order of magnitude of their contribution to the discriminant function, and their abbreviations are explained in Appendix 2.

<table>
<thead>
<tr>
<th>Character</th>
<th>T. venustus</th>
<th>n</th>
<th>T. kanburiensis</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>DV17to15</td>
<td>3.38 (3.0 - 5.0)</td>
<td>20</td>
<td>4.0 (3.5 - 4.5)</td>
<td>6</td>
</tr>
<tr>
<td>SCR1</td>
<td>0.39 (0.1 - 0.8)</td>
<td>20</td>
<td>0.17 (0.0 - 0.2)</td>
<td>6</td>
</tr>
<tr>
<td>ROST</td>
<td>0.45 (0.33 - 0.58)</td>
<td>17</td>
<td>0.33 (0.22 - 0.47)</td>
<td>6</td>
</tr>
<tr>
<td>GULAR</td>
<td>6.9 (5.5 - 9.5)</td>
<td>20</td>
<td>8.6 (7.9 - 9.5)</td>
<td>6</td>
</tr>
<tr>
<td>BTWSUP2</td>
<td>12.85 (11.0 - 16.0)</td>
<td>20</td>
<td>10.33 (9.0 - 12.0)</td>
<td>6</td>
</tr>
<tr>
<td>LAB3</td>
<td>0.15 (0 - 1)</td>
<td>20</td>
<td>0.58 (0 - 1)</td>
<td>6</td>
</tr>
<tr>
<td>LHEAD</td>
<td>19.74 (17.9 - 23.6)</td>
<td>19</td>
<td>21.62 (19.0 - 22.6)</td>
<td>5</td>
</tr>
<tr>
<td>SCS (females only)</td>
<td>56.08 (50 - 66)</td>
<td>13</td>
<td>51.25 (50 - 52)</td>
<td>4</td>
</tr>
</tbody>
</table>

The maximum number of specimens available for that character is 27. The mean values and range of morphological characters important in multivariate discrimination between T. venustus and T. kanburiensis are listed in Table 2.

Table 3. Mean values and range of morphological characters in T. venustus and T. kanburiensis which do not discriminate among species but distinguish the sexes. Data are for the maximum number of specimens available for that character. Size-related characters are adjusted to a common size of SVL (42.0 cm). Characters are listed in order of magnitude of the F-ratio in the ANOVA/ANCOVA.

<table>
<thead>
<tr>
<th>Character</th>
<th>Male</th>
<th>n</th>
<th>Female</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>TAIL</td>
<td>9.15 (± 0.23)</td>
<td>7</td>
<td>6.83 (± 0.22)</td>
<td>15</td>
</tr>
<tr>
<td>PTERY</td>
<td>14.8 (14-16)</td>
<td>6</td>
<td>13.2 (12-14)</td>
<td>9</td>
</tr>
<tr>
<td>SC8to6</td>
<td>16.4 (14.0-18.5)</td>
<td>8</td>
<td>9.9 (5.0-15.5)</td>
<td>18</td>
</tr>
<tr>
<td>DARKVENT</td>
<td>64.4 (0-100)</td>
<td>8</td>
<td>43.1 (0-100)</td>
<td>18</td>
</tr>
<tr>
<td>LVANT</td>
<td>63.25 (62-64)</td>
<td>4</td>
<td>61.6 (58-66)</td>
<td>9</td>
</tr>
<tr>
<td>LKANT</td>
<td>138.75 (133-142)</td>
<td>4</td>
<td>413.55 (125-145)</td>
<td>8</td>
</tr>
<tr>
<td>LVPOST</td>
<td>96.5 (91-99)</td>
<td>4</td>
<td>95.1 (93-103)</td>
<td>9</td>
</tr>
</tbody>
</table>

Some of the ventrals. This is more extensive in males than females, in which the encroachment is just a sprinkling of brown spots. Males and females both have white or bluish spots on the first dorsal scale row, the overall effect being a blurred margin between dorsal and ventral scales. Labial scales are also scattered with white or bluish pigment, and in males are boldly marked with two or more patches of dark pigment. A broad and irregular dark stripe extends from the rear edge of the eye, again this is bolder in males than females. The eye is light orange heavily speckled with brown. The tail is similarly patterned to the body but the colour of the bands is brighter than on the rest of the body. One of the males has a series of white vertebral spots.

