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Taxonomic reassessment of Middle Eastern water frogs: Morphological variation among populations considered as *Rana ridibunda, R. bedriagae* or *R. levantina*

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Abstract

Eight morphometric features of water frogs of 14 localities in Turkey, Syria, Jordan and Israel were compared with those of *Rana ridibunda* in Kazakhstan, Armenia and Greece (Thrace). These study sites include the type localities of *R. ridibunda*, *R. r. caralitana*, *R. esculenta* var. *bedriagae* and *R. levantina*. Multivariate comparisons (principal-component analysis, discriminant analysis) based on the $\log_{10}$-transformed variables demonstrate that the data set includes only two taxa that differ significantly in size and shape. By applying a morphospecies criterion, *R. ridibunda* is represented exclusively by the three reference populations, whereas all other populations (in Turkey, Syria, Jordan and Israel) represent the same species, *R. bedriagae*.

Key words: *Rana ridibunda* – *Rana bedriagae* – morphometry – multivariate comparisons – morphospecies

Introduction

Opinions regarding the number of the Eurasian water frog species (genus: *Rana*) and their geographic ranges have undergone considerable changes in the last three decades. In 1960, Mertens and Wermuth mentioned only *R. esculenta* and *R. ridibunda* as valid species, whereas currently 10 species are recognized (Dubois and Ohler 1994; Gasc et al. 1997). The reassessment of water frog taxonomy was initiated by Berger (1966), who was the first to realize that *R. esculenta* is a hybrid resulting from crosses between *R. lessonae* and *R. ridibunda*. This surprising finding was based on morphometric analyses of the three phenotypes and finally verified by subsequent crossing experiments (Berger 1968). Studies on the interspecific variation of many character complexes such as body size and shape, signals of acoustic communication, chromosome morphology, and electrophoretic mobility of proteins have contributed to our present view. In particular, bioacoustic analyses based on structural features of the advertisement call have provided evidence for the recognition of several new species and their hybrids (Schneider and Sinsch 1992; Sinsch and Schneider 1996): *R. epeirotica* and *R. balcanica* in the western Balkans (Schneider et al. 1984; Schneider et al. 1993), *R. levantina* in Turkey, Israel and Egypt (Schneider et al. 1992), and *R. bergeri* in Italy (Sinsch and Schneider 1996). Moreover, bioacoustic analyses corroborated the specific status of *R. lessonae*, *R. perezi*, and *R. ridibunda* (Günther 1969; Schneider et al. 1979; Schneider and Steinwarz 1990) and shed doubts on that of *R. shqiperica* (Sinsch and Schneider 1996).

Species-specific differences in advertisement calls are always accompanied by corresponding differentiation of other character complexes, such as external morphology, karyotypes and electrophoretic mobility of allozymes. For instance, *R. balcanica* and *R. levantina* significantly differ from *R. ridibunda* in 5 and 4, respectively, out of 12 morphometric ratios (Schneider et al. 1992, 1993). The karyotype of *R. epeirotica* characteristically varies from that of *R. ridibunda* (Belcheva 1985). Finally, allozyme analyses corroborate the bioacoustic and morphometric differentiation (Nevo and Filippucci 1988; Sinsch and Eblenkamp 1994; Sofianidou et al. 1994).

Recent bioacoustic investigations of water frogs at two sites – Damascus (Syria), the type locality of the form *Rana esculenta* var. *bedriagae* described by Camerano (1882), and Birket Ata (Israel), the type locality of *R. levantina* – showed that there is no difference between the advertisement calls of these two groups of frogs (Schneider and Sinsch 1999). Nor do these calls differ from those of the frogs of Lake Beyşehir (Turkey), which were described by Arikan (1988) as the distinct subspecies *R. ridibunda caralitana*. Rigorous application of the bioacoustic method removes all doubt that these three sites are inhabited by the same species, which on the basis of priority of nomenclature should be called *R. bedriagae*. In accordance with previous practice, this conclusion has now been tested by analysing another character complex, the quantitative features of external morphology. Material for this comparison included previously available data as well as many new measurements of specimens in museum collections and of frogs collected on site. This study considerably extends our knowledge of the geographic range of *R. bedriagae* as several new localities were identified which were not surveyed during the the bioacustical sampling.

