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

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(Accepted 18.8.89)

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. graciosus, T. v. lantzi, T. v. amplusis, T. v. kossiwig and T. v. schmidleri. 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 Salamanders. Many species have 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. virgatus* 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.

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

<table>
<thead>
<tr>
<th>SUBSPECIES</th>
<th>ORIGINAL NAME AND SYNONYMS</th>
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<tr>
<td><em>Triturus vulgaris vulgaris</em></td>
<td><em>Lucertus vulgaris</em> (Linnæus 1758)</td>
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<td><em>Triturus vulgaris</em> subspp. typica forma Kummereri* (Wolterstorff 1907)</td>
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<td><em>Triturus vulgaris</em> forma Schreiber* (Wolterstorff 1914)</td>
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<td><em>Triturus vulgaris</em> borealis* Kauri 1959</td>
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<td><em>Triturus vulgaris</em> tataiensis* Dely 1967</td>
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<td><em>Triturus vulgaris meridionalis</em></td>
<td><em>Moige vulgaris</em> subspp. meridionalis* (Boulenger 1882)</td>
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<td><em>Moige vulgaris</em> subspp. kapelana* (Méhely 1905)</td>
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<td><em>Moige vulgaris</em> Boulengeri* (Dunn 1918?)</td>
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<td><em>Triturus vulgaris graecus</em></td>
<td><em>Triturus vulgaris</em> subspp. graecus* (Wolterstorff 1905)</td>
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<td><em>Triturus vulgaris</em> subspp. graeca forma corenensis* (Wolterstorff 1908)</td>
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<td><em>Triturus vulgaris</em> subspp. graeca forma Toniasini* (Wolterstorff 1908)</td>
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<td>Hybrid T. v. vulgaris x T. v. graecus</td>
<td><em>Triturus vulgaris</em> subspp. dalmaticus* (Kolombatovic 1907)</td>
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<td><em>Triturus vulgaris</em> subspp. intermedia* (Kolombatovic 1907)</td>
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<td><em>Triturus vulgaris lantzi</em></td>
<td><em>Triturus vulgaris</em> subspp. typica forma Lantzi* (Wolterstorff 1914)</td>
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<td><em>Triturus vulgaris ampelesensis</em></td>
<td><em>Triturus vulgaris</em> ampelesensis* Fuhrn 1951</td>
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<td><em>Triturus vulgaris</em> ampelesensis* Fuhrn and Freytag 1952</td>
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<td><em>Triturus vulgaris kosswigi</em></td>
<td><em>Triturus vulgaris</em> kosswigi* Freytag 1955</td>
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<tr>
<td><em>Triturus vulgaris schmidleriorum</em></td>
<td><em>Triturus vulgaris</em> schmidleri* Raxworthy 1988</td>
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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 Peraccia (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. schmidleriorum* (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. tomasini* is a synonym of *T. v. graecus* (Schmidtler and Schmidtler 1983).

The latest subspecies to be described is *T. v. schmidleriorum* 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 schmidleri* to *Triturus vulgaris schmidleriorum*. 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 (Gilsen and Kauri 1959). The description
was based on 11 males caught in Northern Sweden. I have examined six specimens of *T. v. hordealis* kindly loaned to me by J. Elmberg which were collected from Stokarret (Skelleftea), Alnön (Medelpad), Vindelgransele (Lykselle) and Strigstjärn (Sabrâ). 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 = 1.4 mm, n = 6) than that seen in good breeding condition males from England (mean = 2.5 mm, 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. hordealis* 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* tataien sis Dely 1967

Dely (1967) described a paedomorphic subspecies *T. v. tataien sis* 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. tataien sis* 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. tataien sis* 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 paedomorphism 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 meridonialis* (Boulenger 1882)
- *Triturus vulgaris gracaeus* (Wolterstorf 1905)
- *Triturus vulgaris lanzi* (Wolterstorf 1914)
- *Triturus vulgaris ampeleus* Fuhn 1951
- *Triturus vulgaris kosswigi* Freytag 1955
- *Triturus vulgaris schmidtlorum* 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 (>1.0 mm 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 meridonialis* (Boulenger 1882)