Morphometric and meristic characters. Females have relatively shorter tails than males, and this is also reflected in the number of subcaudals (ranging in females between 50-52, compared to 61 in the male. Maximum recorded size for females is 58.2 cm SVL, compared to 41.5 cm for the male. The number of ventral scales varies between 172 and 177 in both sexes. Body scales are keeled, although this may vary from weak to strong. Temporal scales and scales on the side of the head between the temporals and supralabials are also usually keeled, as are scales on the rear of the head. The ratio of the upper and lower edges of the rostral scale varies between 0.2 and 0.5 (note that this character is not noticeably allometric as it is not correlated with any linear measurement on the head or body). Supralabials vary between 10 and 11 and sublabials between 11-13. The minimum number of scales between supraoculants varies between 7-9 and there are 9-12 scales between the posterior edges of the supraoculars. The number of scales between the nasals and shield bordering the anterior of the pit varies between 0-1 and there may be up to one scale between the internasals. The third supralabial may be separated from the subocular by up to one scale, but there is always one scale between the fourth and fifth supralabials and the subocular. The supraoculars may be heavily indented on the inner margin with the adjacent head scales, making the edge appear very uneven and irregular. However, a few specimens have regular supraoculars, and they may also be very broad. A few specimens have a suture run-

Coloration appears to be due to sexual dimorphism rather than being a diagnostic difference. Thus, it seems that the diagnosis and characteristics of the two species requires redefinition.

REDESCRIPTION OF VARIATION WITHIN T. KANBURIENSIS

Colour in preservative. The banding pattern seems to be easily lost especially after some time in formalin (Warrell et al., 1992), leaving a uniformly brown dorsal and lateral coloration. In these specimens, the ventral surface appears white, although it is still possible to detect a pale blotch on the first dorsal scale row, and some darker pigment extending onto the edge of the ventral scales. The darker colour also extends onto the sublabial scales and some of the scale rows between these and the genial scales, although it may be patchy. In better preserved specimens, darker blotches are visible on the head and form irregular bands on the body.

Colour in life. This description is based on a specimen freshly preserved in alcohol and on pictures of two living males and one female specimen from the same population. The ground colour of the body is a shade of olive or greyish green. The head is heavily blotched with dull brown or orange brown, and bands of the same colour occur on the body. The ventral surface is creamy white. Brown pigment encroaches onto the edges of

Table 3. Mean values and range of morphological characters in T. venustus and T. kanburiensis which do not discriminate among species but distinguish the sexes. Data are for the maximum number of specimens available for that character. Size-related characters are adjusted to a common size of SVL (42.0 cm). Characters are listed in order of magnitude of the F-ratio in the ANOVA/ANCOVA.
ing partially across the scale, but the supraoculars are never completely divided. There are always 19 scale rows at mid-body, with the reduction from 21 to 19 scale rows occurring between 10 and 28% of the distance between the first ventral scale and the anal scale. Some of these scalation patterns are illustrated in Fig. 4a. There are 2-3 postocular scales, 5-8 scales bordering the subocular scale (not counting the pre- and post-oculars) and 12-14 teeth on the pterygoid and 12-15 on the dentary bone.

**Redescription of Variation within *T. venustus***

*Colour in preservative.* Some specimens have a uniformly dark dorsal and lateral coloration. This is almost certainly a preservation effect since no specimen of *T. venustus* without bands has ever been found (although one aberrant striped individual has been recorded; Gunnewicht, 2002b). The ventral surface appears white, with a pale blotch extending onto some scales of the first dorsal scale row, and some darker pigment extending from the dorsal surface onto the edge of the ventral scales. In better preserved specimens, darker blotches are visible on the head and form irregular bands on the body. Supralabials are lighter than the rest of the head, but may have a number of darker blotches (usually no more than one). Sublabial scales are generally white and unmarked, although in some specimens they appear darker.