Materials and methods

The external morphology was studied in water frogs collected in the Middle Eastern states Turkey ($n = 33$), Syria ($n = 44$), Israel ($n = 37$) and Jordan ($n = 12$). The study sites (Fig. 1) include the type localities of *Rana ridibunda caralitana* Arikan 1988, *R. esculenta* var. *bedriagae* Camerano 1882 and *R. levantina* Schneider et al. 1992. Eight parameters were measured with calipers to the nearest 0.1 mm: 1. snout-vent length (SVL); 2. femur length; 3. tibia length; 4. digitus primus length; 5. callus internus length; 6. maximal head width; 7. snout-eye distance; 8. tympanum diameter. In the same way, we measured 55 specimens of lake frogs, *Rana ridibunda* Pallas 1771 from another three sites (including the type locality) as an outgroup. Localities, numbers and sex of specimens and their assignment to museum collections are summarized in the appendix. All morphometric distances were $\log_{10}$-transformed before applying multivariate statistics.

At the level of populations, a discriminant analysis was run on all data sets which consisted of at least 6 specimens measured, including the reference populations of *R. ridibunda*. At the species level, sets of the $\log_{10}$-transformed data were subjected to principal-component analysis to explore the morphometric variability independent of taxonomic assignment and to reduce the information to statistically unrelated factors. The first principal component (PC1) of morphometric data generally describes differences in size, but size effects may be present in subsequent principal components representing shape (Humphries et al. 1981). Techniques such as shearing have been developed to correct PC2 and PC3 for possible size effects (Bookstein et al. 1985), but they are controversial and size effects may still persist (Rohlf and

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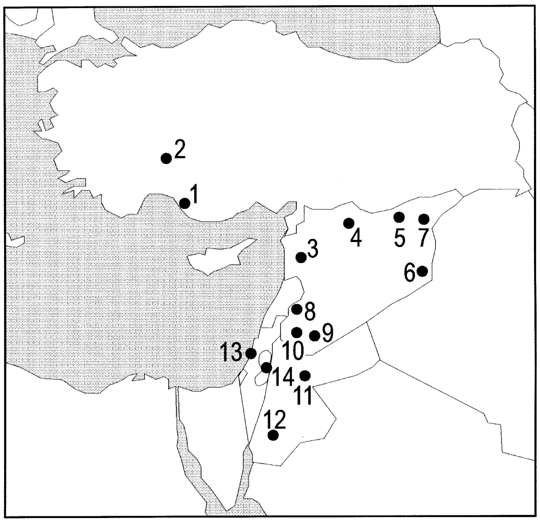

Fig. 1. Map of localities. Turkey: Alanya (1), Beyşehir (2); Syria: Jebel el Ansariye (3), Ar Raqqah (4), Nahr al-Habur (5), Abu Kemal (6), Bahrat Khatuniyah (7), Damascus (8), Quanwat (9), Mzeirib (10); Jordan: Zarqa (11), Wadi Wala (12); Israel: Birket Ata, Hadera (13), Jericho (14). Further information on localities is given in the appendix

Bookstein 1987). The influence of SVL on PC1 was assessed by linear correlation and regression analysis for each species, and slopes and intercepts of regression lines were tested for species-specific differences, using conditional sum of square. Again, discriminant analysis was applied to obtain a further measure of the morphological differentiation between the species.

