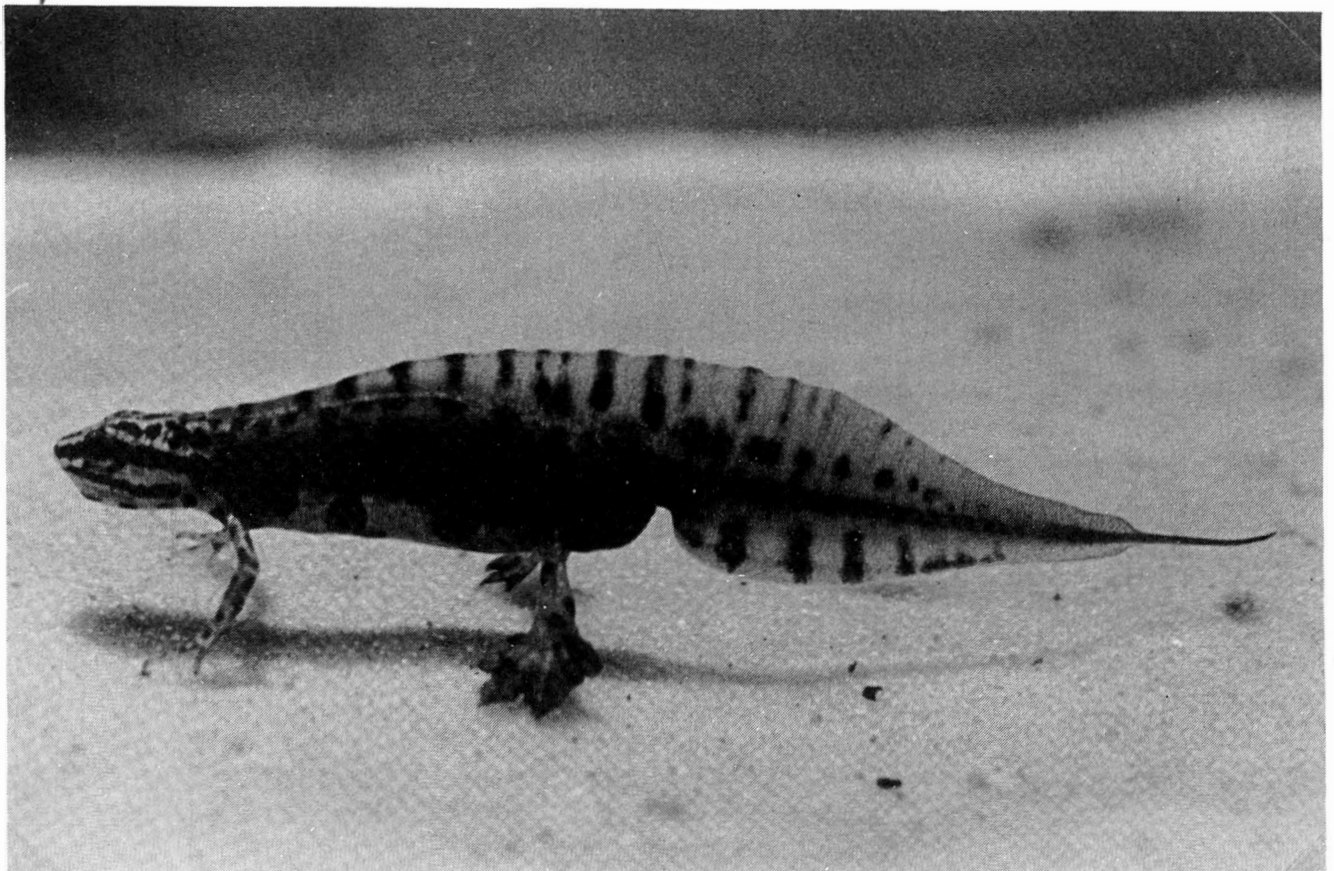


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REVIEW: **A REVIEW OF THE SMOOTH NEWT (*TRITURUS VULGARIS*) SUBSPECIES,** **INCLUDING AN IDENTIFICATION KEY**

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ABSTRACT

A taxonomic revision of the Smooth Newt, *Triturus vulgaris* leads to the recognition of seven subspecies: *T. v. vulgaris*, *T. v. meridionalis*, *T. v. graecus*, *T. v. lantzi*, *T. v. ampelensis*, *T. v. kosswigi* and *T. v. schmidtlerorum*. *T. v. borealis* and *T. v. tataiensis* are considered to be synonyms of *T. v. vulgaris*. An identification key and updated distribution map is provided. These subspecies are recognised by characters which represent non-independent patterns of racial variation, probably produced as a direct consequence of allopatric divergence in isolated glacial refugia. Based on the biological species concept there can be no justification in raising these taxonomic units to species rank.

INTRODUCTION

The recognition of subspecies has always been considered to be of importance to taxonomists working on European Salamandrids. Many species show clear racial differences between geographical areas, particularly within the genus *Triturus* (see Thorn, 1968). At present there are over 30 described subspecies of European newts, although this will certainly be reduced following a full revision of the group. The Smooth newt *Triturus vulgaris* is exceptional among the *Triturus* species in that the degree of secondary sexual character variation seen between subspecies is far greater than that found in the other 11 species. This has resulted in the description of many *T. vulgaris* subspecies and, in the past, some considerable taxonomic confusion.

The aims of this paper are to review and revise the subspecific taxonomy of the Smooth newt, *Triturus vulgaris*, and discuss the values and applications of the subspecies concept. This taxonomic study represents part of a more detailed comparative investigation of the subspecific evolution of courtship behaviour and secondary sexual characters in the Smooth Newt (Raxworthy, 1989 and in prep.).

A HISTORICAL SUMMARY

The original descriptions of the *T. vulgaris* subspecies were based on museum material which was considered to show significant variation between different geographical populations. Usually material was available to museum taxonomists in only very small samples, and this has sometimes resulted in subspecies having been described based on insignificant variation. Male secondary sexual characters have been used extensively to recognise racial variation, indeed most racial variation is restricted to these characters in *T. vulgaris*. These secondary sexual characters include the crest, tail tip, toe flaps, body cross section, dorso-

lateral folds and pigmentation of the male (Fig. 1). However all these features only fully develop during the breeding season when newts are aquatic. Unless fully developed they are of little taxonomic value. This problem is discussed by Steinitz (1965) in relation to *T. vittatus* taxonomy. He found that only two of the five described subspecies were in fact valid and blamed earlier workers for using small samples and animals which were clearly out of full breeding condition.

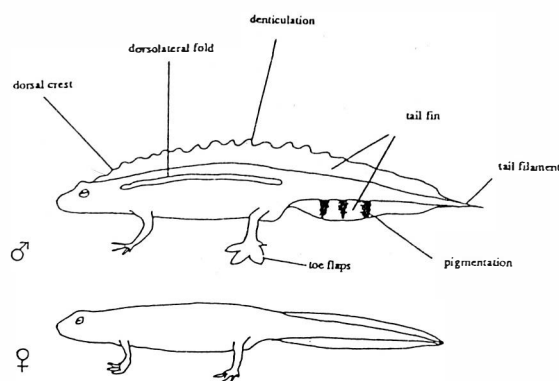


Fig. 1 Some sexually dimorphic characters of *Triturus vulgaris*.

Secondary sexual characters such as the crest, toe flaps and tail filament may all regress over a matter of days if animals are kept under stressful conditions or starved. Also, these characters are not fully developed at the very start and end of the aquatic breeding period (Verrell, Halliday and Griffiths, 1986; Griffiths and Mylotte, 1989).

