

Volume 11, Number 2

April 2001
ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by the
BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

The Herpetological Journal is published quarterly by the British Herpetological Society and is issued free to members. Articles are listed in *Current Awareness in Biological Sciences*, *Current Contents*, *Science Citation Index* and *Zoological Record*.

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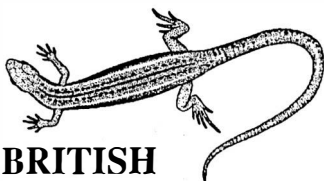
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FRONT COVER: Male *Calumma vencesi* (F. Andreone)

AMPHIBIAN BREEDING SITE CHARACTERISTICS IN THE WESTERN CARPATHIANS, POLAND

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The status of amphibian populations in the eastern part of the Western Carpathians, Poland, was investigated by assessing the number and ecological characteristics of breeding sites. Breeding populations of *Salamandra salamandra*, *Triturus cristatus*, *T. vulgaris*, *T. montandoni*, *T. vulgaris* x *T. montandoni* hybrids, *T. alpestris*, *Bombina variegata*, *Bufo bufo*, *Bufo viridis* and *Rana temporaria* were found. A total of 171 breeding sites together with their surrounding terrestrial habitats were examined for 11 environmental habitat parameters and data on presence/absence of other amphibians were recorded. A Canonical Correspondence Analysis (CCA) was performed to relate the species composition to the set of environmental variables. The first axis clearly differentiated *S. salamandra* from all other species, which were most clearly separated along the second axis. This second axis can be interpreted as a gradient of permanency and abundance of water vegetation. Generally, the CCA showed that environmental gradients were short, which reflects the limited range of habitats available for the amphibians in the area. *G*-tests revealed that two breeding assemblages could be distinguished. The first comprised newts of the genus *Triturus*, together with *B. variegata*; the second assemblage was composed of *Bufo bufo* and *R. temporaria*. The number of breeding species at a site was positively correlated with the surface area, "clay pit" habitat type and depth, but negatively with the "oxbow" and "stream" habitat types. Some 84% of all breeding sites were of human origin, the majority of them being small, transient water bodies such as wheel-ruts and roadside ditches. To keep the amphibian abundance in the study area at the present level, continuous human activity in creating and maintaining such suitable sites is necessary.

Key words: Amphibia, *Triturus montandoni*, breeding site, conservation, habitat choice, Western Carpathians

INTRODUCTION

Dramatic declines of populations of many amphibian species have been reported from all over the world (Wake, 1991; Blaustein, Wake & Sousa, 1994). The causes of these declines seem diverse and not fully understood. Changes in agricultural practices and road construction over the past 50 years have been major causes of loss of breeding sites in Western Europe (Beebee, 1996). Several formerly common and widely spread amphibian species are now considered rare, threatened or even endangered in Western Europe. In most cases the principal reason for these declines has been the loss of the breeding sites (Heusser, 1961; Prestt, Cooke & Corbett, 1974; Beebee, 1977; Oldham & Nicholson, 1986; Stumpel & Tester, 1992). The status of amphibian populations in Eastern Europe is not well known. Objective methods of measuring and monitoring amphibian populations have been applied only recently in some parts of Eastern Europe (Lars Briggs, pers. com.), but there are no published data which would enable comparisons with the data available for Western Europe. The general impression is that many habitats suitable for amphibians still exist in many parts of Eastern Europe due to the fact that envi-

ronmental changes have been much less profound there than in Western Europe. On the other hand, much of Eastern Europe is now undergoing rapid development, with new patterns of land use being introduced, especially in agriculture. These may be expected to have a negative effect on amphibian populations.

The aim of our study was to assess the range of amphibian breeding site characteristics in an area which has preserved traditional forms of land use and which has a relatively rich amphibian fauna. Our study area was situated in the eastern part of the Western Carpathians (Magurski National Park, SE Poland; Fig. 1). Only traditional forms of agriculture have been practised here and since the end of World War II the area has been severely depopulated (Zajdel, 1997). Most of the land formerly used for agriculture and for human settlement has been undergoing the natural process of vegetational succession (Michalik & Michalik, 1997). We concentrated our survey on the quantitative description of breeding sites used by the local amphibians, and searched for associations between habitat characteristics and the presence of particular species. Number of breeding sites may be a better indicator of the present state and future prospects of amphibian populations than population size, which often shows large, natural fluctuations over the years (Pechmann *et al.*, 1991; Green, 1997). Information on breeding site characteristics is important for conserva-

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tion purposes, as maintenance and creation of breeding sites have proven to be among the most effective ways of increasing the number and size of amphibian populations (Beebee, 1996).

Habitat selection by amphibian species has been studied extensively in Europe, but all these studies were restricted to the western part of the continent (e.g. Cooke & Frazer, 1976; Beebee, 1977, 1980, 1981, 1985; Fonseca & Jocque, 1982; Pavignano, Giacoma & Castellano, 1990; Denton, 1991; Ildos & Ancona, 1994; Marnell, 1998; Serra-Cobo, Lacroix & White, 1998). In regions which differ in geological and climatic conditions, these preferences may vary even within the same species. We follow previous studies in inferring a species' preferences by searching for associations between habitat characteristics and the presence of a species, even if the real preferences of the species depend on some unknown and/or unnoticed features of the environment.

One of the most common species in our study area is Montandon's newt (*Triturus montandoni*). This species has the most restricted distribution of all the European newt species (Arntzen & de Wijer, 1989), being confined to the Western and Eastern Carpathians as well as the easternmost part of the Sudeten Mountains. Local declines of this species have been reported (Kuzmin, 1994). The species is also considered as rare by several red-book lists (Baruš *et al.*, 1988; Sytnik *et al.*, 1988; Głowaciński, 1992) and it is included as a strictly protected species in Appendix II of the Bern Convention on the Conservation of European Wildlife and Natural Habitats. The distribution area of *T. montandoni* is limited to the territories of Romania, Ukraine, Slovakia, Poland and, marginally, the Czech Republic (Cogălniceanu, 1997). All these countries have been

undergoing major political and economic changes, which are also likely to change the patterns of land use and agricultural practices. As the status of *T. montandoni* may be expected to suffer from these recent alterations, the need for description of its breeding habitats in an area where this species is still common is urgent.

Specifically, we wanted to answer the following questions: (1) Do the species distributed in our study area show associations with particular characteristics of the breeding sites described by the variables recorded? (2) Which of the measured variables can account best for observed amphibian breeding communities? (3) Do the amphibians present in the area form discernible breeding assemblages? (4) Is there any correlation between the features of the breeding site and the number of amphibian species at a site?

MATERIALS AND METHODS

DATA COLLECTION

The study area (Fig. 1) is situated in low-altitude mountains (maximum height 842 m a.s.l.). The growing season lasts 187 days/year on average. Mean (mean of daily means) temperature in July is 13.9°C; mean temperature in January is -7.7°C. Mean average rainfall ranges from 850 to 1000 mm, with 600-650 mm from April to September (unpublished recordings from a local meteorological station). Geologically, the area is homogeneous, and is situated on Flysch-type strata. The predominant soil type on mountain ridges and slopes is heavy clay (cambisols), whereas alluvial deposits fill the river valleys (Skiba *et al.*, 1999). The mountain ridges and slopes are almost entirely covered by mixed beech-fir forest; alluvial alder and willow woods are found along rivers and streams. Forests cover over 80% of the area (Michalik & Michalik, 1997). Arable land occupies only small areas in larger valleys. Traditional, non-intensive forms of agriculture predominate, especially pasture and hay-meadows (Dubiel, Gawroński & Stachurska, 1997).

The field work was conducted from April to July during three consecutive breeding seasons, in the years 1997-1999. Most of the identified breeding sites were visited during at least two breeding seasons. Our survey covered an area of about 450 square km. Valleys and ridges were much more extensively searched than wooded slopes, which were visited several times in different parts of the area. Such preliminary surveys showed that hardly any amphibian breeding sites were found on the wooded slopes, except for streams which were the breeding sites for *Salamandra salamandra*. Only the unsurfaced tracks on the slopes supported substantial numbers of amphibian breeding sites and for this reason they were searched intensively.