Results

The discriminant analysis based on eight $\log_{10}$-transformed morphometric distances resulted in four significant canonical variables (discriminant functions) which explained 95.8% of the total variance (Table 1). Each of the plots of the individual discriminant scores showed a considerable overlap between the three *R. ridibunda* reference populations and the other ones, but taken together, provided a remarkable distinction among many populations (Fig. 2A,B, Table 1C). Two groups of populations with high rates of within-group erroneous classifications could be distinguished: one group exclusively consisted of the *R. ridibunda* reference populations, the second group included all other populations. This result confirms the conclusion based on the features of the advertisment calls (Schneider and Sinsch 1998), that the studied region is inhabited by only two water frog species, *R. ridibunda* and *R. bedriagae*. In terms of body size, there were remarkable interpopulational differences in the maximum snout-vent length (SVL) reached by *R. bedriagae* (Fig. 2B). The maximum size registered in the highland population of Lake Beyşehir (Turkey) was 123 mm SVL, about 30 mm more than in any other population. In contrast, the minimum size at which sexual maturity is attained was similar in all populations.

Principal-component analysis at the level of species showed that the first three principal components explained 94.0% of the total variation. PC1 had an eigenvalue of 6.8 and in itself explained 84.5% of the total variation. This canonical variable significantly correlated with SVL in the two taxa ($p < 0.001$; Fig. 3A), but the species-specific regression lines went parallel, i.e. only the intercepts differed significantly ($p < 0.01$). The relation between the digitus primus length and SVL exemplifies the allometric differences between the two taxa (Fig. 3B). In the range between 40 mm and 80 mm SVL, the length of the digitus primus alone is sufficient to assign almost every individual to the correct taxon. Finally, *R. bedriagae* attains sexual maturity at a smaller size than *R. ridibunda* (44 mm vs. 62 mm) and, at least at highland sites, grows larger. PC2 (eigenvalue 0.48) and PC3 (eigenvalue 0.28) accounted for 6.0% and 3.5% of the total variance, respectively. The range of variability caused by differences in shape completely overlaps in the two species, but the range of variation is smaller in *R. bedriagae* than in *R. ridibunda* (Fig. 4A). Still, a highly significant discriminant function which is based on the eight $\log_{10}$-transformed morphometric variables can be derived (Table 2). The classification of specimens has a precision of at least 88.9% correct assignments, i.e. the overlap between the frequency distributions of the species-specific discriminant scores is relatively small (Fig. 4B).

Discussion

The taxonomic reassessment of the palaearctic water frogs during the past three decades was initiated by the classical morphometric analysis of the three phenotypes present in central Europe (Berger 1966). While current progress in understanding the evolutionary history of this group is mainly based on bioacoustic and chemotaxonomic studies, investigations on the potential morphological differentiations among the taxa still remain important: (1) significant differences in morphology back up taxonomic assignments based on other character complexes; (2) the identification of noncalling individuals in the field is facilitated; and (3) formaldehyde-preserved specimens in museum collections become informative for estimates of the present and former geographic range of taxa. Lake frogs from the Balkans (*R. balcanica*) and Israel (*R. levantina*) which were formerly considered as *R. ridibunda* (Günther 1990) are generally similar in size and shape, but nevertheless specific differences in the temporal structures of their advertisement calls and in their gene pools were found to be associated with significant differences in morphometry (Schneider et al. 1992; Schneider et al. 1993; Gavrilovic et al. 1996). The morphometric data analysed in this study enable us to evaluate quantitatively the morphological variation among water frogs of the Middle East (Turkey, Syria, Jordan, Israel) and to compare it with the bioacoustic variation found in frogs of the same area (Schneider and Sinsch 1999).

Morphological variation

At first glance, the water frogs of Lake Beyşehir in the Taurus mountains and those inhabiting the Mediterranean coast of Turkey appear to be rather distinct – an impression given by the large difference in size and the peculiar belly colouration of the highland frogs. However, size-adjusted multivariate comparisons leave no doubt that body proportions are the same in the frogs of both regions and the apparent dissimilarity is exclusively due to size. In turn, size sometimes positively correlates with altitude (Lüdecke 1997) or simply reflects a greater life expectancy (= longer growth period), as in Alpine populations of *R. temporaria* and *B. bufo* (Ryser 1988; Grossenbacher, pers. comm.). Consequently, morphometric variation does not provide any evidence for a taxonomically relevant differentiation and entirely agrees with the bioacoustic diagnosis that the two regions are inhabited by the same species (Schneider and Sinsch 1998). Lowland and highland specimens of the populations studied in Turkey merely represent the extremes of a continuous size distribution.