*Colour in life.* This description is based on macrophotographs of five specimens (one male, four females) captured alive in south Thailand. The ground colour of the body is dull olive or bluish-green (male) to grass-green (female). The head is heavily blotched with dull brown, and bands of the same colour occur on the body. The ventral surface is a similar, slightly lighter colour, than the dorsal surface. Brown pigment encroaches onto the edges of some of the ventrals, although the extent of the encroachment is variable and some females have virtually immaculate ventral scales. Males and females both have a white spot on the first dorsal scale row, which is more regular than in *T. kanburiensis* and therefore forms a clear margin between the dorsal and ventral scales although in the male there are also white flecks on some ventral scales. The labials are the same green colour as the rest of the dorsal surface, and in both sexes are boldly marked with at least one brown patch. A broad and irregular dark stripe may extend from the rear edge of the eye, not appearing to be different in intensity in males and females. The eye is light orange heavily speckled with brown. The tail is patterned and coloured identically to the body.

*Morphometric and meristic characters.* Females have relatively shorter tails than males, also reflected in the number of subcaudals (ranging in females between 50-66, compared to 68-72 in males). Females reach a slightly larger size than males but this is not a marked difference (maximum recorded 48.6 cm SVL compared to 43.4 cm for males). The number of ventral scales varies between 166 and 183 in both sexes. Body scales are always keeled, with a range from weak keeling to strong keeling. Temporal scales, scales between the temporals and supralabials, and scales on the rear of the head are also weakly to strongly keeled, The ratio of the upper and lower edges of the rostral scale varies between 0.3 and 0.6 (note that this character is not noticeably allom-
metric as it is not correlated with any linear measurement on the head or body). Supralabials vary between 9 and 11 and sublabials between 10-13. The minimum number of scales between supraoculars varies between 6-10 and there are 11-16 scales between the posterior edges of the supraoculars. The number of scales between the nasals and shield bordering the anterior of the pit varies between 0 and 1, and there may be 0-1 internasal scale. There may be up to 1 scale between the third and fourth supralabial and the subocular, and 1-2 scales between the fifth supralabials and the subocular scale. The inner edge of the supraoculars may be smooth or slightly indented by the adjacent head scales (especially towards the rear of the scale). There may be 21 or 19 scale rows at mid-body, with the reduction from 21 to 19 scale rows occurring between 59 and 67% of the distance between the first ventral scale and the anal scale in the former case, or between 4.5 - 23% of this distance in the latter. There are 1-4 postocular scales, 5-8 scales bordering the subocular scale (not counting the pre- and post-ocular's) and 12-16 pterygoid and 13-16 dentary teeth. Some of the head scation patterns are illustrated in Fig 4b.

**DIAGNOSIS**

*T. kanburiensis* can best be distinguished from *T. venustus* by its coloration, which is always less saturated in the former (Fig. 5). The ventral colour is white or cream rather than a shade of green. Males also have more boldly marked labial scales in *T. kanburiensis*. The white lateral stripe is less obvious in *T. kanburiensis*, appearing rather as a blurring of the boundary between dorsal and ventral coloration. There is no single scation character that can unequivocally distinguish between the two species. However, the rostral tends to be more triangular in shape, there tends to be fewer scales between the rear edges of the supraoculars, and more likely to be at least one scale between the third supralabial and the subocular, in *T. kanburiensis* than in *T. venustus*. The scale reduction from 17 to 15 scale rows (the most posterior on the body) is more likely to involve higher scale rows in *T. venustus* than in *T. kanburiensis*.