T. vulgaris was originally described by Linnaeus in 1758 which he placed in the genus *Lacerta* with the European lizards. His form became the first nominal subspecies upon the discovery more than one hundred and twenty years later of the next subspecies, *T. v. meridionalis* which was described by Boulenger (1882). At around the turn of the century many more

SUBSPECIES	ORIGINAL NAME AND SYNONYMS
<i>Triturus vulgaris vulgaris</i>	<i>Lacerta vulgaris</i> (Linnaeus 1758) <i>Triton vulgaris</i> subsp. <i>typica</i> forma <i>Kammereri</i> (Wolterstorff 1907) <i>Triton vulgaris</i> forma <i>Schreiberi</i> (Wolterstorff 1914) <i>Triturus vulgaris borealis</i> Kauri 1959 <i>Triturus vulgaris tataiensis</i> Dely 1967
<i>Triturus vulgaris meridionalis</i>	<i>Molge vulgaris</i> subsp. <i>meridionalis</i> (Boulenger 1882) <i>Molge vulgaris</i> subsp. <i>kapelana</i> (Méhely 1905) <i>Molge vulgaris Boulengeri</i> (Dunn 1918)
<i>Triturus vulgaris graecus</i>	<i>Triton vulgaris</i> subsp. <i>graeca</i> (Wolterstorff 1905) <i>Triton vulgaris</i> subsp. <i>graeca</i> forma <i>corcyrensis</i> (Wolterstorff 1908) <i>Triton vulgaris</i> subsp. <i>graeca</i> forma <i>Tomasinii</i> (Wolterstorff 1908)
Hybrid <i>T. v. vulgaris</i> x <i>T. v. graecus</i>	<i>Triton vulgaris</i> subsp. <i>dalmatica</i> (Kolombatovic 1907) <i>Triton vulgaris</i> subsp. <i>intermedia</i> (Kolombatovic 1907)
<i>Triturus vulgaris lantzi</i>	<i>Triturus vulgaris</i> subsp. <i>typica</i> forma <i>Lantzi</i> (Wolterstorff 1914)
<i>Triturus vulgaris ampelensis</i>	<i>Triturus vulgaris ampelensis</i> Fuhn 1951 <i>Triturus vulgaris vulgaris</i> (ampelensis-Form) Fuhn and Freytag 1952
<i>Triturus vulgaris kosswigi</i>	<i>Triturus vulgaris kosswigi</i> Freytag 1955
<i>Triturus vulgaris schmidtlerorum</i>	<i>Triturus vulgaris schmidtleri</i> Raxworthy 1988

TABLE 1: Original subspecific names and post-1882 synonyms of *T. vulgaris*.

subspecies were described. The most prolific taxonomist of this time was Wolterstorff who described in all a total of five forms, although only two are still recognised. The post-1882 synonyms are given on Table 1 for all recognised subspecies. All earlier synonyms refer to the nominate form and are given by Mertens and Wermuth (1960). A brief summary of recent taxonomic changes since then is given below:

Mertens and Wermuth (1960) included *T. italicus* as a subspecies of *T. vulgaris*, despite the detailed and well illustrated description given by Peracca (1898a,b) who rightly considered this to be a good species. Mertens and Wermuth's taxonomic view was followed by Steward (1969) in his review of the European Urodeles. However Mancino (1961) provided strong evidence that *T. italicus* was a good species based upon his hybridisation experiments between *T. italicus* and *T. vulgaris*. This was supported by Thorn (1968) who gave *T. italicus* species rank in his review of *Triturus* and this has been followed by all more recent studies.

Thorn (1968) recognised all the presently subspecies with the exception of *T. v. schmidtlerorum* (which had not been described then) and also *T. v. tataiensis* (which had only just been described by Dely in 1967). He also included three other subspecies: *T. v. schreiberi*, *T. v. dalmaticus* and *T. v. borealis*.

The situation regarding the Dalmatian coast *T. vulgaris* subspecies remained confusing with five subspecies having been described from this region of Yugoslavia. This is especially evident when referring to the descriptions given by Steward (1969) for *T. v. dalmaticus*, *T. v. graecus* and *T. v. schreiberi*. The differences he gives (based on the original descriptions) are strikingly unconvincing. Schmidtler and Schmidtler (1983) finally resolved the taxonomic status of these

forms by making a detailed survey of the Adriatic region. They considered *T. v. schreiberi* to be a synonym of *T. v. vulgaris*, which they found established in the type locality area. *T. v. dalmaticus* and *T. v. intermedia* are considered to be forms collected in the intergradation zone between *T. v. vulgaris* and *T. v. graecus*, while *T. v. tomasinii* is a synonym of *T. v. graecus* (Schmidtler and Schmidtler 1983).

The latest subspecies to be described is *T. v. schmidtlerorum* collected from Turkey (Raxworthy, 1988). It had been suspected earlier to deserve subspecific status by both Eiselt (1966) and Schmidtler and Schmidtler (1967), although this view was not supported by Özeti (1964). The subspecific name of this subspecies has been changed from *Triturus vulgaris schmidtleri* to *Triturus vulgaris schmidtlerorum*, because this subspecies was named after two people: J. J. Schmidtler and J. F. Schmidtler and therefore the original subspecific name was grammatically incorrect (Raxworthy, 1989).

A population of *T. vulgaris* discovered in the Sava Valley, north Yugoslavia, resembles the nominate form but may deserve subspecific status (Schmidtler and Schmidtler 1983) following further studies. There is also a possibility that specimens from the Danube basin may also represent another new subspecies (Schmidtler, pers. com.).

PROPOSED REVISION

Triturus vulgaris borealis Kauri 1959

T. v. borealis was recognised by its low crest, smaller body spots, general marked 'longitudinal ridges' on the back and in some specimens a thread like appendage (Gilsén and Kauri 1959). The description

was based on 11 males caught in Northern Sweden. I have examined six specimens of *T. v. borealis* kindly loaned to me by J. Elmberg which were collected from Stokärret (Skelefteå), Alnön (Medelpad), Vindelgransele (Lykselle) and Strigtjärn (Sabrå). There is no evidence of true dorso-lateral folds or a tail filament (as defined by Raxworthy, 1988) and body pigmentation does not differ significantly from the nominate form. The crest however is slightly lower (mean = 1.4mm, $n = 6$) than that seen in good breeding condition males from England (mean = 2.5mm, $n = 19$), although the small sample size does not allow a firm conclusion to be made on this. Kauri found that this northern race is subject to a poor diet and has a shorter period of activity than populations further South. Crest development is known to be dependent upon food availability (Halliday, 1977) and therefore the slightly lower crest seen in *T. v. borealis* might be due to local environmental factors. Translocation experiments would readily support or reject this hypothesis. However based on the material examined I conclude that these specimens belong to the nominate subspecies.

Triturus vulgaris tataiensis Dely 1967

Dely (1967) described a paedomorphic subspecies *T. v. tataiensis* from Tata, Hungary. The adults had external gills and the males had poorly developed secondary sexual characters. This paedomorphic condition, which is seen in *T. vulgaris* is most suitably be described as facultative partial neoteny (Raxworthy, 1989, in prep.). From the description of *T. v. tataiensis* it is clear that it is separated from the nominate form by paedomorphic features only. Paedomorphic specimens examined during this study from Smilic, Yugoslavia, show similar features, although they belong to the nominate subspecies.

The paedomorphic and metamorphic condition represent the two states of a polymorphism. The phenotypic expression of the paedomorphic condition is known to be affected by environmental conditions (e.g. Gabrion, Sentein and Gabrion, 1977), since paedomorphs usually undergo metamorphosis when subject to laboratory conditions. The unstable nature of the paedomorphic condition and the fact that it only represents a different morph within a population invalidate the use of this character being used in taxonomic studies regarding the description of subspecies. The paedomorphic *T. v. vulgaris* described by Dely (1967) as *T. v. tataiensis* should therefore be rejected unless other evidence can be produced which demonstrated clear differences between this form and the nominate subspecies.