All the amphibian species recorded for this area lay their eggs in water and have aquatic larvae. A water body was recorded as a breeding site if either eggs or larvae were present, or – in the case of newts (genus *Triturus*) – if adults were present. Occurrence of adult

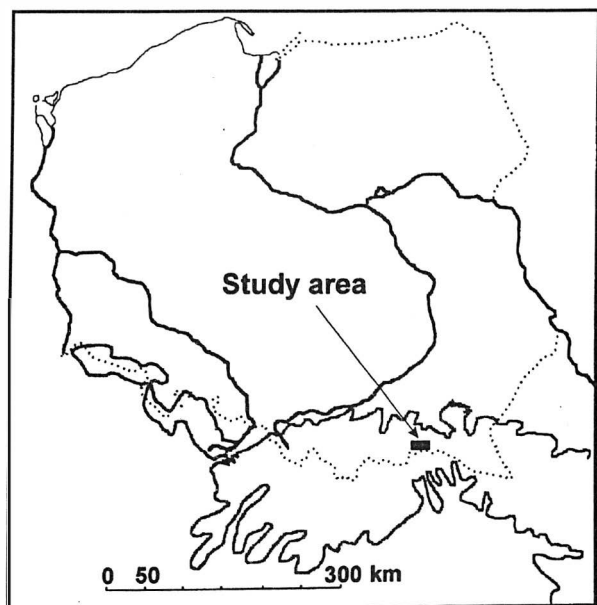


FIG. 1. Map of Poland with the study area indicated. A contour line at 300 m a.s.l. is shown.

TABLE 1. Environmental variables recorded and the scoring system used.

Variable	Variable states
Altitude [m a.s.l.]	1, <400; 2, 400-499; 3, 500-599; 4, >600.
Breeding habitat	Wheel-rut, puddle or small pool, ditch, bomb hole, clay pit, fish pond, gravel pit, artificial basin, oxbow, stream.
Area [m ²]	1, <1; 2, 1-2; 3, 2-10; 4, 10-100; 5, >100.
Depth [cm]	1, <10; 2, 10-20; 3, 21-50; 4, >50.
Bottom characteristics	Mineral, organic/mineral, organic
Substrate	Alluvial deposits, heavy clays (cambisoils) on Flysch-like sediments.
Aquatic vegetation	1, no vegetation; 2, along the edges only; 3, dispersed throughout the surface; 4, emergent and submerged vegetation over the whole area.
Turnover	Standing water, low turnover, high turnover
Permanence	1, ephemeral; 2, transient but not ephemeral; 3, permanent under normal climatic conditions; 4, permanent.
Surrounding terrestrial habitat	Mixed woodland; meadow/pasture, residual alluvial forest, village
Situation in relief	Valley, slope, ridge

newts in spring in a water body is strongly correlated with their reproduction there (pers. obs.). The presence of mature individuals, eggs and/or larvae was ascertained by visual inspection and/or dip-netting. Since both eggs and larvae of *T. montandoni* are indistinguishable from *T. vulgaris* under field conditions, the presence of either of these species was always verified by observation of mature newts. Presence of *T. cristatus* was established both by the examination of plants for the eggs, which could be identified as belonging to this species by their characteristic colour, size and shape, and by the presence of either larvae or mature individuals. For each anuran species a site was classified as a breeding site if eggs and/or tadpoles were found in it.

Very often in our study area amphibians used wheel-ruts as breeding sites. We therefore regarded sites that were more than 10 m apart as separate sites, as the chance of coalescence of such areas even after heavy rains was very small. For each breeding site the altitude a.s.l. was read from 1: 50 000 maps, and at the site we recorded the following characteristics: breeding habitat (i.e. the type of water body), area, depth, bottom characteristics, substrate, aquatic vegetation, turnover, permanence, surrounding terrestrial habitat and situation in relief (for details see Tables 1 and 2). The category "high turnover" was applied only to streams, "low turnover" designates such places as ditches, seepages and some oxbows. We classified the bottom characteristics in three categories: "mineral" – stones, gravel or clay; "organic" – bottom completely covered with decomposing plant material; "mineral/organic" – bottom partly covered by organic deposits. Breeding sites were situated on two types of substrate, either alluvial deposits (i.e. sand, gravel, stones) or heavy clays (cambisoils). We classified as "ephemeral" such places as very shallow puddles and flooded wheel-ruts formed after rain on unsurfaced tracks and without aquatic veg-

etation, which may, in the absence of rain, dry up very quickly (i.e. within a few weeks). Deeper wheel-ruts on roads and some ditches with aquatic vegetation situated in more damp surroundings – which indicated that they may last for a month or longer in the absence of precipitation – were classified as "transient". Stable water bodies which dried out in some years during the study were classified as "permanent under normal conditions". Under "surrounding terrestrial habitat", the terms "mixed woodland" or "residual alluvial forest" indicate that the water body was located no further than 100 m from the woodland. When no woodland was present at this distance, "meadow/pasture" or "village" was used. Water temperature, pH, conductivity and oxygen concentration were not measured because these parameters are highly dependent on inspection date, especially for small water bodies, which predominated in our study area. Additionally, we recorded whether each site was natural or of anthropogenic origin. We present these data in Table 2. In total, we sampled 171 breeding sites of amphibians (Table 2).

DATA ANALYSIS

Canonical Correspondence Analysis (CCA) was applied to investigate the relationship between amphibian breeding communities and the values of environmental variables (Ter Braak & Prentice, 1988). When the data collected include presence/absence of a species and environmental variables are coded in a nominal and/or ordinal scale, as was the case with our data, CCA is the most appropriate method for detecting relationships between species composition and environment (Ter Braak, 1986). The joint effect of the environmental variables on the species is represented in this method through a few ordination axes which can be considered as composite environmental gradients influencing species composition. CCA leads to an ordination diagram that simultaneously displays the approximate optima of

the species in the low-dimensional (usually two-dimensional) environmental subspace, and environmental variables. Species optima are represented by points and direction and rate of change of variables by arrows on the diagram; nominal variables are represented by points. The ordination axes are weighted sums of the environmental variables. Altitude, aquatic vegetation, area, depth and permanence were coded as ordinal variables whereas all the others were nominal and were coded as dummy variables (Table 1). This resulted in a total of 30 variables included in the analysis. We performed forward stepwise analysis with CANOCO to establish which of the environmental variables were most important in shaping the composition of amphibian communities. The statistical significance was established by randomization tests with 999 permutations. Only variables with $P < 0.05$ were included in the model and used for constructing the diagram (Table 3, Fig. 2). We also tested specific associations between some species or groups of species using 2×2 G -tests of independence ($df = 1$ in all cases).

To determine which environmental factors are useful in predicting the number of species reproducing at a given site, we performed forward stepwise multiple regression with the number of species recorded as a dependent variable and the variables listed in Table 1 as the independent ones (coded as for CCA). Computations were performed using STATISTICA (StatSoft, 1997) and CANOCO (Ter Braak & Šmilauer, 1998).

RESULTS

ENVIRONMENTAL ASSOCIATIONS

In the study area we found breeding sites of *Salamandra salamandra*, *Triturus cristatus*, *T. vulgaris*, *T. montandoni*, hybrids between the two latter species, *T. alpestris*, *Bombina variegata*, *Bufo bufo*, *Bufo viridis* and *Rana temporaria*. The most common species was *B. variegata* which occurred in 48.5% of the breeding sites. The second commonest species was *R. temporaria* (31.6%). The rarest species were *T. vulgaris* (3.5%), *T. cristatus* (2.9%) and *Bufo viridis* (1.8%) (Table 2). The widest range of breeding habitat types was used by *R. temporaria* and *B. variegata* (8 and 5 respectively). The narrowest range was found for *S. salamandra* and *Bufo viridis* (2 types for both) (Table 2).

The total range of amphibian breeding habitats in our study area is quite narrow, as can be seen from the CCA diagram (Fig. 2). As revealed by the randomization tests only 11 out of 30 environmental variables were significant in structuring the amphibian communities (Table 3, Fig. 2).

The first axis differentiated the breeding habitat of *S. salamandra* from all other species. This is hardly surprising, since all but one (93.3%) of its breeding sites were small mountain streams where no other amphibian species reproduced. Since other species were not separated along the first CCA axis it was not shown on the plot. The second axis showed the strongest correla-

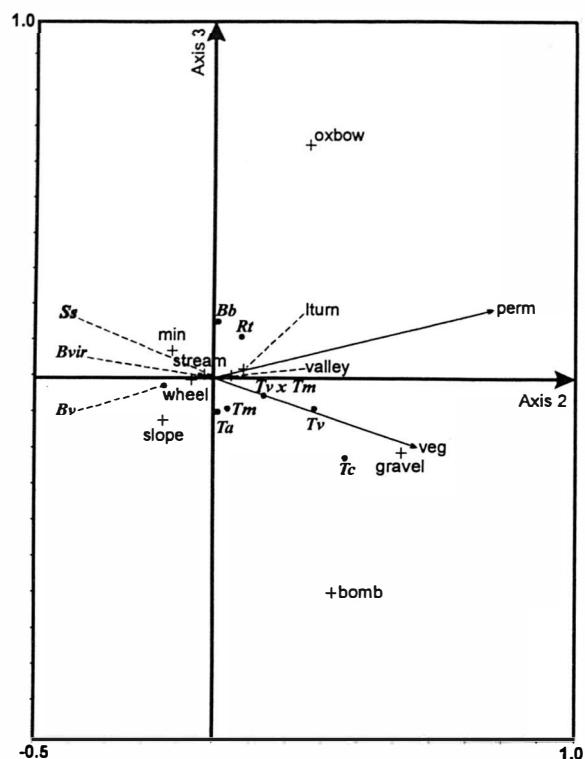


FIG. 2. Ordination diagram showing the positions of species (dots) and environmental variables in a plane of the second and third CCA axes. Nominal variables are shown as crosses, quantitative ones as arrows. Abbreviations: bomb, bomb hole; gravel, gravel pit, lturn, low water turnover; min, mineral bottom; perm, permanence; veg, aquatic vegetation, wheel, wheel-rut; Ss, *Salamandra salamandra*; Tc, *Triturus cristatus*; Tv, *T. vulgaris*; Tm, *T. montandoni*; Tv x Tm, hybrids between *T. vulgaris* and *T. montandoni*; Bv, *Bombina variegata*; Bb, *Bufo bufo*; Bvir, *Bufo viridis*; Rt, *Rana temporaria*.