Southern Smooth newt

The dorsal crest is low and smooth edged (<1.5 mm 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 gracaeus* (Wolterstorf)

Balkan Smooth newt

The dorsal crest is low (<1.0 mm 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 lanzi* (Wolterstorf 1914)

Lantz's Smooth newt

The dorsal crest is of medium height (>1.0 mm 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. geneus*. Vilusi, Yugoslavia. (C. J. Raxworthy).

Fig. 5  *T. v. lanzi*. Tbilisi, U.S.S.R. (B. Ardabyevski).
Fig. 6  *T. v. anpelesis*. Valea Dosului, Romania. (D. Cogalniceanu).

Fig. 7  *T. v. kosswigi*. Adapazari, Turkey. (C. J. Raxworthy).
Fig. 8  *T. v. schmidtlerorum*. 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 dorso-lateral folds but the body is slightly square-shaped dorsally. The toe 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), Kalezic (1983), Sparreboom and Arntzen (1987) and Tarkhnishvili (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.

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**Fig. 10** The subspecies distribution of *T. vulgaris*. 
The tail tip usually tapers gradually to a fine point, showing no distinct transition from the rest of the tail, Fig. 11(f). There are obvious well developed dorso-lateral folds on the body, Fig. 11(d). Dorso-lateral folds may be present, Fig. 11(k) or absent, Fig. 11(j).

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.) are visible. 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. korsswigi

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. ampeleensis

**DISCUSSION**

**PHYLLOGENETIC 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 (Raggianti, 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, Fuhm, Sová and Dumitrescu, 1975, Pecio and Rafinski, 1985).

Within *T. vulgaris* two main groups can be recognised (Raxworthy, 1989). The 'graeceus' group is comprised of *T. vulgaris*, *T. ampeleensis* and *T. korsswigi*. The 'vulgaris' group is comprised of *T. vulgaris*, *T. lanzi* and *T. schmidtlerorum*. T. v. meridionalis and *T. ampeleensis* represent intermediate forms, with stronger affinities to the 'graeceus' group for *T. vulgaris*, and stronger 'vulgaris' affinities for *T. ampeleensis*. Outgroup comparison suggests that the 'graeceus' 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.).
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 Yugoslav *T. vulgaris* subspecies have also been supported by electrophoretic evidence (Kalezić, 1984).

The glacial refugia identified by tree pollen analysis by consequence of climatic changes in the Pleistocene. Italien and widespread Central European subspecies (Arntzen and Raxworthy, in prep.). The 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 (Cullum 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 superspecies (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. grceus* (Schmidtler and Schmidtler, 1983). Rumania: *T. v. vulgaris* x *T. v. ampelesis* Cogalniceanu pers. comm.) and in Turkey *T. v. vulgaris* and *T. v. kossaigyi* (Tabrizi, 1980).
The size of some of these intergradation zones (up to 160 km 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.

ACKNOWLEDGEMENTS

I should like to thank all the following colleagues who have contributed information and advice. In particular I should like to mention Begôña Arano, Pim Arntzen, Frantisek Andreone, Nick Arnold, John Baker, Barry Burke, Barry Clarke, Dan Cogalniccanu, Johan Elmborg, Cristina Giacoma, Richard Griffiths, Tim Halliday, Lottie Hosie, Milos Kalezic, Herbert Macgregor, Giorgio Maccarone, Giorgio Mancino, Phil McGowan, Jan Rafinski, Julie Roberts, Joseph Schmidtter, Max Sparreboom, David Tarkhishvili, Paul Verrell and Robert Vignali. This study was supervised by Tim Halliday and funded by the Science and Engineering Research Council. I am grateful to Pim Arntzen and Joseph Schmidtter for their comments on an earlier version of this work.

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