Table 1. Discriminant functions based on eight log_{10}-transformed morphometric variables to distinguish among 11 water frog populations including three reference populations (R1-R3) of *R. ridibunda*. (A) Statistical significance; (B) Unstandardized coefficients of the discriminant functions; (C) Classification success

(A)

Discriminant function	Eigenvalue	Relative percentage	Canonical correlation	Wilks Lambda	Chi-square	Degrees of freedom	Statistical significance
1	3.75	47.1	0.8886	0.0142	614.5	80	$p < 0.0001$
2	1.83	22.9	0.8038	0.0676	389.3	63	$p < 0.0001$
3	1.55	19.2	0.7799	0.1910	239.2	48	$p < 0.0001$
4	0.52	6.6	0.5857	0.4876	103.8	35	$p < 0.0001$

(B)

log_{10} (variable)	Discriminant function 1	Discriminant function 2	Discriminant function 3	Discriminant function 4
snout-vent length	23.22	−10.32	−33.95	31.27
femur length	22.47	−6.82	38.01	−4.26
tibia length	2.84	26.94	−14.49	−20.54
digitus primus length	−15.64	−12.08	6.83	2.77
callus internus length	0.67	1.30	0.63	−12.06
maximal head width	−22.16	−16.67	9.14	6.76
snout-eye distance	2.04	8.42	−1.72	−11.98
tympanum diameter	−10.91	−1.08	−16.01	−5.16
constant	−28.15	15.70	20.52	−7.96

(C)

Actual group		Predicted group 1	2	8	10	11	12	13	14	R1	R2	R3
1	Alanya, Turkey	14 (67%)	0	0	0	2 (10%)	1 (5%)	3 (14%)	1 (5%)	0	0	0
2	Beyşehir, Turkey	0	8 (67%)	0	0	0	1 (8%)	2 (16%)	0	1 (8%)	0	0
8	Damascus, Syria	1 (14%)	0	2 (29%)	2 (29%)	0 (14%)	1 (14%)	1	0	0	0	0
10	Mzeirib, Syria	1 (9%)	0	4 (36%)	4 (36%)	0	0 (18%)	2	0	0	0	0
11	Zarqa, Jordania	0	0	0	0	6 (100%)	0	0	0	0	0	0
12	Wadi Wala, Jordania	0	0	0	0	0	6 (100%)	0	0	0	0	0
13	Birket Ata, Israel	0	2 (20%)	1 (10%)	0	1 (10%)	0	5 (50%)	0	1 (10%)	0	0
14	Jericho, Israel	0	0	0	0	0	0	0	23 (86%)	2 (7%)	2 (7%)	0
R1	Atyrau, Kazakhstan	1 (25%)	0	0	0	0	0	0	0	2 (50%)	1 (25%)	0
R2	Hankavan, Armenia	0	2 (7%)	0	0	0	0	0	1 (3%)	5 (17%)	21 (70%)	1 (3%)
R3	Valtos, Greece	0	0	0	0	0	0	0	0	0	0	21 (100%)

Comparisons on the level of populations reveal a remarkable similarity (= low power of discrimination) with respect to external morphology among all Middle Eastern populations from Turkey to Israel. The morphometric features of these frogs contrast sharply with those of *R. ridibunda* specimens of the reference populations, especially with respect to hind limb morphology. The significant deviation from the taxonomically well-defined outgroup indicates that the Middle Eastern water frogs