tion with water habitat permanency and amount of water vegetation (Table 3) and contributed most to the species ordering (Fig. 2). The distribution range of species along the third CCA axis (explaining 11.3% of variance) is quite narrow. The most noticeable feature shown by this axis is that *Bufo bufo* and *R. temporaria* are grouped together, which is because these species were more often found in oxbows than the others (Fig. 2). The sum of the eigenvalues of the first four axes was 1.483 and accounted for 91.1 % of the total variance in the distribution of amphibian species at the sites studied with respect to the 11 significant variables (Table 3).

As can be seen from Fig. 2, more permanent and richly vegetated habitats were breeding places for *T. cristatus* and *T. vulgaris*. These two species were mainly found in larger and deeper water bodies like old gravel pits and bomb holes (*T. cristatus*). *T. vulgaris* was also found in richly vegetated wheel ruts and there was a clear geographic pattern in its distribution: this species occurred mainly in the northern part of the area adjacent to the lowlands and seems to have spread to the south along the Wisłoka river valley only (data not shown). In the case of *T. vulgaris* x *T. montandoni* hybrids, the main factor responsible for their occurrence was also the geographic location of the sites. Hybrids

	All sites <i>n</i>	%	<i>Ss</i> <i>n</i>	<i>Tc</i> <i>n</i>	<i>Tv</i> <i>n</i>	<i>Tm</i> <i>n</i>	<i>TvxTm</i> <i>n</i>	<i>Ta</i> <i>n</i>	<i>Bv</i> <i>n</i>	<i>Bb</i> <i>n</i>	<i>Bvir</i> <i>n</i>	<i>Rt</i> <i>n</i>
% of all sites <i>n</i>			8.8 15	2.9 5	3.5 6	26.9 46	4.7 8	26.3 45	48.5 83	21.6 37	1.8 3	31.6 54
<i>Breeding habitat</i>												
Wheel-rut	98	57.3	1	—	3	33	6	26	58	25	2	26
Puddle or small pool	10	5.8	—	1	—	2	—	3	6	1	—	5
Ditch	23	13.5	—	—	1	4	1	8	15	1	1	6
Bomb hole	3	1.8	—	1	—	3	—	3	—	—	—	—
Clay pit	3	1.8	—	1	—	1	—	3	3	1	—	2
Fish pond	2	1.2	—	—	—	—	—	1	—	2	—	2
Gravel pit	3	1.8	—	2	2	2	—	1	—	1	—	2
Artificial basin	2	1.2	—	—	—	1	—	—	1	—	—	1
Oxbow	13	7.6	—	—	—	—	1	—	—	6	—	10
Stream	14	8.2	14	—	—	—	—	—	—	—	—	—
All sites	171											
<i>Altitude [m a.s.l.]</i>												
<400	16	9.4	—	2	2	5	—	3	3	5	—	12
400-499	90	52.6	5	1	3	27	4	25	45	15	1	25
500-599	42	24.6	9	2	—	11	2	10	21	8	2	10
>600	23	13.5	1	—	1	3	2	7	14	9	—	7
All sites	171											
<i>Area [m²]</i>												
NA – coded as 0	14	8.2	14	—	—	—	—	—	—	—	—	—
<1	2	1.2	—	—	—	—	—	1	1	—	—	—
1-2	36	21.1	—	—	—	10	1	8	26	5	—	1
2-10	69	40.4	1	—	3	19	4	20	34	10	2	25
10-100	45	26.3	—	4	1	16	2	14	21	18	—	24
>100	5	2.9	—	1	2	1	1	2	1	4	1	4
All sites	171											
<i>Depth [cm]</i>												
> 10	6	3.5	2	—	—	2	—	1	2	—	—	1
10-20	125	73.1	12	1	2	32	3	26	68	21	1	32
21-50	30	17.5	1	1	2	6	5	12	13	11	2	15
>50	10	5.8	—	3	2	6	—	6	—	5	—	6
All sites	171											
<i>Bottom characteristics</i>												
Mineral	98	57.3	14	—	1	23	—	14	55	24	1	26
Organic/mineral	29	17.0	—	2	3	8	3	11	15	5	1	14
Organic	44	25.7	1	3	2	15	5	20	13	8	1	14
All sites	171											
<i>Substrate</i>												
Alluvial deposits	17	9.9	—	2	2	3	1	1	2	6	—	11
Heavy clays (cambisoils) on Flysch-like sediments	154	90.1	15	3	4	43	7	4				

TABLE 2. (continued...)

	All sites		<i>Ss</i>	<i>Tc</i>	<i>Tv</i>	<i>Tm</i>	<i>TvxTm</i>	<i>Ta</i>	<i>Bv</i>	<i>Bb</i>	<i>Bvir</i>	<i>Rt</i>
	<i>n</i>	%	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>	<i>n</i>
<i>Aquatic vegetation</i>												
No vegetation	19	11.1	14	—	—	1	—	1	3	—	1	1
Along the edges only	69	40.4	—	—	1	16	—	13	40	17	—	19
Dispersed on the surface	58	33.9	—	—	2	21	4	18	32	12	1	21
Emergent and submerged vegetation over the whole area	25	14.6	1	5	3	8	4	13	8	8	1	13
All sites	171											
<i>Turnover</i>												
Standing water	106	62.0	1	4	3	33	3	31	63	27	2	33
Low turnover	51	29.8	—	1	3	13	5	14	20	10	1	21
High turnover	14	8.2	14	—	—	—	—	—	—	—	—	—
All sites	171											
<i>Permanence</i>												
Ephemeral	14	8.2	—	—	—	2	—	2	11	2	—	—
Transient but not ephemeral	57	33.3	—	—	—	17	1	14	40	12	—	13
Permanent under normal climatic conditions	65	38.0	2	1	4	20	7	23	30	13	3	26
Permanent	35	20.5	13	4	2	7	—	6	2	10	—	15
All sites	171											
<i>Presumed origin</i>												
Natural	33	19.3	14	—	—	—	1	1	5	7	—	13
Man-made	138	80.7	1	5	6	46	7	44	78	30	3	41
All sites	171											
<i>Surrounding terrestrial habitat</i>												
Mixed woodland	84	49.1	15	—	1	20	4	24	37	15	2	17
Meadow/pasture	53	31.0	—	2	2	17	3	16	31	11	1	16
Residual alluvial forest	31	18.1	—	3	3	9	1	5	12	11	—	19
Village	3	1.8	—	—	—	—	—	—	3	—	—	2
All sites	171											
<i>Situation in relief</i>												
Valley	108	63.2	1	5	5	38	3	30	51	25	—	45
Slope	49	28.6	14	—	—	6	4	11	23	3	2	3
Ridge	14	8.2	—	—	1	2	1	4	9	9	1	6
All sites	171											

were found in the northern part of the area studied and in the Wisłoka river valley, where their parental species co-occur. In the ordination diagram sites populated by hybrids occupy an intermediate position along the second CCA axis between the two parental species.

In contrast to *T. cristatus* and *T. vulgaris*, the two remaining newt species (*T. alpestris* and *T. montandoni*) were more often found in less permanent sites with less abundant aquatic vegetation, as can be seen from the ordination diagram (Fig. 2) and Table 2. *T. montandoni* was a relatively common species in the study area, occupying 26.9% of all breeding sites. These were mainly water-filled wheel-ruts, with small surface area, with

little or no turnover of water. This habitat type comprised 71.7% of breeding places for this species. Similar sites were occupied by *T. alpestris*; most often it was found breeding in water-filled wheel-ruts and roadside ditches (75.6% of all its breeding places) with no or little water turnover. Breeding sites of *T. alpestris* were found almost as often as those of *T. montandoni* (in 26.3% of recorded amphibian breeding places); in most cases these two newt species occurred syntopically.

B. variegata, the commonest species in the area (48.5% of all sites) occupies the opposite end of the environmental gradient represented by the second CCA

TABLE 3. Results of CCA. Significance of the individual variable contributions to the model (P), correlations of variables with CCA axes, and the variances explained by the axes.