Gislén and Kauri (1959) for similar reasons questioned on what basis Radovanovic (1951a) distinguished his new paedomorphic subspecies of *T. alpestris*. They presumed it was because these animals were permanently paedomorphic, although in fact Radovanovic (1951b) himself reports that some captive animals did undergo partial metamorphosis before they died. Rocek (1974), Gabrion *et al* (1977) and Breuil and Thuot (1983) all have considered paedomorphosis to be an unreliable indicator of subspecific status for *Triturus* newts, and Breuil and

Guillaume (1984) have found the electrophoretic studies were unable to separate the metamorphic form from the paedomorphic form.

THE *TRITURUS VULGARIS* SUBSPECIES

A total of seven subspecies are recognised in this study. These are:

Triturus vulgaris vulgaris (Linnaeus 1758)

Triturus vulgaris meridionalis (Boulenger 1882)

Triturus vulgaris graecus (Wolterstorff 1905)

Triturus vulgaris lantzi (Wolterstorff 1914)

Triturus vulgaris ampelenis Fuhn 1951

Triturus vulgaris kosswigi Freytag 1955

Triturus vulgaris schmidtlerorum Raxworthy 1988

A brief description of the seven recognised subspecies is presented below. Because fully developed male secondary sexual characters are used to distinguish subspecies, only these features are considered here. Body size is not a diagnostic feature of subspecies (Raxworthy, 1988). Because of the well known differences in body size between populations of newts (Bell, 1966, Tucic and Kalezic, 1984, Clifford, 1986) body size is considered to be largely influenced by local environmental factors.

Triturus vulgaris vulgaris (Linnaeus 1758)

Common Smooth newt

The dorsal crest is high along the body (>1.0mm at mid-body) and deeply notched by rounded denticulations. There is no tail filament, the tail usually tapers to a blunt end. There are no dorso-lateral folds. The body cross section is rounded. The toe flaps are moderately or poorly developed. Fig. 2 and Fig. 8.

Triturus vulgaris meridionalis (Boulenger 1882)

Southern Smooth newt

The dorsal crest is low and smooth edged (<1.5mm at mid-body). The tail tapers to a fine point but there is no tail filament. Weak dorso-lateral folds are present. The body cross section is square-shaped dorsally. The toe flaps are strongly developed. Fig. 3.

Triturus vulgaris graecus (Wolterstorff)

Balkan Smooth newt

The dorsal crest is low (<1.0mm at mid-body) and smooth edged. The tail ends in a long filament. The dorso-lateral folds are strongly developed and the body cross section square-shaped dorsally. The toe flaps are strongly developed. The lower margin of the tail fin is usually unspotted. The belly has many small spots. Fig. 4.

Triturus vulgaris lantzi (Wolterstorff 1914)

Lantz's Smooth newt

The dorsal crest is of medium height (>1.0mm at mid-body) and denticulated by almost spine shaped serrations. The tail gradually tapers to a long fine thread (but there is no tail filament as defined by Raxworthy, 1988). No dorso-lateral folds. The body cross section is slightly square-shaped dorsally. The toe flaps are moderately well-developed. Fig. 5.

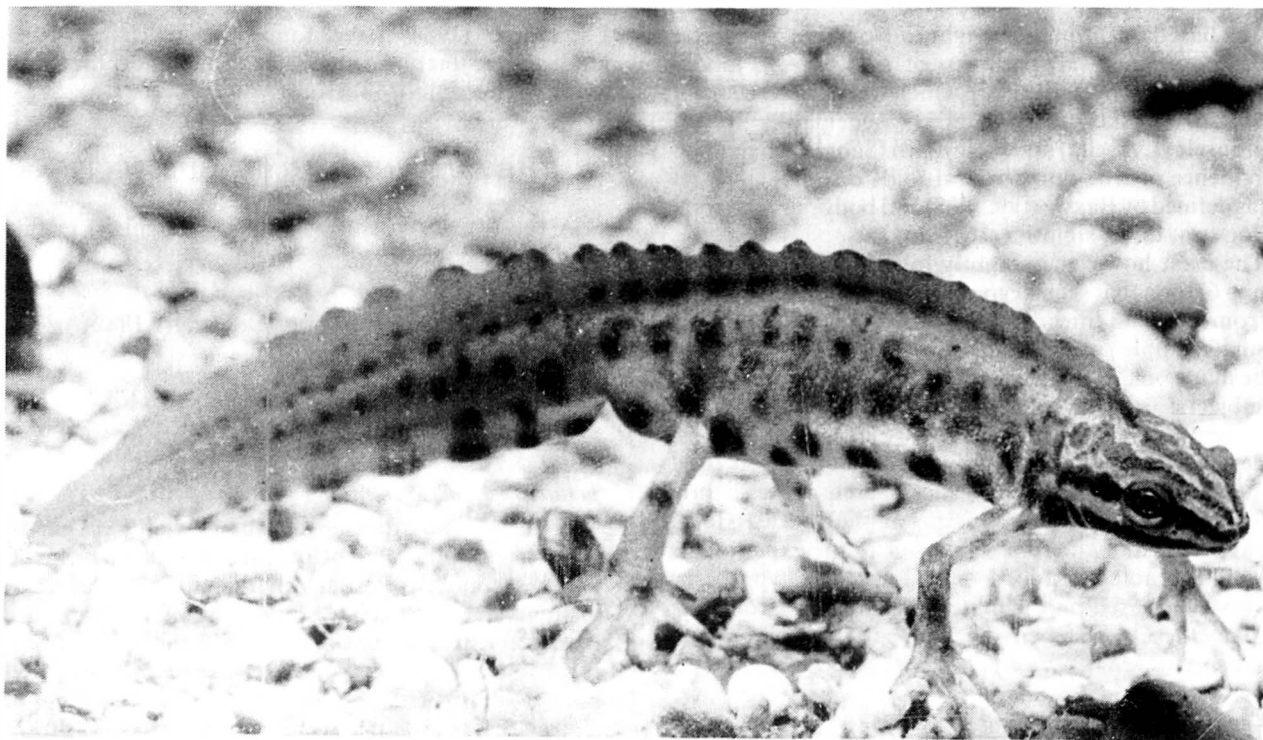


Fig. 2 *T. v. vulgaris*, Oxford, England. (T. R. Halliday).