**COMPARISONS**

Although this paper is focused primarily on the species *T. kanburiensis* and *T. venustus*, Vogel (1991) has provided diagnostic characters to separate *T. venustus* from some other species with which it co-occurs and/or has been confused in the past. These include *T. purpureomaculatus*, *T. erythrunus*, *T. macrops* and *T. albolabris*, *T. popeiorum*, *T. stejnegeri* and *T. sumatr anus*. The first four of these are all members of the *albolabris* group (sensu Malhotra & Thorne, 2000). Vogel (1991) stated that *T. venustus* could be separated from members of the *albolabris* group by separation of the first supralabial shield from the nasal shield. However, this is incorrect. In fact it is very rare that these scales are not fused to some extent in both *T. venustus* and *T. kanburiensis*. Only one out of the 26 specimens examined had a completely divided nasal and first labial scale, and even this only showed this character state on one side. Thus this character actually serves to diagnose *T. venustus*/*T. kanburiensis* from all other *Trimeresurus* species except members of the *albolabris* group. *Trimeresurus purpureomaculatus* is very distinctive and Wardell et al. (1992) have provided a table of characters that serves to distinguish this species from *T. venustus*/*T. kanburiensis*. *Trimeresurus erythrunus* can be distinguished by a higher number of scales at mid body (23 and above), and is not currently known to overlap in range with *T. kanburiensis*, although this is possible. However, confusion with *T. albolabris* and *T. macrops* is still likely, especially in preserved specimens of *T. venustus* which have 21 scale rows at mid-body and in which the distinctive banding pattern has faded. *Trimeresurus albolabris* may be distinguished by its narrow supraoculars and larger head, but *T. macrops* is similar to *T. venustus* in head shape and in having broad supraoculars. *Trimeresurus macrops* can be distinguished by a number of scation differences (Table 4) such as the scale reduction from 10 to 8 rows on the tail (SC108) and from 6 to 4 rows (SC640) occurring further towards the tip and a lower ventral scale count (VSC). Although the range of *T. macrops* does not appear to overlap with that of either *T. kanburiensis* or *T. venustus* according to Regenass & Kramer (1981), in fact it has a much wider distribution (Viravan et al., 1992; personal observation).

**DISTRIBUTION AND NATURAL HISTORY**

Based on verifiable records, *T. venustus* and *T. kanburiensis* are presently known only from Thailand. *Trimeresurus kanburiensis* is known from the western province of Kanchanaburi, which is on the border with Myanmar, and it seems likely that it will also be found in

---

**FIG.**

TABLE 4. Mean values and range of scalation characters distinguishing between *T. venustus* (with 21 scale rows at mid-body) and *T. macrops* (from central and northeastern Thailand), but are not sexually dimorphic. Data are for the maximum number of specimens available for that character. Characters are listed in order of magnitude of the F-ratio in the ANOVA/ANCOVA.

<table>
<thead>
<tr>
<th>Character</th>
<th><em>T. venustus</em></th>
<th>n</th>
<th><em>T. macrops</em></th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC10to8</td>
<td>5.15 (2.9–8.3)</td>
<td>17</td>
<td>9.17 (5.8–13.6)</td>
<td>15</td>
</tr>
<tr>
<td>DV17to15</td>
<td>3.28 (3–4)</td>
<td>17</td>
<td>4.26 (3.5–4.5)</td>
<td>15</td>
</tr>
<tr>
<td>VSC</td>
<td>174.4 (166–183)</td>
<td>17</td>
<td>166.1 (159–173)</td>
<td>15</td>
</tr>
<tr>
<td>BSCK</td>
<td>0.9 (0.5–1)</td>
<td>17</td>
<td>0.6 (0.5–1)</td>
<td>12</td>
</tr>
<tr>
<td>VENTEDGE</td>
<td>8.2 (7–9)</td>
<td>17</td>
<td>7.4 (7–8.5)</td>
<td>14</td>
</tr>
<tr>
<td>SC6to4</td>
<td>62.7 (50.9–71.8)</td>
<td>17</td>
<td>73.0 (60.1–85.9)</td>
<td>15</td>
</tr>
<tr>
<td>SOCBORD</td>
<td>6.4 (5.5–8)</td>
<td>17</td>
<td>7.2 (5.5–9)</td>
<td>15</td>
</tr>
<tr>
<td>Dv21TO19</td>
<td>3.9 (3.5–5)</td>
<td>17</td>
<td>4.3 (3–5)</td>
<td>15</td>
</tr>
</tbody>
</table>

Myanmar eventually. Although precise localities are not available for some specimens, all specimens with known localities come from a relatively short distance around the provincial capital Kanchanaburi. In the course of searching for the species, we found very few villagers who recognised pictures of them; those who did were engaged in bamboo cutting in the limestone hills. This is in accord with the details in Warrell et al. (1992) which describes the case history of a woman who was bitten by this species while cutting bamboo. The scarcity of the species until recently is more likely to be due to the fact that they are confined to higher parts of these hills, and may also have a limited activity period since these hills get extremely arid during the dry season.