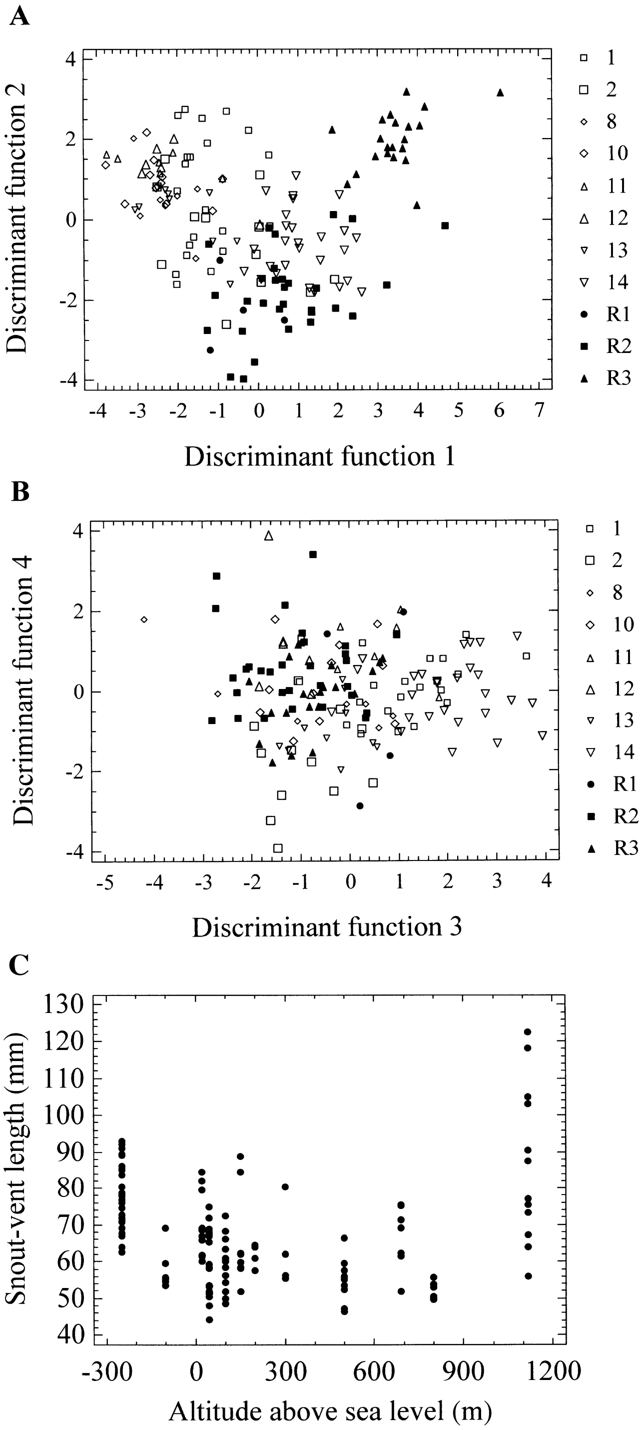

Fig. 2. Morphometric variation among Middle Eastern water frog populations including three reference populations of *R. ridibunda*. (A, B) Discriminant plots of individual scores (based on eight $\log_{10}$-transformed variables) obtained for 11 localities with $N \geqslant 6$ specimens (Table 1). (C) Variation of frog size (SVL) among populations at different altitudes (excluding the reference populations)