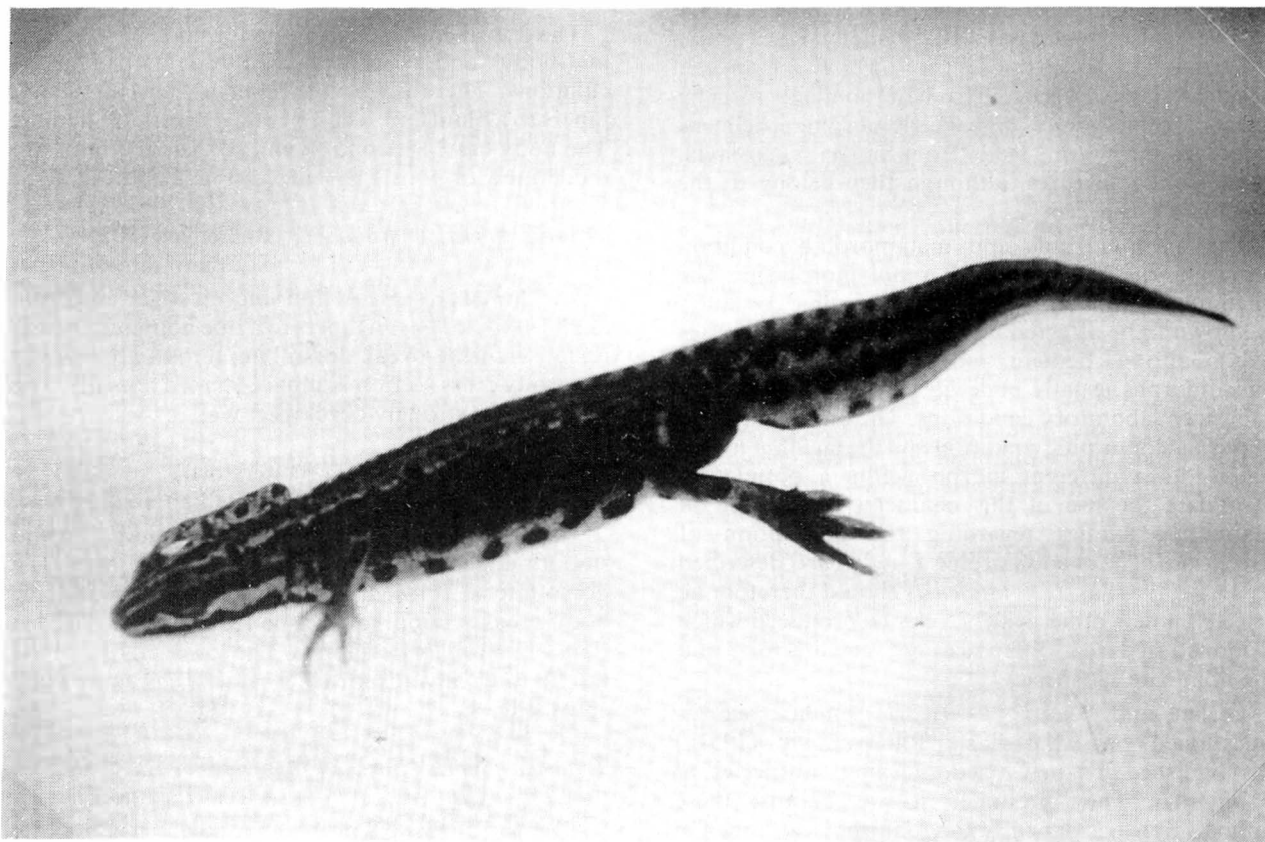


Fig. 3 *T. v. meridionalis*, Torino, Italy. (C. J. Raxworthy).

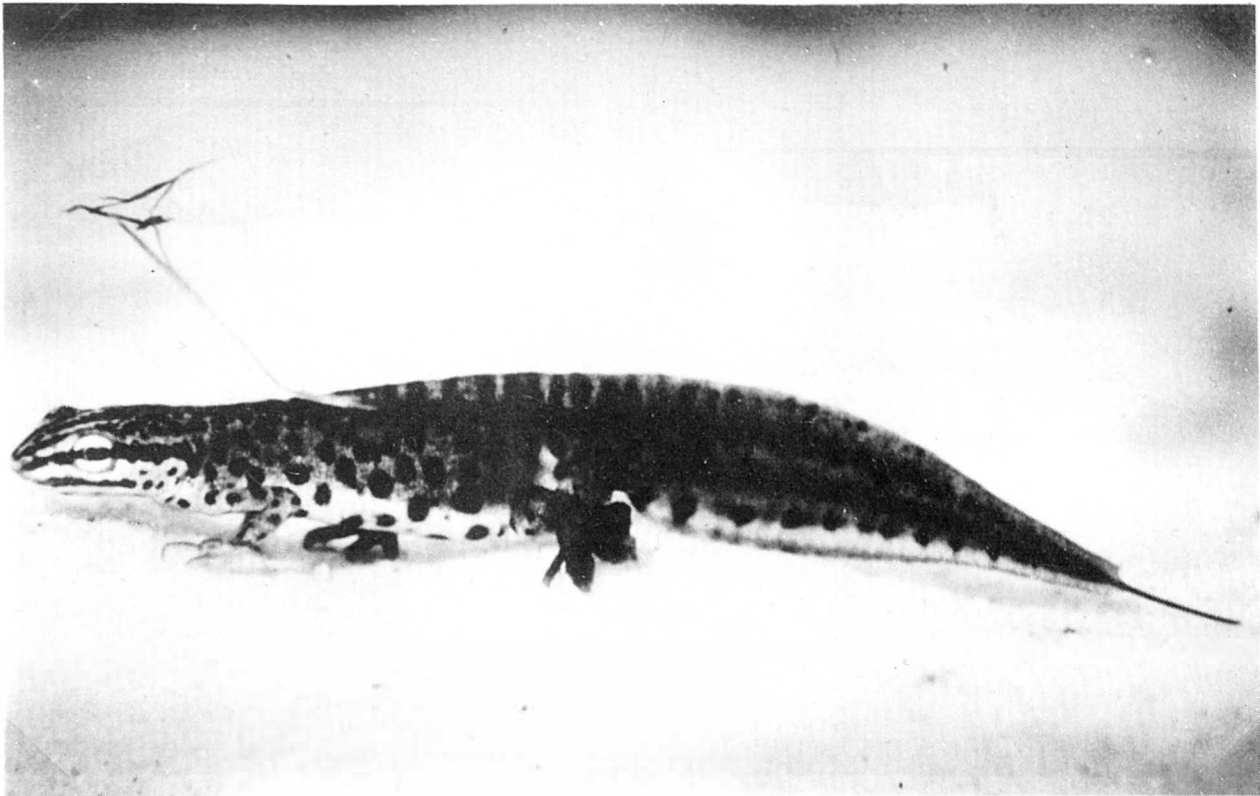


Fig. 4 *T. v. graccus*, Vilusi, Yugoslavia. (C. J. Raxworthy).

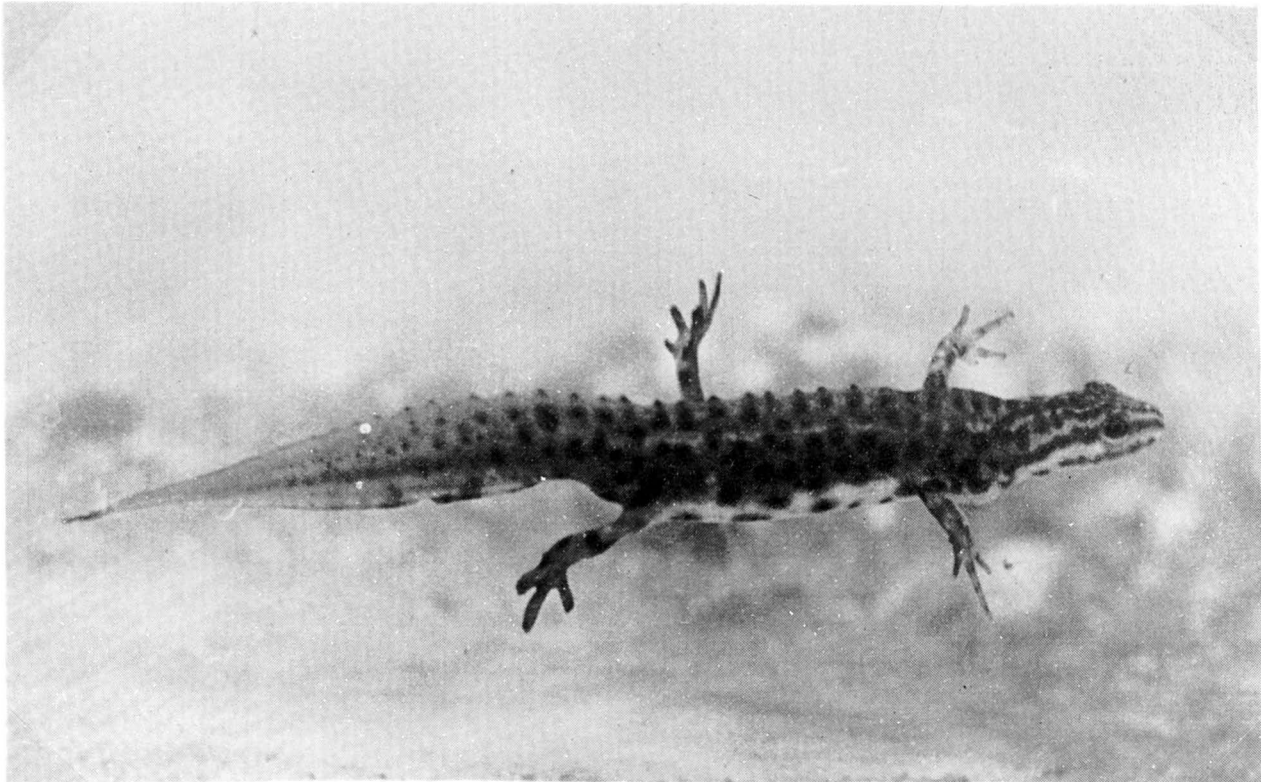


Fig. 5 *T. v. lantzi*, Tbilisi, U.S.S.R. (B. Ardabyevski).