Variable	P	Axis 1	Axis 2	Axis 3	Axis 4
correlations of variables with axes					
Aquatic vegetation	0.043	-0.409	0.552	-0.186	0.171
Bomb hole	0.030	-0.035	0.230	-0.415	-0.182
Gravel pit	0.016	-0.048	0.501	-0.196	-0.343
Low water turnover	0.020	-0.150	0.243	0.073	0.367
Mineral bottom	0.002	0.190	-0.539	0.359	-0.374
Oxbow	0.001	-0.057	0.290	0.722	0.090
Permanence	0.001	0.320	0.766	0.192	-0.033
Slope	0.006	0.409	-0.343	-0.278	0.508
Stream	0.001	0.999	-0.023	0.009	-0.012
Valley	0.002	-0.304	0.322	0.032	-0.544
Wheel-rut	0.006	-0.256	-0.336	-0.032	0.181
Eigenvalue (λ)		0.932	0.226	0.183	0.142
Cumulative percentage of species-environment relation variance explained		57.3	71.1	82.4	91.1

axis; this signifies the least permanent and the least vegetated sites (Fig. 2). Table 2 also shows that *B. variegata* was found breeding most often in small, even ephemeral wheel-ruts and roadside ditches with standing water, mineral bottom and often very scarce aquatic vegetation or even none at all. Such habitats constituted 88% of breeding sites for this species.

R. temporaria was the second commonest species in the area (31.6% of all sites). It bred most often in wheel-ruts and roadside ditches (52.2% of its breeding sites), and also in oxbows (18.5%). *R. temporaria* quite often spawned in lentic water, 38.9% of all breeding sites had at least some water turnover; this can be seen also from the position of the species in Fig. 2. Generally in our study area *R. temporaria* only rarely reproduced in very shallow temporary pools.

Breeding habitats of *Bufo bufo* were similar to those of *R. temporaria*. It was the only other amphibian species, besides *R. temporaria*, found breeding regularly in oxbows (16.2 % of its breeding places, see also Fig. 2), although most often *Bufo bufo* spawned in larger wheel-ruts filled with water (67.6%) (Table 2).

TABLE 4. Species abundance at the breeding sites.

n of species	n of breeding sites	% of all breeding sites
1	90	52.6
2	50	29.2
3	20	11.7
4	6	3.5
5	3	1.8
6	1	0.6
7	1	0.6

Bufo viridis was found in three locations only, two were wheel-ruts and one was a ditch.

SPECIES ASSOCIATIONS AND ABUNDANCE

Associations between some amphibian species/groups were tested using G -tests of independence. These tests revealed that *T. montandoni* often bred together with *T. alpestris* ($G=7.58$, $P<0.0001$). All the newt species taken as a group were positively associated with *B. variegata* ($G=10.86$, $P<0.0001$), but no association was found between the newts and either *Bufo bufo* or *R. temporaria* ($G=2.99$, $P=0.13$). These two latter species often co-occurred ($G=3.08$, $P<0.0001$). There was no significant association between the presence of *B. variegata* and other anuran species ($G=1.48$, $P=0.22$).

We also tested which environmental factors most significantly influenced the number of species breeding in a site. In more than a half of cases (52.6% of all the breeding sites) only one species was found (Table 4). The maximum number of seven species breeding in one locality was recorded at one site only. This breeding locality had some exceptional characteristics since it was formed by many closely-spaced wheel-ruts and pools which we treated as a single breeding site. Six species were found only at another breeding site, which was an old clay pit. Generally, as revealed by stepwise multiple regression, five environmental variables influenced the species abundance significantly. We found positive relationships between the number of species and area ($b=0.346$, $P<0.005$); "clay pit" habitat type ($b=0.195$, $P<0.005$) and depth ($b=0.167$, $P<0.05$). Negative relationships were found for the "stream" habitat type ($b=-0.232$, $P<0.05$) and "oxbow" habitat type ($b=-0.192$, $P<0.05$).

DISCUSSION

Out of 18 amphibian species found in southern Poland as a whole, in the area studied we recorded only nine. Our study area was outside the geographic and/or ecological range of such species as *Pelobates fuscus*, *Bombina bombina*, *Bufo calamita*, *Rana ridibunda*, *R. arvalis* and *R. dalmatina* (Juszczyk, 1987; Szymura & Rafiński, 1997; Hofman & Szymura, 1998). However, despite intensive search, we could not find such species as *Hyla arborea*, *R. lessonae* and *R. esculenta*, although the study area was located within the broad distributional limits of these species. We also failed to identify any environmental factor(s) which could explain their absence. It seems that *Bufo viridis*, which was recorded at only three sites, reaches its local distributional and/or ecological limits in the area.

The amphibians in the Magurski NP seem not to be as selective in breeding habitat choice as the same species studied in different areas of Europe (Pavignano *et al.*, 1990; Ildos & Ancona, 1994; Serra-Cobo *et al.*, 1998), though the methods of analysis used by the latter authors are not readily comparable to ours. One possible reason is that in our area only a narrow range of suitable habitats (breeding sites available) was present. On the other hand, we cannot reject the possibility that the relatively low selectiveness found in our study resulted from our arbitrary choice of environmental variables and the way we coded them. Narrow habitat range of amphibian breeding communities in the Magurski NP was revealed also by CCA analysis; both first and second axes were shorter than 1 SD.

The narrowest breeding niche was found for *S. salamandra*, which in the area studied bred almost exclusively in small mountain streams. But even for this species there are reports of it using seepages, roadside ditches, small puddles and wells as breeding places, especially in the more eastern part of the Carpathians (Świerad, 1988; personal observations).

The most successful species in the study area was *B. variegata*. It spawned even in very transient habitats like small pools, ditches and wheel-ruts which are the most common water bodies in the Magurski NP. Such small water bodies constituted 76.3% of all amphibian breeding sites there. The prolonged breeding season (April–August) and relatively rapid larval development period of *B. variegata* facilitates high reproductive success for this species even in transient pools (Rafińska, 1991). This species selects similar types of breeding habitats in other parts of its distribution (MacCallum *et al.*, 1998).

More permanent roadside ditches and wheel-ruts left by heavy forestry vehicles were very often used as breeding sites by smaller species of newts: *T. vulgaris*, *T. montandoni* and *T. alpestris*. In such sites the newts often co-occurred with *B. variegata*, though the shallowest and the most temporary places used for breeding by *B. variegata* were typically avoided by the newts. The newts often occupied breeding sites where no other

amphibian species was present (46% of all breeding sites for newts), but when another amphibian species was found at the same site it was usually *B. variegata* which co-occurred with newts in 33% of their localities. This resulted in a positive association between the presence of newts and *B. variegata*.

Generally, the four newt species reproduced in sites with at least some vegetation. Aquatic and at least partly submerged marginal vegetation provide the main substrates used for egg deposition by all newt species (Miaud, 1995). Both *T. cristatus* and *T. vulgaris* were rare species in our study area (found at five and six sites respectively), so we cannot generalize our findings with respect to environmental associations. Nevertheless, our data are in agreement with those reported by other authors (see below).

T. cristatus was found only in places with abundant submerged vegetation. However, this may be a secondary effect, because we found this species only in larger and more permanent waters which were usually rich in vegetation (the only habitat types we found this species in were gravel pits, a clay pit, a bomb hole and a large pool). Association with similar water bodies for *T. cristatus* was also reported from Western Europe (Beebee, 1975; Cooke & Frazer, 1976), but such a correlation was not found by Denton (1991). The specific requirements of *T. cristatus* may be the main cause of its being the rarest newt species in many areas of Europe and therefore the subject of serious conservation concern (Baille & Groombridge, 1996; Beebee, 1996). On the other hand, our own observations (unpublished) indicate that this species can show greater ecological plasticity in other parts of its distribution (the Polish Eastern Carpathians) as we have found it breeding there also in small water bodies such as roadside ditches and water-filled wheel-ruts.

T. vulgaris also bred in more vegetated places than the other two newt species (Table 2). Associations between aquatic vegetation and the presence of *T. vulgaris* were found by Fonseca & Jocque (1982), Ildos & Ancona (1994) and Marnell (1998). Although the association of *T. vulgaris* with abundant aquatic vegetation was clear, our observations should be treated with caution as this species was found at six sites only.

Our analysis demonstrated that *T. montandoni* and *T. alpestris* often occurred together, which may indicate that they share similar requirements. They seem not to depend so much on the presence of rich aquatic vegetation as *T. cristatus* and *T. vulgaris*. We did not find an obvious relationship between the presence of the woodland within 100 m of the breeding site and the presence of newts. In several studies a strong dependence by newts on the presence of forest or scrub habitat in the vicinity of the breeding site was found (Beebee, 1980, 1985; Pavignano, 1988). Lack of such an association in the present study may be explained by the general abundance of forest habitats in our study area.