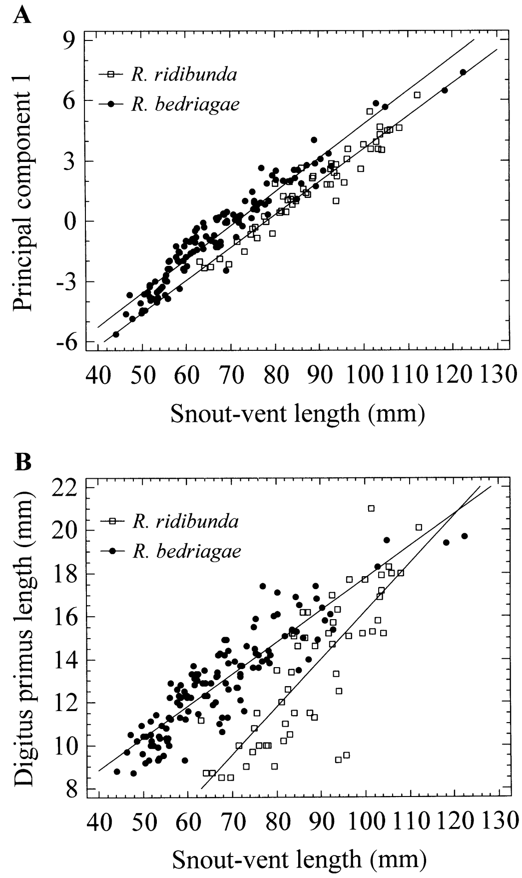

Fig. 3. Morphometric variation between *R. ridibunda* and *R. bedriagae*. (A) Individual scores of PC1 (based on eight $\log_{10}$-transformed variables) in relation to SVL. Regression models: $PC1 = -12.78 + 0.16 * SVL$; $r = 0.960$ (*R. ridibunda*); $PC1 = -12.01 + 0.17 * SVL$; $r = 0.963$ (*R. bedriagae*). (B) Size dependence of digitus primus length. Regression models: $DPL = 210.16 - 5.93 * SVL$; $r = 0.721$ (*R. ridibunda*); $DPL = 128.27 - 2.99 * SVL$; $r = 0.789$ (*R. bedriagae*)

are not conspecific with *R. ridibunda*. Moreover, the frogs originating from 14 populations in Turkey, Syria, Jordan and Israel belong to a homogeneous group which does not provide any indication for a further taxonomic subdivision.

Taxonomic implications

The morphological differentiation among the populations studied parallels that of the advertisement calls (Schneider and Sinsch 1998): The data set of 14 water frog populations inhabiting the Middle East includes only one morphospecies, the Levantine frog, *R. bedriagae*. This is the first evidence from quantitative morphology that *R. bedriagae* from Syria and *R. levantina* from Israel are conspecific. In contrast, the synonymy of the two names proposed by Dubois and Ohler (1994) is no more than a casual speculation without adequate data base ($n = 2$ specimens originating from Damascus). Instead of using the discriminant function provided by Schneider et al. (1992) to support conspecificity, they vaguely state: 'Various measurements of these specimens give values that fall within the ranges given for *Rana levantina*'.

Our bioacoustic (Schneider and Sinsch 1999) and morphometric analyses prove that *R. ridibunda caralitana* is conspecific with *R. bedriagae*. In this case, Dubois and Ohler (1994) suggested the now proven synonymy even without any supporting evidence. This is certainly not a scientific way to solve taxonomic problems.

Finally, there remains the question whether these high-altitude *R. bedriagae* deserve to be placed in a separate subspecies as proposed by Arikan (1988). The only diagnostic feature of