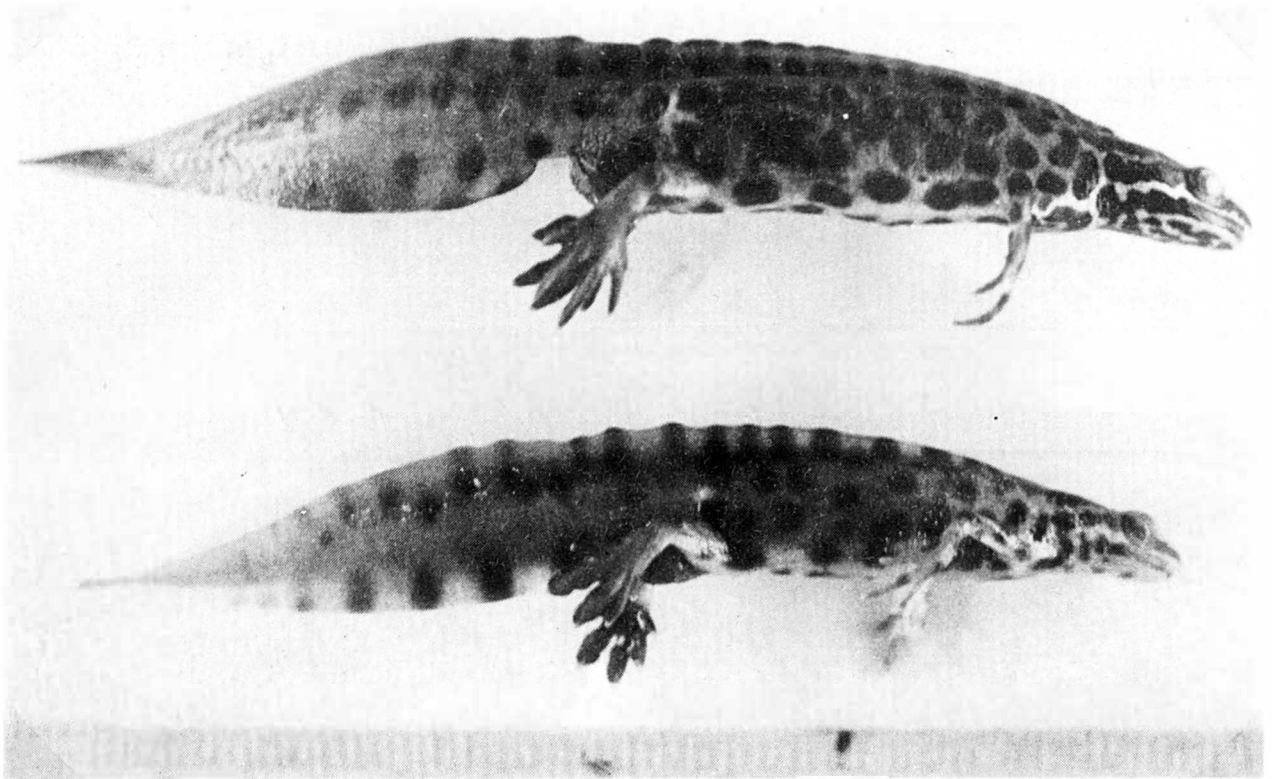


Fig. 6 *T. v. ampelensis*. Valea Dosului, Rumania. (D. Cogalniceanu).

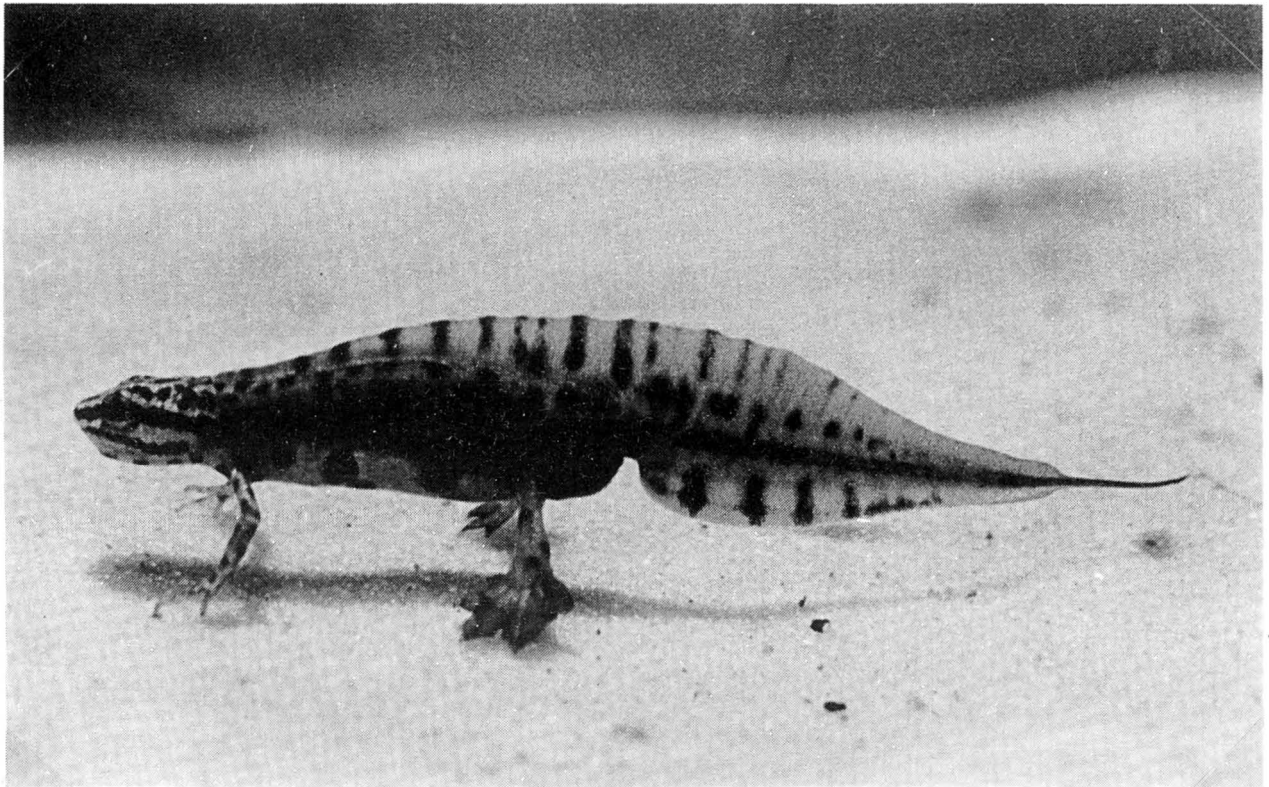


Fig. 7 *T. v. kosswigi*. Adapazari, Turkey. (C. J. Raxworthy).