*T. venustus* is currently only known from the southern provinces of Nakhon Si Thammarat, Surat Thani and Krabi. Considering the popularity of *T. venustus* in captivity, it is surprising how little has been written about its natural history, possibly because almost all captive specimens have been bought from dealers. In December 1997, the authors were taken to a limestone outcrop near Thung Song, where local people often find the snakes making some of his personal collection of *T. venustus*. The new generic names can be found in Malhotra & Thorpe (2004).

ACKNOWLEDGEMENTS

We are grateful to the large numbers of people who have assisted us in the field, or supplied us with tissue samples for analysis. These include Lawan Chanhome (Queen Savoabha Memorial Institute, Thailand), Jenny Daltry (Flora and Fauna International), Wolfgang Wüster (University of Wales Bangor), Tanya Chan-ard, Jarujin Nabhitabhata (National Science Museum of Thailand), Kamthorn Thirakhupt and Peter Paul van Dijk (Chulalongkorn University, Thailand), Kamphol Udomritthiruj (Aquacorp, Thailand), Merel J. Cox, and Jonathan Murray. We also thank Kamphol Udomritthiruj for providing details of coloration and photographs of live *T. kanburiensis*, Gernot Vogel for making some of his personal collection of *T. venustus* available to us for examination, and Andreas Gumprecht for providing a translation of papers in German. We gratefully acknowledge the National Science Council of Thailand for permission to carry out fieldwork. This study was funded by the Leverhulme Trust (F174/1 and F174/0), the Wellcome Trust (057257/Z/99/Z and 060384/Z/00/Z), and the Darwin Initiative (162/6/65), with additional support for fieldwork from the Royal Society, the Percy Sladen Trust, the Bonhote Trust, and the Carnegie Trust.

REFERENCES


Accepted: 26.5.03
APPENDIX 1

SPECIMENS USED IN THE MORPHOLOGICAL ANALYSIS

Museum abbreviations are as follows: UF: State University of Florida at Gainesville; BMNH: the Natural History Museum, London; PSGV: Gernot Vogel's private collection; AFS: author’s field collection number. Figures in parentheses are the number of males and females respectively. The holotype of *T. kanburiensis* is indicated in italics.

KANCHANABURI PROVINCE

No precise locality: BMNH 194.6.1.8.91 (F); BMNH 2002.51; Erawan National Park (Prathat Caves): UF61846 (1F); Sai Yok Military Camp: BMNH 1987.943 (F), BMNH 1992.535; Tanousri, 25 km NW of Kanchanaburi: BMNH 1988.383 (F).

NAKHON SI THAMMARAT PROVINCE

Thung Song: PSGV 220-222 (2M, 1F), BMNH 1988.384-386 (1M, 2F); BMNH 1987.944 (1F); AFS97B.8-12 (2M, 3F); Khao Luang area: BMNH 2002.52 (M), AFS4 (F).

KRABI PROVINCE


NO LOCALITY

UF (uncatalogued) (2F).

APPENDIX 2

MORPHOLOGICAL CHARACTERS USED, AND THEIR ABBREVIATIONS.

(A) SCALATION

Scale counts recordable on both sides of the body were averages of right and left counts.

VSC: the number of ventral scales (VS), not including anal scale, recorded by the Dowling (1951) method (i.e. the first VS is the one which contacts the first dorsal scale row on both sides).

SCS: the number of pairs of subcaudal scales. Any unpaired scales are treated as a pair.

SUPLAB: the number of supralabials on the left and right hand side.

SUBLAB: the number of supralabials on the left and right hand side.

POSTOC: number of postocular scales.

PREOC: number of preocular scales.

BORSUPOC: the number of scales bordering the supraocular scales, not counting pre- or post-oculars.

BTWSUPOC1: the minimum number of scales between the supraoculars.

BTWSUPOC2: the number of scales between the posterior edge of the supraoculars.

INTNAS: the number of scales separating the internasal scales.

NASPIT: the number of scales between the nasal and the scale bordering the anterior edge of the pit (formed by the fused second supralabial and loreal scale).

LABNAS: the degree of fusion of the first supralabial and nasal scale (1: fully fused, 0: not fused).