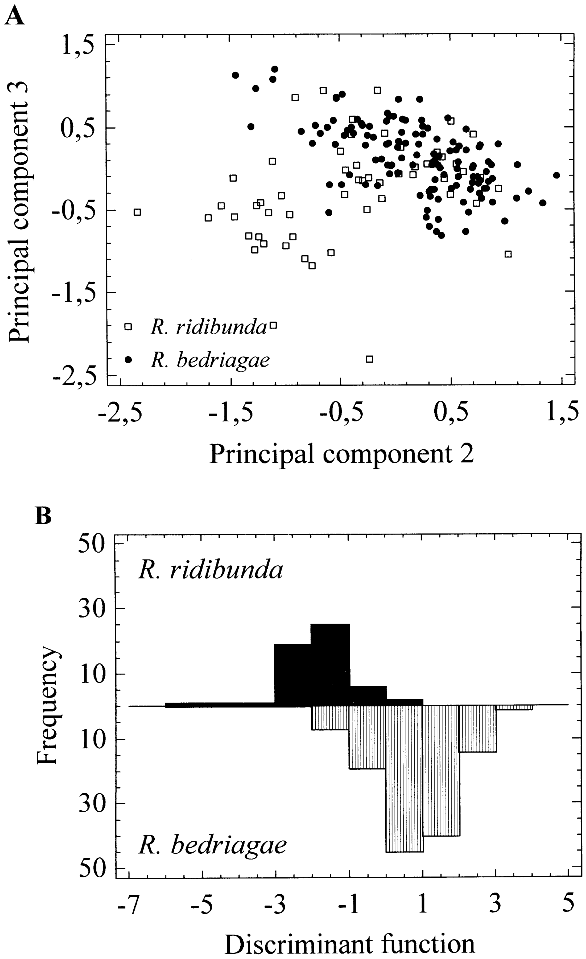

Fig. 4. Morphometric variation between *R. ridibunda* and *R. bedriagae*. (A) Variation in shape: PC2 vs. PC3. (B) Frequency histogram (class width: 1 unit) of the discriminant scores (Table 2)

these frogs is orange coloration of the venter. Considering that many anuran species are polymorphic with respect to coloration, we agree with Bodenheimer (1944) that a colour variation alone does not justify a distinct subspecific status.

Range of distribution

This study extends our knowledge of the range of geographic distribution of *R. bedriagae* by demonstrating its presence in large regions of Syria and Jordan. Thus, the combined morphological (this study) and bioacoustic evidence (Schneider and Sinsch 1999) indicates that the mainland distribution of this species includes the Aegean coast and the southern part of highland Anatolia in Turkey, Syria, Jordan, Israel and Egypt. Its presence in Lebanon is most probable.

Yet, the exact limits of geographic distribution remain unknown. The absence of *R. bedriagae* in Armenia and in Gülşehir, Turkey suggests that the northern limit is located in Anatolian highlands. Likely candidates for occurrence of *R. bedriagae* are Iraq in the east and Lybia in the west. Another open biogeographic problem is the status of the water frog populations inhabiting the Aegean islands: *R. ridibunda* is present on Samothraki Island, Greece (Schneider and Sinsch 1992; Schneider et al. 1993), *R. balcanica* on Thasos Island, Greece (Sofianidou et al. 1994), and *R. bedriagae* in Cyprus (Böhme and Wiedl 1994). These three species may have immigrated to the islands from the neighbouring mainland, but introduction by man to the more distant islands may also have played a role in establishing the present composition of the local frog fauna.

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Table 2. Discriminant function based on eight $\log_{10}$-transformed morphometric parameters to distinguish between *R. ridibunda* and *R. bedriagae* (A) Statistical significance; (B) Unstandardized coefficients of the discriminant functions; (C) Classification success

(A)

Eigenvalue	Relative percentage	Canonical correlation	Wilks Lambda	Chi-square	Degrees of freedom	Statistical significance
1.538	100	0.7785	0.3940	163.0	8	$p < 0.0001$

(B)

Log_{10} (variable)	Discriminant function
snout-vent length	−39.73
femur length	6.03
tibia length	2.89
digitus primus length	11.81
callus internus length	1.20
maximal head width	7.19
snout-eye distance	6.87
tympanum diameter	−2.02
constant	30.18

(C)

	Predicted species	
Actual species	*R. ridibunda*	*R. bedriagae*
R. ridibunda	51 (92.7%)	4 (7.3%)
R. bedriagae	14 (11.1%)	112 (88.9%)

Zusammenfassung

Taxonomische Neubewertung von Wasserfröschen aus dem Mittleren Osten: Morphologische Variation bei Populationen, die als Rana ridibunda, R. bedriagae oder R. levantina angesehen werden

Bei Wasserfröschen von vierzehn Standorten aus der Türkei, Syrien, Jordanien und Israel wurden acht morphometrische Korpermaße pro Individuum gemessen und mit denjenigen von *Rana ridibunda* aus Kasachstan, Armenien und Griechenland (Thrakien) verglichen. Zu diesen Standorten gehören die Typuslokalitäten von *R. ridibunda*, *R. r. caralitana*, *R. esculenta* var. *bedriagae* und *R. levantina*. Multivariate Vergleiche (Hauptkomponentenanalyse, Diskriminanzanalyse) basierend auf den $\log_{10}$-transformierten Meßstrecken zeigen, daß nur zwei Taxa im Sinne von Morphospezies vorkommen, die sich signifikant in Größe und Gestalt unterscheiden: *R. ridibunda*, und *R. bedriagae*. *R. ridibunda* ist durch die drei Referenzpopulationen vertreten, *R. bedriagae* durch alle anderen untersuchten Populationen aus der Türkei, Syrien, Jordanien und Israel.