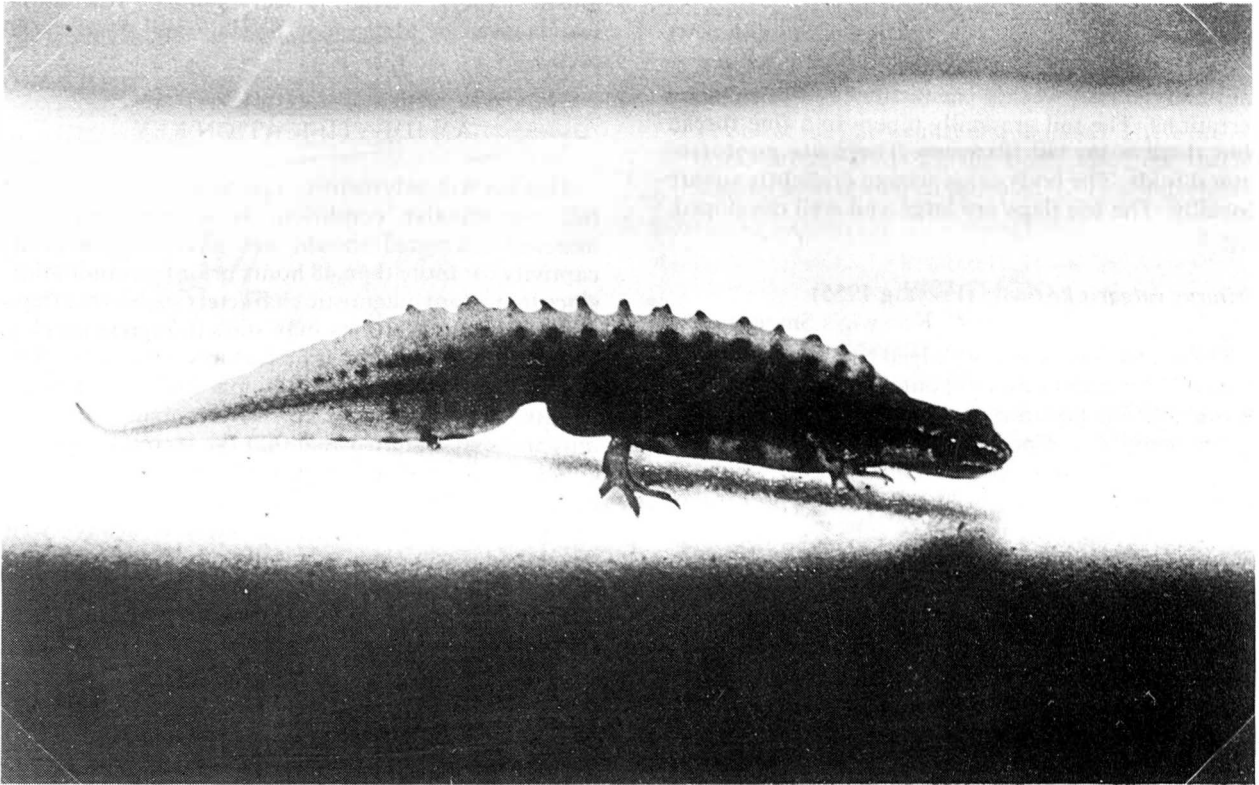


Fig. 8 *T. v. schmidlerorum*, Karacabey, Turkey. (C. J. Raxworthy).

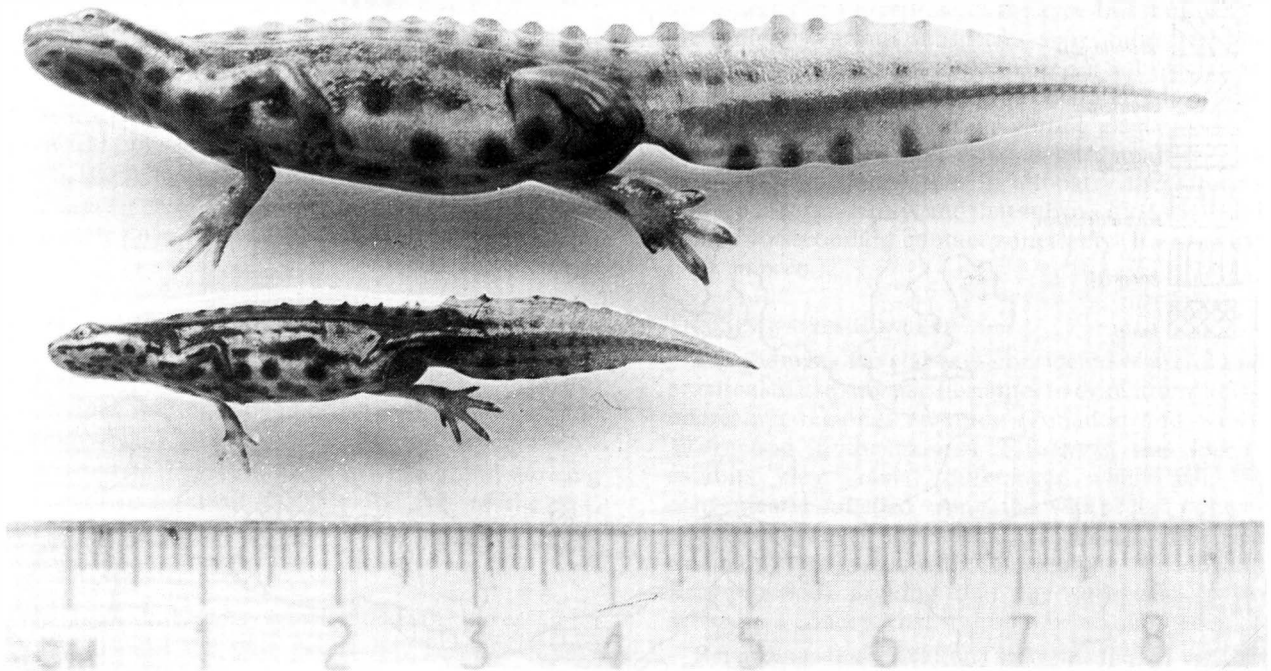


Fig. 9 Top: *T. v. vulgaris*, Milton Keynes, England. Bottom: *T. v. schmidlerorum*, Karacabey, Turkey. (C. J. Raxworthy).

Triturus vulgaris ampelensis (Fuhn 1951)

Apuseni Smooth newt

The dorsal crest is of medium height (>1.0mm at mid-body) and weakly denticulated by rounded serrations. The tail gradually tapers to a fine thread (but there is no tail filament). There are no dorso-lateral folds. The body cross section is slightly square dorsally. The toe flaps are large and well developed. Fig. 6.

Triturus vulgaris kosswigi (Freytag 1955)

Kosswig's Smooth newt

The dorsal crest is smooth edged and very low on the body (<1.0mm at mid-body) but high at the basal area of the tail. The tail ends in a long tail filament. There are strongly developed dorso-lateral folds and the body cross section is square-shaped dorsally. The toe flaps are broad and very well developed. Fig. 7.

Triturus vulgaris schmidtlerorum (Raxworthy 1988)

Schmidtler's Smooth newt

The dorsal crest is of medium height (>2.0mm at mid-body) and denticulated by almost spine shaped serrations. The tail gradually tapers to an elongated point (but no tail filament). There are no dorsal-lateral folds but the body is slightly square-shaped dorsally. The tow flaps are only very weakly developed. Fig. 8 and Fig. 9.

Fig. 10 shows the geographical distribution of each subspecies based on the distribution information given by Schmidtler and Schmidtler (1967, 1983), Kalezić (1983), Sparreboom and Arntzen (1987) and Tark-

hnishvili (pers. comm.). A very similar distribution map is given by Macgregor, Sessions and Arntzen (in prep.).

AN IDENTIFICATION KEY

This key will only identify aquatic males which are in full reproductive condition. It is preferable that material examined should not have been kept in captivity for more than 48 hours prior to examination since important diagnostic characters such as toe flaps and crest denticulations may start to regress quickly under some conditions. The features used in this key can all be examined readily on live unrestrained aquatic animals, but the key works equally well with museum material provided that the secondary sexual characters are fully developed. This can be determined by examination of the crest and toe flaps. In all subspecies, one of these characters is always well developed for animals in full breeding condition. Occasionally animals may have suffered natural damage to the tail tip. Under these circumstances it is best to avoid using the tail tip features in the key.