LAB3: minimum number of scales separating 3rd supralabial and subocular.

LAB4: minimum number of scales separating 4th supralabial and subocular.

LAB5: minimum number of scales separating 5th supralabial and subocular.

ROST: the ratio of the anterior margin of the rostral scale to the posterior margin.

SOCBORD: the number of scales bordering the subocular scale (not including pre- or post-oculars).

BSCK: the keeling of scales at mid-body.

KTEMP: the keeling of the temporal scales.

KHEADSC: the keeling of the scales on the back of the head.

VENTEDGE: the number of scales between the edge of the mouth and the ventral scales, starting at and including the last sublabial.

GULAR: the number of scales between the first ventral (see above) and second pair of sublabials (which meet ventrally).

(B) SCALE REDUCTION FORMULA

Recorded as a series of characters, each referring to a specific reduction. Each position will have two characters, the dorso-ventral (DV) position of the reduction (the lowest of the two merging scale rows), and the ventral scale (VS) position (counted from the head), which is the ventral scale to which the scale reduction traces diagonally. Before analysis, the VS position was transformed into the percentage of the total number of ventral scales (%VS), to control for variation.

VS23to21: ventral scale position of the reduction from 23 to 21 scale rows.

DV23to21: dorsoventral position of reduction from 23 to 21 scale rows.

VS21to19: ventral scale position of the reduction from 21 to 19 scale rows.

DV21to19: dorsoventral position of reduction from 21 to 19 scale rows.

VS19to17: ventral scale position of the reduction from 19 to 17 scale rows.

DV19to17: dorsoventral position of reduction from 19 to 17 scale rows.

VS17to15: ventral position of the reduction from 17 to 15 scale rows.

DV17to15: dorsoventral position of reduction from 17 to 15 scale rows.
VALIDITY OF TRIMERESURUS VENUSTUS

SC10to8: subcaudal scale position of the reduction from 10 to 8 scale rows.
DV10to8: dorsoventral position of reduction from 10 to 8 scale rows.
SC8to6: subcaudal scale position of the reduction from 8 to 6 scale rows.
SC6to4: subcaudal scale position of the reduction from 6 to 4 scale rows.

(C) BODY DIMENSIONS

All measurements are made on the right side of the head only unless this was damaged, in which case they were done on the left.

SVL: distance between the tip of the snout and the cloaca.
TAIL: distance between the anterior edge of the first subcaudal scale and the tip of the tail.
WHHEAD: width of the head measured between the outer edges of the supraoculars.
LHEAD: length of the head measured between the tip of the snout to the posterior edge of the lower jawbone.
DEYE: diameter of the eye measured between the edges of the scales surrounding it.
EYE2NOS: distance between the eye and the nostril, measured between the suture between the second and third preocular (from the bottom) and the inner edge of the nostril.
WSUPOC: the width of the supraoculars measured in mm, at the widest part.
LSUPOC: the length of the supraoculars measured in mm.
WINTNAS: the width of the internasals (in mm).

(D) INTERNAL CHARACTERS

VS positions are transformed to % VS before analysis (see scale reductions).

PTERY: the number of pterygoid teeth.
DENT: the number of dentary teeth.
HTANT: VS position of the thyroid gland.
HTPOST: VS position of the rear edge of the ventricle.
LVANT: VS position of the anterior tip of the liver.
LVPOST: VS position of the tip of the superficial lobe of the liver.
RKANT: VS position of the anterior tip of the right kidney.
CLOPOST: SC position of the posterior tip of the cloacal gland in the tail base (females only).

(E) COLOUR PATTERN

STRIFE: presence of a lateral stripe (0, absent; 1, indistinct; 2, distinct).
SCRSTR: number of scale rows involved in stripe.
OCSTRIFE: presence of postocular stripe (0, absent; 1, indistinct; 2, distinct).
SCRROC: number of scale rows involved in postocular stripe.
BAND: the number of bands (counted on the right side) between the head and vent.
WBAND: the average width of three bands at mid-body, counted in numbers of scales covered.
WGAP: the average width of the gap between three bands at mid-body, counted in numbers of scales covered.
SCR1: the proportion of the first scale row covered by the light area.
DARKVENT: the percentage of ventral scales with dark pigment.