Breeding sites of *T. montandoni* were found almost exactly as often as those of *T. alpestris*; nevertheless, the latter species was clearly not so abundant in Magurski NP as the former. We estimated the sizes of amphibian populations by dip-netting for some sites only but we do not report these here. The ratio of *T. montandoni* to *T. alpestris* was close to 2:1, as estimated from the data collected at 46 sites. This is most probably a geographical phenomenon, as in the Polish Carpathians the abundance of *T. alpestris* declines with the increase of *T. montandoni* towards the east (Szyndlar, 1980; Juszczuk, 1987; Świerad, 1988). The question of whether this is solely a result of the history of the postglacial colonization, or depends on some unknown environmental factor(s) along the west-east axis relevant to the requirements of these newts remains unanswered.

In our study area *Bufo bufo* and *R. temporaria* seem to have similar requirements and often spawned at the same sites. They usually used as breeding sites deeper wheel-ruts and roadside ditches, and seemed to avoid more shallow and transient water bodies. In our study area *R. temporaria* did not avoid sites with slowly running water (38.9 % of its breeding places). Together with *B. bufo*, they were the only amphibian species that often spawned in oxbows. This indicates that as early breeders, *R. temporaria* and *B. bufo* are perhaps more tolerant of relatively low temperatures during embryonic and larval development than other amphibian species occurring in Magurski NP. Although we have not collected any data on long term temperature fluctuations in the breeding places, oxbows – which are usually relatively deep and large water bodies – are generally cooler than small temporary pools.

The scarcity of larger water bodies is a salient feature of the area studied. Water bodies larger than 100 sq. m constituted only 2.9% of all breeding sites. Some of them may be of special importance for amphibian communities since they host large populations of several species. Being the most stable breeding habitats they probably serve as source populations for the whole metapopulation. For this reason such large multi-species breeding sites deserve special attention in the maintenance of amphibian populations. On the other hand, small water bodies – which in this area predominated – may give high reproductive success, especially in the years with high rainfall throughout the reproductive period. The impact of invertebrate predators can be significantly lower in smaller, more transient breeding sites, and it seems that at least some amphibian species actively choose smaller water bodies for breeding to avoid predation (MacCallum *et al.*, 1998). Conservation measures for *Bufo calamita* in Britain showed that this species more successfully colonized smaller and shallower water bodies than larger ones, most probably because of lower predation pressure and weaker competition from other amphibian species (Beebee, 1996).

Many authors have reported the negative relationship between the presence of fish and that of

amphibians (Beebee, 1977; Brönmark & Edenhamn, 1994; Ildos & Ancona, 1994; Aransson & Stenson, 1995), although a positive association was found for *B. bufo* by Beebee (1985). In our study area, still waters with fish were extremely rare (four oxbows and two fish ponds), so the impact of fish on amphibians could not be assessed.

Nearly all of the sites recorded in the study area were of human origin (84.2%). Natural sites were confined to streams – which were only used for breeding by *S. salamandra* – and the oxbows, where the only species reproducing were *R. temporaria* and *B. bufo*. To prevent the reduction of amphibian population size, and to maintain the whole biodiversity of this and similar areas, the active protection of man-made habitats is very important. The commonest types of amphibian breeding habitat in the Magurski National Park were water-filled wheel-ruts and roadside ditches found along tracks and minor roads. Any modernization of roads used for local traffic, especially in woods, will cause a dramatic decline of the number and size of amphibian populations. For example, the existence of *T. montandoni* in Magurski NP is almost entirely dependent on the presence of roadside ditches and wheel-ruts. Similar environmental conditions seem to predominate in many of the mountainous regions of Eastern Europe. In order to preserve the present status of amphibian populations there, active maintenance of existing – and creation of new – breeding sites is needed. Such conservation practices have proved to be very successful for the preservation of amphibian breeding populations in Western Europe (Laan & Verboom, 1990; Arntzen & Teunis, 1993; Fog & Briggs, 1997; Beebee, 1996).

ACKNOWLEDGEMENTS

We would like to thank Dr Jacek M. Szymura for helpful suggestions on the manuscript. The paper benefited from comments made by the editor and two reviewers. Dr Z. Dzwonko introduced us to CCA analysis. A. Bieniek, J. Dziadosz, W. Kilarski, M. Krawczyk, K. Rogowski, K. Sarnecka and A. Szydio helped with data collection in the field. The work was in part financed by grant PD 9017 from the Magurski National Park.

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Accepted: 8.11.00

TWO NEW CHAMELEONS OF THE GENUS *CALUMMA* FROM NORTH-EAST MADAGASCAR, WITH OBSERVATIONS ON HEMIPENIAL MORPHOLOGY IN THE *CALUMMA FURCIFER* GROUP (REPTILIA, SQUAMATA, CHAMAELEONIDAE)

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During herpetological surveys in N.E. Madagascar two new species of *Calumma* chameleons belonging to the *C. furcifer* group were found and are described here. The first species, *Calumma vencesi* n. sp., was found at three rainforest sites: Ambolokopatrika (corridor between the Anjanaharibe-Sud and Marojejy massifs), Besariaka (classified forest south of the Anjanaharibe-Sud Massif), and Tsararano (forest between Besariaka and Masoala). This species is related to *C. gastrotaenia*, *C. guillaumeti* and *C. marojezensis*. *C. vencesi* n. sp. differs in having a larger size, a dorsal crest, and – in females – a typical green coloration with a network of alternating dark and light semicircular stripes. Furthermore, it is characterized by a unique combination of hemipenis characters: a pair of sulcal rotulae anteriorly bearing a papillary field; a pair of asulcal rotulae showing a double denticulated edge; and a pair of long pointed cylindrical papillae bearing a micropapillary field on top. The second species, *Calumma vatosoa* n. sp., found in ericoid habitat on the summit of the Tsararano Chain, is conspicuous due to its bright greenish coloration, with a longitudinal midlateral whitish band, and a yellowish spot in the middle of each flank. The hemipenis ornamentation includes a feature exclusive to this species which has not been described in any other species of the genus *Calumma*: the coexistence of three pairs of rotulae. This species is perhaps related to *C. peyrierasi*. The distribution of the species belonging to the *C. furcifer* group is also discussed from the point of view of biogeographic patterns and refuge massifs.

Key words: *Calumma*, Madagascar, chameleon, hemipenial morphology

INTRODUCTION

According to the revision of the family Chamaeleonidae proposed by Klaver & Böhme (1986, 1997) and complementary studies (Hofman *et al.*, 1991), two genera endemic to Madagascar and neighbouring islands are ascribed to the subfamily Chamaeleoninae: *Furcifer* and *Calumma*. Whereas most *Furcifer* species are typical inhabitants of deciduous habitats with a marked dry season – including degraded areas of this type – the *Calumma* species seem to be restricted to rainforests within the eastern region of Madagascar. Most of the latter exclusively occur in mid- and high-altitude rainforests, thus showing a rather narrow range of microthermal preferences: the highest elevational record belongs to *Calumma tsaratananensis*, collected at about 2500 m on the Tsaratanana Massif (Brygoo & Domergue, 1968). A phenetic classification based on external morphology proposed by Brygoo (1971) and reviewed by Glaw &

Vences (1994) identified five species groups within the genus *Furcifer* and four within the genus *Calumma*. The *Calumma furcifer* group has been recently reviewed by Böhme (1997), giving evidence for the elevation to full species status of the taxa formerly regarded as *C. gastrotaenia* subspecies: *C. guillaumeti*, *C. marojezensis* and *C. andringitraensis*. The description of *C. glawi* by Böhme (1997) made the *C. furcifer* group the richest species assemblage within the genera *Calumma* and *Furcifer*, with seven species.

During recent survey work in northern Madagascar, we had the opportunity to find several new species of amphibian and reptile and to obtain new records for others (e.g., Andreone *et al.*, 1998; Nussbaum *et al.*, 1998; Jesu *et al.*, 1998; Mattioli, 1998), thus stressing the importance of this geographic area. In particular, we collected two chameleons that did not fall into any known taxon, and therefore are regarded as new species. In this paper we describe them and summarize information on their distribution and phenetic relationships. Furthermore, we provide data on the hemipenis morphology and a preliminary key to the identification of the males of all the known species of this group.