- 1 The crest is obviously denticulated along the body. Fig. 11(a,b). 2
- The crest is approximately smooth edged along its entire length. Fig. 11(c). 4
- 2 The tail tip gradually tapers to a fine point, frequently with a very fine thread like end. Fig. 11(d). The body cross section is slightly squares

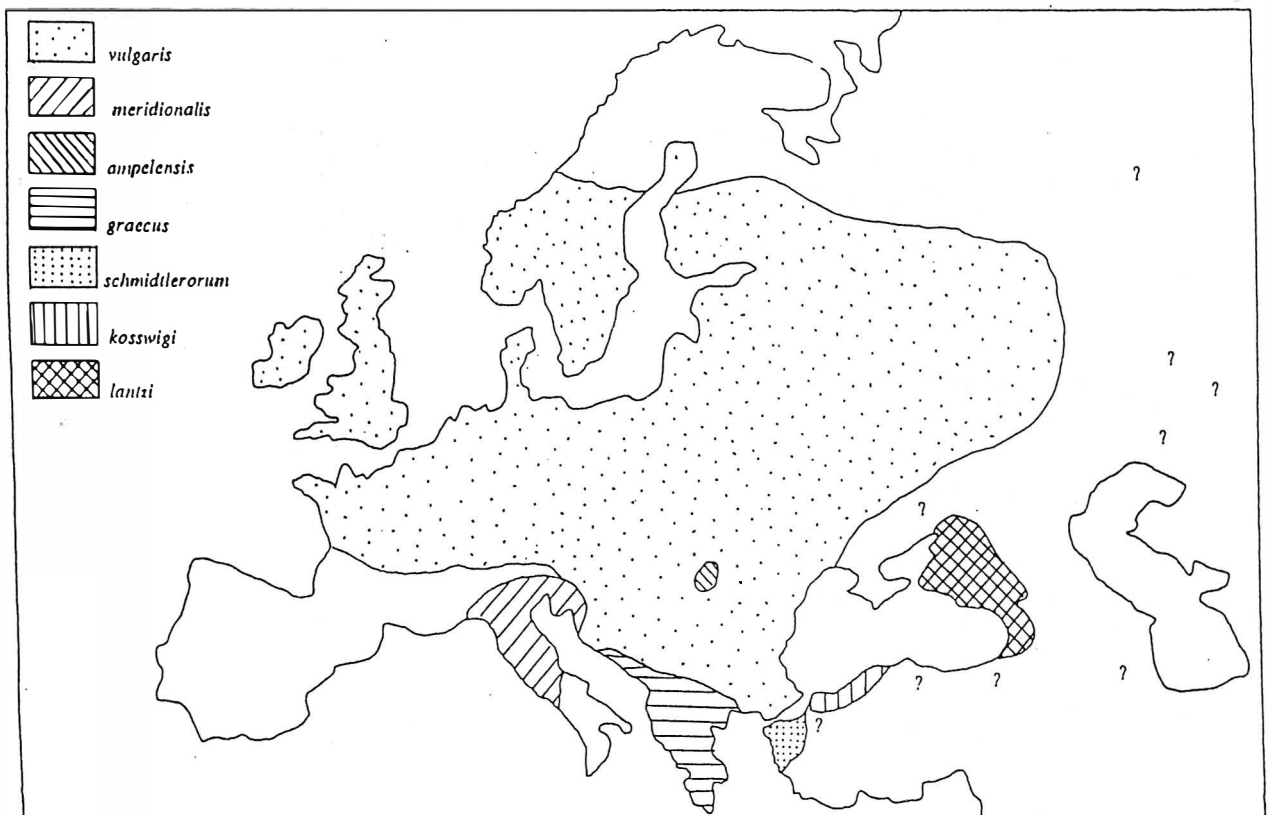


Fig. 10 The subspecies distribution of *T. vulgaris*.

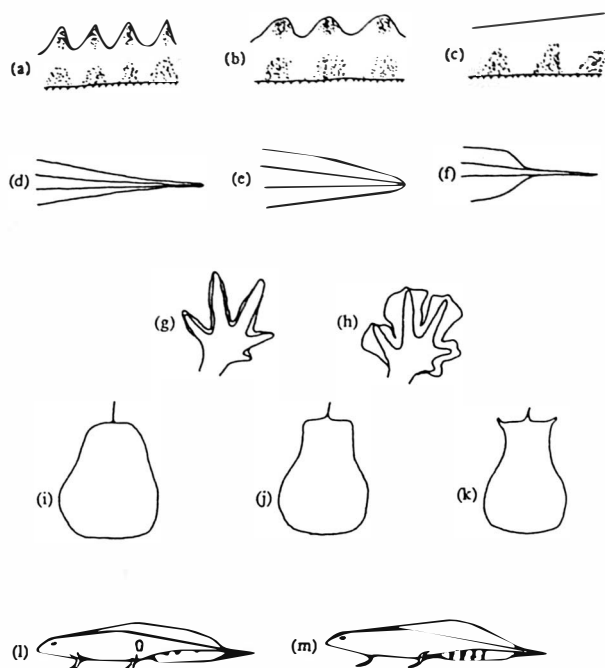


Fig. 11

shaped dorsally, Fig. 11(j). The crest denticulations may be pointed, Fig. 11(a), or rounded, Fig. 11(b).

- 3 The tail tip usually tapers gradually to a blunt point, Fig. 11(e). The body cross section is rounded in the dorso-lateral region, Fig. 11(i). The crest denticulations are rounded, Fig. 11(b). *T. v. vulgaris*
- 3 The toe flaps are not obvious, Fig. 11(g). The crest denticulations are almost pointed and extend onto the tail past the cloaca, Fig. 11(a).

T. v. schmidtlerorum

The toe flaps can be seen easily, Fig. 11(h). The denticulations may be rounded or pointed and extend onto the tail past the cloaca. *T. v. lantzi*

The toe flaps are large and very obvious, Fig. 11(h). The crest denticulations are rounded Fig. 11(b) and usually do not extend on to the tail past the cloaca.

T. v. ampelensis

- 4 The tail tip ends in a long tail filament which is devoid of tail fin and shows a distinct transition from the rest of the tail, Fig. 11(f). There are obvious well developed dorso-lateral folds on the body, Fig. 11(k).
- 5 The tail tip tapers gradually to a fine point, showing no distinct transition from the rest of the tail, Fig. 11(d). Dorso-lateral folds may be present, Fig. 11(k) or absent, Fig. 11(j).

- 5 No large dark spots typically touch the lower tail fin margin and the pale pelvic line is usually very obvious, Fig. 11(l). Only small spots on the belly (<1.5mm dia.)

T. v. graecus

Large dark spots typically touch the lower tail fin margin and the pale pelvic line is absent or very

poorly developed, Fig. 11(m). Usually a few large spots on the belly (>1.5mm dia.). *T. v. kosswigi*

- 6 The crest is always smooth edged. There are weak dorso-lateral folds on the body. *T. v. meridionalis*
- The crest may be weakly denticulated. There are no dorso-lateral folds on the body although this is slightly square shaped dorsally. *T. v. ampelensis*

DISCUSSION

PHYLOGENETIC ASPECTS

The two most closely related species to *T. vulgaris* are *T. helveticus* and *T. montandoni*. The three species form their own monophyletic group (Rafinski and Arntzen, 1987, Arntzen and Sparreboom, 1987, Macgregor *et al.* in prep.). Hybridisation studies (Macgregor *et al.* in prep.), cytological evidence (Ragghianti, Bucci-Innocent and Mancino, 1978) and electrophoretic evidence (Rafinski and Arntzen, 1987) all indicate that *T. vulgaris* is most closely related to *T. montandoni*. Sympatric populations are known in Central Europe and natural hybrids have been reported which may be common in some populations (Hofmann, 1908, Geyer, 1953, Fuhn, Sova and Dumitrescu, 1975, Pecio and Rafinski, 1985).