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Appendix:

Geographical origin of specimens examined morphometrically

The altitude of the localities above sea level is also given. The numbers of localities refer to Fig. 1. Institutional abbreviations are as follows: SMF Senckenberg Museum Frankfurt; ZFMK Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

Turkey

Locality 1: Alanya, Prov. Antalya, 10 m above sea level.

1st sample: 5 males, 5 females, ZFMK 40192–40201, collected in April 1983;

2nd sample: 1 male, 1 female, unpreserved, collected by H. Schneider in April 1994;

3rd sample: 10 males, unpreserved, collected by H. Schneider in April 1996.

Locality 2: Beyşehir, Prov. Konya, 1116 m above sea level (type locality of *R. ridibunda caralitana*).

1st sample: 1 male, unpreserved, collected by H. Schneider in April 1994;

2nd sample: 2 males, 8 females, unpreserved, collected by H. Schneider in April 1996.

Syria

Locality 3: Jebel el Ansariye, about 150 m above sea level.

1 male, 3 females, ZFMK 60901–6904.

Locality 4: Ar Raqqah (35°56′N, 39°01′E), about 150 m above sea level.

1 male, 3 females, SMF 75349–75352, collected by H. Martens.

Locality 5: Nahr al-Habur, about 500 m above sea level.
4 males, 2 females, SMF 73715–73717, 73721, 73723–73724, collected by H. Martens in October 1988.
Locality 6: Abu Kemal, Euphrates River, about 200 m above sea level.
4 males, ZFMK 61785–61788.
Locality 7: Bahrat Khatuniyah (36°24′N, 41°13′E), about 300 m above sea level.
1 male, 3 females, SMF 75467–75470, collected by H. Martens.
Locality 8: Barada River, surroundings of Damascus, 690 m above sea level (type locality of *R. bedriagae*).
1st sample: 1 male, SMF 5900, collected by H. Simon in 1882;
2nd sample: 4 males, 2 females, SMF 75688–75689, 75693–75696, 75699, collected by H. Martens.
Locality 9: Quanwat (32°45′N, 36°37′E), Jebel Al-Arab, about 500 m above sea level.
2 males, 3 females, SMF 75610–75613, collected by H. Martens
Locality 10: Mzeirib (32°42′N, 36°01′E), about 100 m above sea level.
4 males, 8 females, SMF 75644–75655, collected by H. Martens.

Jordan
Locality 11: Zarqa, about 800 m above sea level.
4 males, 2 females, SMF 76454–76459.
Locality 12: Wadi Wala, about 100 below sea level.
6 females, SMF 76469–76474.

Israel
Locality 13: coastal plain: Birket Ata, Hadera, 20 m above sea level (type locality of *R. levantina*).
4 males, 5 females, ZFMK 52836–52844, collected by E. Nevo in 1992.
Locality 14: Jordan valley: Jericho, 250 m below sea level. 11 males, 17 females, ZFMK 52836–52844 and unpreserved, collected by E. Nevo in 1992.

Reference populations of *Rana ridibunda* for the outgroup comparison

Kazakhstan
(R1) Atyrau, formerly Guryev (type locality of *R. ridibunda*), 2 males, 2 females, unpreserved, collected by H. Schneider and E. M. Egiasarjan in May 1990.

Armenia
(R2) Hankavan, 19 males, 11 females, unpreserved, collected by H. Schneider and E. M. Egiasarjan in May 1990.

Greece
(R3) Valtos, Thrace, 12 males, 9 females, unpreserved, collected by T. S. Sofianidou in March 1990.