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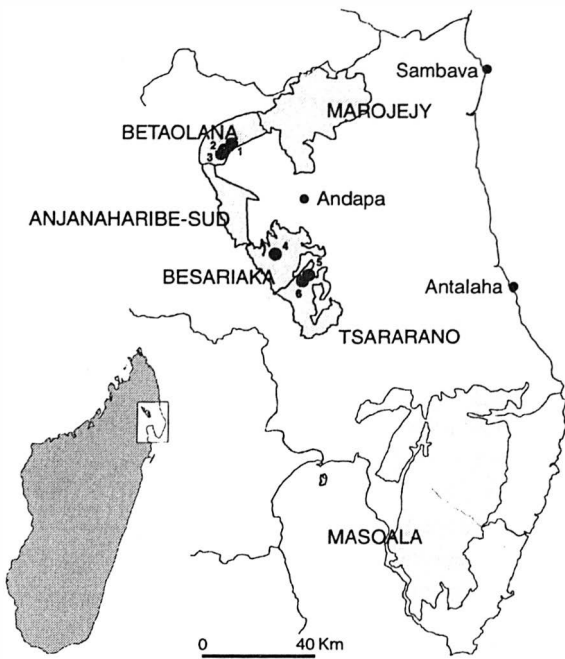


FIG. 1. Map of N.E. Madagascar with sites where some taxa belonging to the *Calumma furcifer* group were found during field surveys. 1-3, campsites 1-3 at Ambolokopatrika Corridor (collecting localities of *Calumma vencesi* n.sp.); 4, campsite 1 at Forêt de Besariaka (Betaolana Ridge) (collecting locality of *C. vencesi* n. sp.); 5, campsite 1 at Forêt de Tsararano (collecting locality of *C. vencesi* n.sp.); 6, campsite 2 at Forêt de Tsararano (collecting locality of *C. vatsoa* n. sp.). Area borders refer to the political boundaries of protected areas (PN de Marojejy, RS d'Anjanaharibe-Sud, PN de Masoala) and classified forests (Forêt de Besariaka, Forêt de Tsararano). Based upon FTM (Foiben-Taosarintanin'I Madagasikara/Institut Géographique et Hydrogéographique National) maps and a digital elaboration of GIS Service at WWF Madagascar.

MATERIALS AND METHODS

STUDY SITES AND PERIODS

The sites where the two new species were found are described below, and a map is given in Fig. 1. Latitudes and longitudes were given according to GPS prospecting, maps and IUCN/UNEP/WWF (1987). A more detailed description of these sites is given by Andreone *et al.* (2000).

(1) *Ambolokopatrika*. This forest is situated northwest of the Andapa Basin, between the Anjanaharibe-Sud and Marojejy massifs (Betaolana Ridge). The vegetation of the forest belongs to the domains of East and Central Madagascar (Humbert, 1955). Due to human activity, the Ambolokopatrika corridor is currently a mosaic of fairly intact forest, "savoka" (a degraded vegetational formation mainly constituted of herbaceous species) and secondary forest. At Ambolokopatrika three study sites were chosen, all within the Andapa Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), "Andemakatsara" (Campsite 1), 14°31.8'S, 49°26.5'E, 810-875 m (27 May - 3 June 1997); "Andranomadio" (Campsite 2),

14°32.4'S, 49°26.3'E, 860-910 m (4-12 June 1997 and 29 November-8 December 1997); "Antsinjorano" (Campsite 3), 14°32.6'S, 49°25.8'E, 950-1250 m (9-20 December 1997). The forest around Campsites 1 and 2 is a mid-altitude rainforest, while at Campsite 3 it is transitional between lowland and mid-altitude rainforest; at all sites there are patchworks of, on the one hand, fairly rather intact, and on the other, somewhat altered rainforest.

(2) *Besariaka*. This classified forest is about 60 km south of Andapa. It is delimited to the north by the RS d'Anjanaharibe-Sud, and to the south by the Tsararano Chain. The elevational range is 470-1232 m. Capture of the first newly described species occurred at "Ambinanin'ny miaka-midina" (Campsite 1), 14°50.8'S, 49°35.7'E, 940-995 m (4-15 June 1996). This campsite is within the Andapa Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province). There the forest is rather degraded, especially in parcels far from streams. This is apparently due to several reasons, among which are the use of forest areas for cattle, the cutting of trees by villagers, and the use of well established path systems to search for "bilahy" bark (used to make the local alcoholic beverage named "betsabetsa"), and for hunting.

(3) *Tsararano*. This chain, formed by several hills (altitude 400-1269 m) and the forest of the same name lie south of the Andapa Basin, midway between the Anjanaharibe-Sud Massif and the Masoala Peninsula. The collections were made at two sites: "Antsarahan'ny tsararano" (Campsite 1), 14°54.4'S, 49°41.2'E, 700-850 m (29 November - 7 December 1996), and "Andatony anivo" (Campsite 2), 14°54.8'S, 49°42.6'E, 600-750 m (8-18 December 1996). Both of the campsites are included within the Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province). The forest of Tsararano appears to be quite intact, most likely due to its distance from large sized villages. As elsewhere, paths are being cut for the collection of local products and for the hunting of lemurs.

According to Goodman & Lewis (1998) the Andapa region is characterized by a humid and tropical climate. The mean temperature ranges from 18°C in July to 25°C in February. The relative humidity is about 87%, but reaches 97% in March and April. The annual precipitation is slightly more than 2000 mm. On average it rains 271 days per year. The "dry" season lasts about two months (September and October), with 41.1 mm and 52.6 mm of rain distributed throughout 14.7 and 15.1 days respectively.

CAPTURE AND PRESERVATION TECHNIQUES

Chameleons were captured by hand during the night when they are paler and more visible, with the aid of battery powered torches. Some specimens were photographed to obtain information on their natural coloration. Later they were euthanased, fixed in 10% formalin or in 90% ethanol, and preserved in a final so-

lution of 75% ethanol. The voucher specimens are now housed at the Museo Regionale di Scienze Naturali (Torino), and Parc Botanique de Tsimbazaza (Antananarivo).

ACRONYMS, MORPHOMETRY AND HEMIPENIS TERMINOLOGY

Throughout the text the following acronyms have been used: BM(NH), Natural History Museum, London (formerly the British Museum of Natural History); MNHN, Muséum national d'Histoire naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; MZUT, Museo di Zoologia dell'Università di Torino (collection now housed at the MRSN); MSNG, Museo Civico di Storia Naturale "G. Doria", Genova; PBZT-FN, Parc Botanique et Zoologique de Tsimbazaza, Antananarivo; ZFMK, Zoologisches Forschungsinstitut und Museum "Alexander Koenig", Bonn; PN, Parc National (National Park); RNI, Réserve Naturelle Intégrale (Strict Nature Reserve); RS, Réserve Spéciale (Special Reserve). Some specimens quoted in the species description (paratypes), and marked with an asterisk (*) currently bear the MRSN acronym, but will be later housed at PBZT. We also analysed several specimens belonging to the species of the *Calumma furcifer* group. All morphological measurements (Tables 1-2) were taken by one of us (F. Mattioli) with a dial calliper (precision at 0.1 mm): head length (HL), head depth (HD), head width (HW), socket diameter (SD), snout-vent length (SVL), tail length (TL), axilla-groin distance (AGD). For hemipenis morphology, we followed the terminology proposed by Klaver & Böhme (1986) and Böhme (1988).

The drawings of the external morphology of heads and hemipenes were made by tracing pictures obtained from slides in order to maintain the correct proportions; these were then enhanced with details gathered from direct observations using a binocular microscope.

On the basis of a few dissected specimens which all showed completely developed gonads, we assumed that all other specimens of a similar size were adults. The only exception was represented by the specimen MRSN R11682.2: in this case the dissection revealed the presence of incompletely developed ovaria, thus indicating that it had not reached maturity.

RESULTS

CALUMMA VENCESI NEW SPECIES

Diagnosis. A medium-sized chameleon (snout-vent length up to 73 mm), included in the *Calumma furcifer* group (*sensu* Glaw & Vences, 1994) by virtue of the absence of occipital lobes, absence of gular and ventral crest, markedly acute rostral profile and greenish coloration. This new species differs from all the others in the group in the following combination of morphological features: homogeneous scalation, divided canthi rostrales, absence of rostral appendage, evident lateral crests, evident nuchal fold, markedly oblique parietal

profile, double longitudinal ventral white line, weakly developed dorsal crest, rings made by 1-2 rows of white scales on upper surfaces of fingers [described as "*bagues au niveau des doigts*" by Brygoo (1978) in regard to *Calumma marojezensis*, formerly *Chamaeleo gastrotaenia marojezensis*]. Concerning the hemipenis ornamentation, it differs in that (1) a pair of sulcal rotulae anteriorly bear a papillary field, and (2) a pair of asulcal rotulae showing a double denticulated edge and a pair of long pointed cylindrical papillae bear a micropapillary field on top.

Holotype. MRSN R1690, Forêt d'Ambolokopatrika (Campsite 2), 870 m, 14 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina.