Within *T. vulgaris* two main groups can be recognised (Raxworthy, 1989). The 'graecus' group is comprised of *T. v. graecus* and *T. v. kosswigi*. The 'vulgaris' group is comprised of *T. v. vulgaris*, *T. v. lantzi* and *T. v. schmidtlerorum*. *T. v. meridionalis* and *T. v. ampelensis* represent intermediate forms, with stronger affinities to the 'graecus' group for *T. v. meridionalis*, and stronger 'vulgaris' affinities for *T. v. ampelensis*. Outgroup comparison suggests that the 'graecus' group represents the ancestral state, while the 'vulgaris' group subspecies show more derived characters (Raxworthy, 1989, in prep.). Subspeciation of *T. vulgaris* appears to have occurred in the Pleistocene, when populations during glacial periods became fragmented and isolated into small refuges areas. It is suggested that in allopatry these forms evolved independently, and that subspecific fusion was limited to secondary contact zones only (Raxworthy, 1989, in prep.).

THE SUBSPECIES CONCEPT

Taxonomists have always considered it useful and practical to use subspecific names to draw attention to interesting regional variation (Amadon and Short, 1976), and in the case of *T. vulgaris*, this species exhibits clear racial differences which can be conveniently labelled using the subspecies nomenclature. However the subspecies concept has been frequently criticised, with for example Wilson and Brown (1953) arguing that the subspecies is so arbitrary a concept that it should be abandoned.

Regarding the situation seen in the *T. vulgaris* subspecies, all subspecies are defined, based on the development of morphological male secondary sexual characters, which are stable outside hybrid zones (Schmidtler and Schmidtler, 1983). These morpho-

logical characters do not show independent patterns of distribution and therefore this leads to the recognition of clearly defined (and non arbitrary) subspecific taxa. By use of such characters subspecies boundaries become real biological concepts represented by intergradation zones which can be readily identified (Fig. 12). The *T. alpestris* subspecies also appear to show non-independent geographical variation for both morphological and electrophoretic characters. Arano (1988) has found that most of the *T. alpestris* subspecies (described using morphological criteria) are supported by electrophoretic patterns of variability and the Yugoslavian *T. vulgaris* subspecies have also been supported by electrophoretic evidence (Kalezić, 1984).

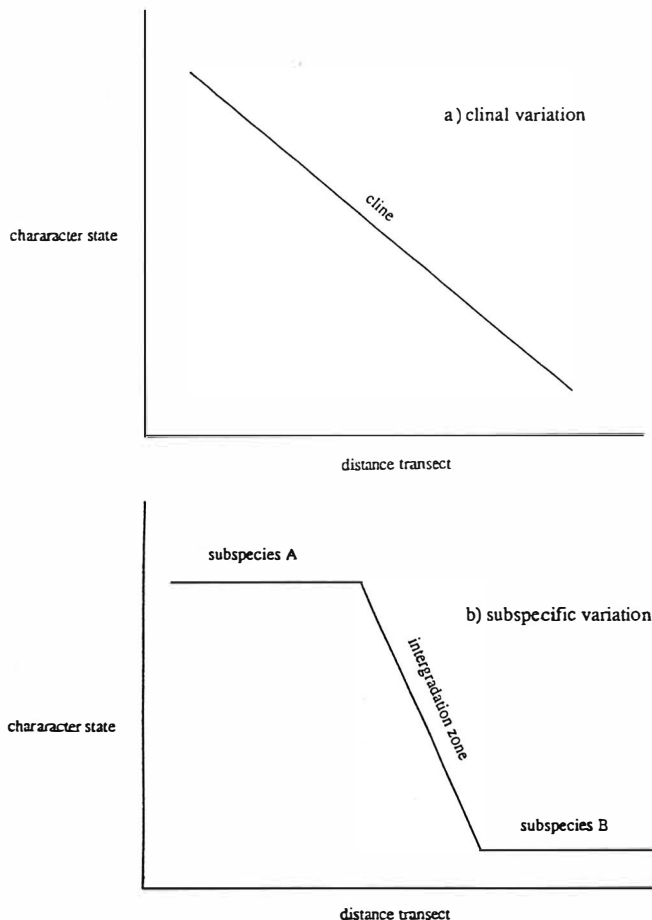


Fig. 12 The difference between clinal variation and subspecific variation.

The subspecific phylogenies of *T. vulgaris* and *T. alpestris* show a surprising level of biogeographical congruence, based on completely different types of data: morphological and courtship behaviour for *T. vulgaris* (Raxworthy, 1989) and electrophoretic evidence for *T. alpestris* (Arano and Arntzen, 1987, Arano, 1988). Both phylogenies have ancestral Balkan subspecies and a more derived lineage giving rise to the Italian and widespread Central European subspecies (Arntzen and Raxworthy, in prep.). The *T. vulgaris* subspecies appear to have arisen as a direct consequence of climatic changes in the Pleistocene. The glacial refugia identified by tree pollen analysis by

Huntley and Birks (1983) shows close correlations with the centres of current subspecies distributions of *T. vulgaris* subspecies (Raxworthy, 1989). It is therefore possible to propose the appropriate refugia where most subspecies were confined during at least the last glacial period.

The biogeographical congruence of subspecific phylogenies, the congruence of different taxonomic data sets and the correlation of subspecies distributions with glacial refugia provide strong evidence that these subspecies represent valid biological entities. Therefore I conclude that these subspecies are not arbitrary concepts, but rather represent real non-independent patterns of geographical variation.

SUBSPECIES OR SPECIES?

Is it appropriate to consider raising the taxonomic status of the *T. vulgaris* subspecies to the species level? Biological species are defined by Mayr (1942) as 'groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups'.

Natural hybridisation is usually rare between *Triturus* species (the exception being between *T. montandoni* and *T. vulgaris*, and *T. cristatus* and *T. marmoratus*). When hybridisation is induced artificially in the laboratory, post-zygotic isolation mechanisms always result in unfit hybrids, e.g. between *T. marmoratus* and *T. cristatus* (Lantz, 1947), *T. vulgaris* and *T. helveticus* (Scali and Mancino, 1968) and the *T. cristatus* superspecies (Callan and Spurway, 1951, Wallis and Arntzen, 1989). In all these cases post-zygotic isolating mechanisms prevent genetic fusion and are therefore contribute to the reproductive isolation of each species. Geyer (1953) however has reported viable hybrid *T. vulgaris-montandoni* in the first and second generation. Although wild *T. vulgaris* x *montandoni* hybrids are well known (see earlier), recent studies have found mutually exclusive parapatric distribution patterns between these two species (Rafinski pers. comm., in Arntzen and Sparreboom submitted). Evidence for ecological and ethological pre-mating isolation mechanisms have been found in some species (Halliday, 1977, Arntzen, 1986) which would prevent gene flow between species.

Only a very limited amount of work has been undertaken concerning hybridisation experiments between the *T. vulgaris* subspecies. Lantz (1947) noted that intra-specific crosses between various subspecies of *T. vulgaris* were obtained without difficulty, yielding offspring which are normal in every respect. Observations made during this study found both reciprocal mixed pairs of *T. v. vulgaris* and *T. v. meridionalis* showed successful courtship with sperm transfer.

T. vulgaris subspecific intergradation zones have now been recognised and described throughout much of Europe. Intergradation zones have been found in: Yugoslavia: *T. v. vulgaris* x *T. v. meridionalis* and *T. v. vulgaris* x *T. v. graecus* (Schmidtler and Schmidtler, 1983). Rumania: *T. v. vulgaris* x *T. v. ampelensis* (Cogalniceanu pers. comm.) and in Turkey *T. v. vulgaris* and *T. v. kosswigi* (Tabrizi, 1980).

The size of some of these intergradation zones (up to 160km in length along the Dalmatian coast) and the reported normal fitness of hybrids do not provide any evidence of reproductive isolation between these subspecies. There is obvious gene flow occurring at these secondary contact zones, although subspecific fusion may be very slow if migration is low and there is some degree of subspecific assortative mating (Raxworthy, 1989). Clearly, there can be no question of raising these taxonomic units to species rank based on the biological species concept.

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