Paratypes. MRSN R1703.1-2, Forêt de Besariaka (Campsite 1), 950 m, 7 May 1996, leg. J. E. Randrianirina; MRSN R1681, Forêt de Besariaka (Campsite 1), 945 m, 9 June 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1682.1-2*, Forêt de Besariaka (Campsite 1), 970 m, 12 June 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1683.1-2, Forêt de Tsararano (Campsite 1), 700 m, 20 October 1996, leg. J. E. Randrianirina; MRSN R1684, Forêt de Tsararano (Campsite 1), 730 m, 28 November 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1685*, Forêt de Tsararano (Campsite 1), 730 m, 2 December 1996, leg. F. Andreone and J. E. Randrianirina; MRSN R1686.1 and R1686.2*, Forêt d'Ambolokopatrika (Campsite 2), 875 m, leg. F. Andreone, G. Aprea and J. E. Randrianirina 30 November 1997; MRSN R1687.1-2, Forêt d'Ambolokopatrika (Campsite 2), 860 m, 4 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina; MRSN R1688, Forêt d'Ambolokopatrika (Campsite 2), 865 m, 12 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina; MRSN R1689.1-3, Forêt d'Ambolokopatrika (Campsite 3), 960 m, 11 December 1997, leg. F. Andreone, G. Aprea and J. E. Randrianirina; PBZT-FN 6661 [specimen not measured], Forêt d'Ambolokopatrika (Campsite 1), 850 m, 29 May 1997, leg. F. Andreone and J. E. Randrianirina; PBZT-FN 6662 [specimen not measured], Forêt d'Ambolokopatrika (Campsite 1), 850 m, 29 May 1997, leg. F. Andreone and J. E. Randrianirina; PBZT-FN 6690 [specimen not measured], Forêt d'Ambolokopatrika (Campsite 1), 850 m, 2 June 1997, leg. F. Andreone and J. Randrianirina.

DESCRIPTION OF THE HOLOTYPE

External morphology. Adult male in a good state of preservation with fully everted hemipenes. Scales homogeneous, except on vicinity of cranial crests and parietal region (upper side of the cranium), in which they are a little bit larger. Head (Fig. 2) shows slightly developed orbital and parasagittal crests and rather developed lateral crest. The parasagittal crests joined at occiput apex. Absence of occipital lobes and gular crest. Canthi rostrales divided and rostral appendage

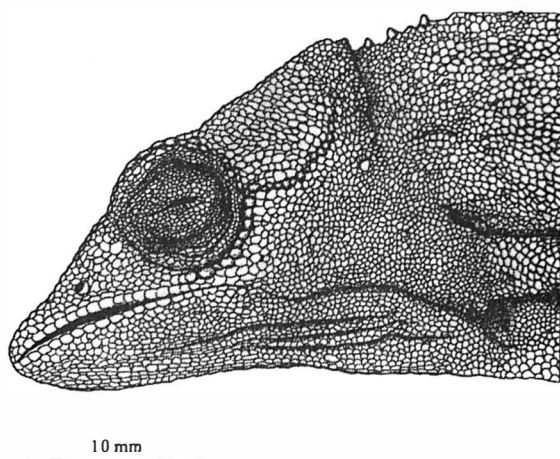


FIG. 2. Lateral view of the head of *Calumma vencesi* n. sp. (MRSN R1690, male, holotype).

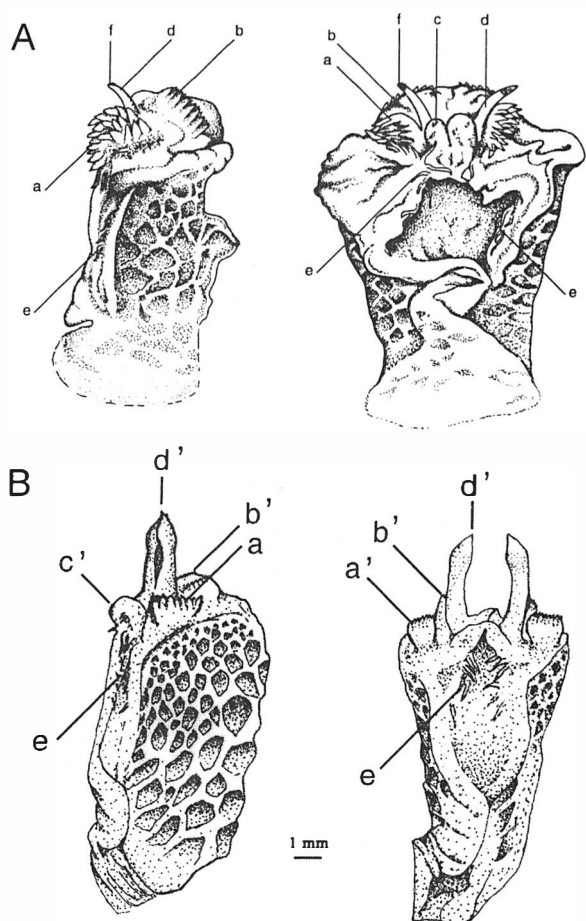


FIG. 3. Hemipenis morphology (lateral and sulcal view) of *Calumma vencesi* n. sp. (MRSN R1690, male, holotype) (A), compared with *Calumma marojezensis* (MRSN R1701) (B). Main ornamental structures: sulcal rotulae bearing papillary field (a); asulcal rotulae bearing a double denticulated edge (b); pair of hypertrophic papillae (c); pair of long pointed cylindrical papillae (d); double row of pointed papillae on sulcal lips (e); micropapillary field (f); sulcal rotulae (a'); asulcal rotulae (b'); two hypertrophic papillae joined together (c'); pair of long pointed cylindrical papillae enlarged on top (d'). Same letters mark presumably homologous structures.

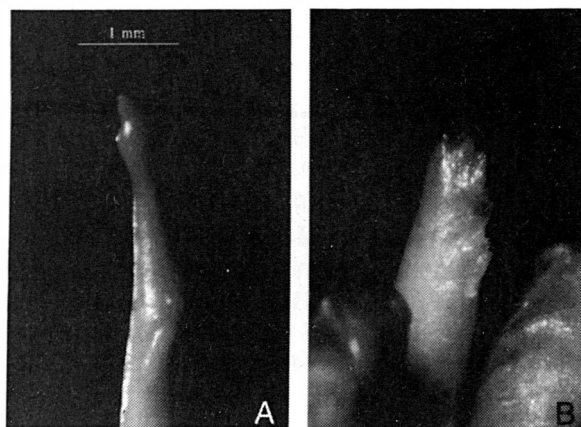


FIG. 4. Comparison between the tips of the cylindrical papillae of *C. marojezensis* (A) and the tips of the cylindrical papillae of *C. vencesi* n. sp. bearing a micropapillary field (B).

absent. Scales enlarged around nostrils. Markedly acute rostral profile and oblique parietal profile. At nape level a dermal fold extends on back for 2 mm. Occiput apex slightly raised forming a pointed helmet. Dorsal crest consisting of ten spines with different degrees of development distributed along the whole body length, but absent on tail. Deep axillary pockets. Number of scales at widest point of flanks: 58. Absence of ventral crest. Evident rings – often joined to each other – consisting of 1–2 rows of white scales on upper surfaces of fingers.

Hemipenial morphology. Hemipenis (Fig. 3) clavate, caliculated, capitate, slightly flattened on sulcal plane. Sulcal lips markedly divergent. Sulcus with ridges and distally limited by a fleshy outgrowth sited at the point at which the sulcal lips join each other. Caput ornamentation consists of: (1) a pair of large sulcal rotulae bearing a papillary field on sulcal side; (2) a pair of smaller asulcal rotulae showing a double denticulated edge; (3) a pair of rounded hypertrophic papillae in sulcal central position; (4) a pair of long pointed cylindrical papillae – longer than any other ornamentation structures – bearing a micropapillary field on top (Fig. 4), sited between the pair of sulcal rotulae and the pair of central papillae; (5) a double row of twelve pointed thin papillae of various sizes respectively starting on left and right of the pair of central papillae and descending along the sulcal lips. Hemipenis length around 10 mm, i.e. 13.7% of snout-vent length.

Coloration in life. The male holotype (Fig. 5, photographed during the night) is characterised by a rather light green coloration on the back. Small scattered darker spots are also evident. A thin, pale line runs midlaterally from the head (at the level of the occiput indentation) to the hindlegs. Two light spots surrounded by a darker border are also visible along this line. Belly light green-whitish, with a double whitish longitudinal stripe bordered by reddish lines (like in most *C. gastrotaenia*). This light and reddish coloration

is also visible around the cloaca. A thin reddish stripe continues also on to the lower part of the tail-base.

Coloration in preservative. Predominantly greyish-blue, with many fine black spots on truncus, limbs and tail. Head blue with the exception of a few whitish areas on temporal region and throat (the latter sprinkled with black single scale-sized spots). Dorsum dark bluish shading into lighter tonalities approaching the ventral region, a few whitish areas above the limb insertions. Three white spots in longitudinal alignment running along mid-flanks. Axillary pockets white. Two longitudinal, ventral, white lines, separated by a thin medio-ventral dark blue line, originating at the proximal ends of arms and running all along the venter; a single longitudinal, ventral, white line running all along the tail.

Variation. The analysis of paratypes, belonging to three different populations (Ambolokopatrika, Besariaka, Tsararano), permits a first assessment of intraspecific variability, which can be summarized as follows: the mean total length in females is significantly smaller than in males [respectively 119.6 ± 9.58 mm (mean \pm SD) compared to 135.8 ± 4.79 mm; $t=4.48$, $df=15$, $P<0.05$], while there is no significant difference in mean SVL (respectively 62.9 ± 7.57 mm compared to 68.9 ± 3.14 mm; $t=2.19$, $df=15$, $P>0.05$); the female paratypes belonging to the Besariaka population (MRSN R1703.2, R1681, R1682.1) show a significantly larger size than all the other females (respectively 129.00 ± 6.24 mm compared to 114.00 ± 5.96 mm; $t=3.39$, $df=6$, $P<0.05$); the occiput apex is not heightened, thus meaning that the helmet is flattened, in most paratypes (MRSN R1703.1-2, R1681, R1682.1, R1682.2, R1683.1, R1683.2, R1684, R1685, R1686.1-2, R1687.1, R1688, R1689.1, R1689.3); a few specimens (MRSN R1689.1-2) show a reduced nuchal fold. The number of spines forming the dorsal crest is variable (1-4 in females, 2-13 in males), while its mean value, although higher in males than in females (males: 8.44 ± 4.67 ; females: 3.5 ± 0.93) is not significantly different (Mann-Whitney $U=16$, $P>0.05$); the dorsal keel is wavy and the rostral profile is extremely acute in the male paratype from Besariaka (MRSN R1703.1); the rings on the upper surfaces of the fingers are often joined together. The cylindrical papillae on the hemipenis apex may be much less developed (probably due to incomplete evagination); the number of pointed papillae forming the double row running along the sulcal lips is variable, but never smaller than ten; the white spots on the flanks may be less than three or absent, but always on the same line; the fine black spots on the flanks are found on all paratypes, even if their density may differ greatly from specimen to specimen. In life the coloration of females is very conspicuous (Fig. 6): the back and the flanks are light green shading to yellowish, with a network of darker irregular stripes that create a type of semicircular banding – rather interconnected (in the depicted

specimen this delineates something of a midlateral clear band), two brownish darker spots are situated on each flank overlapping the light band, scattered spots are visible more than in males and are more contrasted when lying upon the yellowish light coloration, the head is somewhat darker than the rest of the body especially on the parietal region, the eyes are brownish, the pupil is blackish with a light surround, as in males the belly is lighter with a whitish median longitudinal band internally bordered by two thin reddish lines; three females (MRSN R1683.1-2, R1684) belonging to Tsararano population show the dark stripes on the flanks even in preservative, this feature being less evident in the specimen MRSN R1684. MRSN R1682.2 turned out to be much smaller than all the other paratypes (SVL=45.0 mm; T=30.0 mm), and is therefore considered a young female, as confirmed by its dissection.

Etymology. We wish to dedicate this new species to Miguel Vences (Cologne, Germany), in recognition of his outstanding research activity on Malagasy herpetofauna.

Habitat and habits. *Calumma vencesi* n. sp. was found at the three forests between 700 and 960 m, thus showing an altitudinal range of about 260 m. It is, however, likely that the minimum altitudinal limit is lower, at about 600 m, while the maximum altitude be as much as 1000 m. This appears to be consistent with what is known for the various species belonging to the *Calumma gastrotaenia* complex, which usually have a narrow altitudinal distribution. At all the sites *C. vencesi* n. sp. appears to prefer rather intact parcels of forest. At Besariaka it was never found in cleared areas. As with other species in this group, it has been found almost homogeneously throughout the forest, without showing a clear preference for the riverine habitats (= forest at a distance lower than 20 m from the river). At the sites where it has been found *C. vencesi* n. sp. turned out to be rather abundant, and within a single search period (about 4 hours) we usually found between three and 10 specimens. At some locations, it seemed to be more common, although the reasons for this were not clear. Despite our intensive survey activity we never detected individuals during the day. Almost all the specimens were found at an elevation of 10-90 cm from the ground, usually hanging on to a leaf and having the head oriented upwards. We never observed phenomena of territoriality or other aggressive interactions.

CALUMMA VATOSOA NEW SPECIES

Diagnosis. A medium-sized chameleon (snout-vent length 60 mm), ascribed to the *Calumma furcifer* group (see later) due to the following characters: absence of occipital lobes, absence of gular and ventral crest, markedly acute rostral profile and greenish coloration. Assignment to the other *Calumma* group including medium-sized chameleons (*C. nasuta* group) cannot be supported because of the absence of the soft dermal

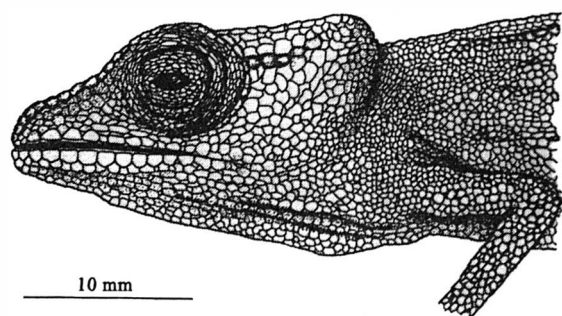


FIG. 7. Lateral view of the head of *Calumma vatosoa* n. sp. (MRSN R1628, male, holotype).

rostral appendage and the completely different hemipenis ornamentation. This new species differs from all the others of the group for the following combination of external morphological features: heterogeneous scalation, canthi rostrales joined at snout tip, absence of rostral appendage, evident lateral crests, flattened helmet, absence of dorsal crest and presence of axillary pockets. In terms of hemipenis ornamentation, there is a feature exclusive to this species which has not been described in any other species of the genus *Calumma*: the coexistence of three pairs of rotulae.

Holotype. MRSN R1628, adult male, Forêt de Tsararano (Campsite 2), 665 m, 14 December 1996, leg. F. Andreone and J. E. Randrianirina.

DESCRIPTION OF HOLOTYPE

External morphology. Adult male in good state of preservation. Hemipenes fully everted. Scalation heterogeneous: scales are uniformly small along the flanks, but significantly larger on head, limbs, dorsal keel and tail. Scale shape rounded on throat and limbs. Head (Fig. 7) shows slightly developed parietal and sagittal crests joined at mid length of parietal crests, rudimental orbital crests and lateral crests starting at

mid orbit and approaching occiput following helmet profile. Absence of occipital lobes and gular crest. Canthi rostrales joined at snout tip. Acute rostral profile. Flattened helmet extends on dorsum for 2 mm. Absence of dorsal crest. Evident axillary pockets. Forty-nine scales at widest point of flanks.

Hemipenial morphology. Hemipenis clavate, calculated, capitate, considerably flattened on sulcal plane (Fig. 8). Sulcal lips markedly divergent. Caput ornamentation consists of the following: a pair of tiny sulcal rotulae (similar to auriculae) parallel to the sulcal plane; a pair of large apical rotulae, slightly concave on asulcal side; a pair of large asulcal rotulae in lateral position; two pairs of papillae in latero-sulcal positions, each of them with a shorter esternal papilla. Hemipenis length around 4.4 mm, i.e. 7.3% of snout-vent length.

Coloration in life. The single collected specimen possessed unusual coloration, until now unique among the *Calumma* chameleons (Fig. 9). Flanks and back have a greenish background, which – depending on the light exposure – varied from light to dark green. Warty scales of the flanks appear darker at their tip. A midlateral white stripe runs from the upper lip, past the front edge of the eye, to a position a few millimetres behind the hindlimbs. This band is wider towards the anterior end, and thinner posteriorly. The flanks are therefore divided by this white band: on the upper and lower sides a network of blackish lines is visible, more evident on the hind part of the back and on the tail. These lines are almost parallel (except for the lower “branches”) and run diagonally towards the anterior part of the body. At mid flank the greenish coloration becomes almost yellowish-orange, forming an irregular wide spot. A more or less yellowish area is also visible in the first half of the tail. The superior part of the head and the helmet are dark greenish-brown, with a darker line which passes throughout the eye and stops at the helmet’s posterior edge. Except for this dark stripe the eyelids are turquoise with a thin yellowish area just around the pupil. The coloration of the legs is similar to that of the back, although they appear a little darker, with the tubercles clearly visible and generally lighter than the background. The belly is much lighter than the rest of the body and is almost greyish-yellow, but without any well-delineated stripe. At the level of the axillae the coloration is lighter, almost whitish.

Coloration in preservative. In preservative the holotype faded, and the green coloration almost disappeared, changing to a dark bronze with shades through to black. The throat and venter were paler than in life. Conspicuous spots absent, unless due to scale wear.

Etymology. The Malagasy word “vatosoa” is a compound of “vato” (meaning stone), and “soa” (meaning beautiful), and in general it is used to indicate a crystal, jewel or precious stone. We assign this name to the new chameleon from Tsararano for its wonderful live coloration, which could indeed be a symbol for Malagasy beauty and for herpetological conservation. In addition,

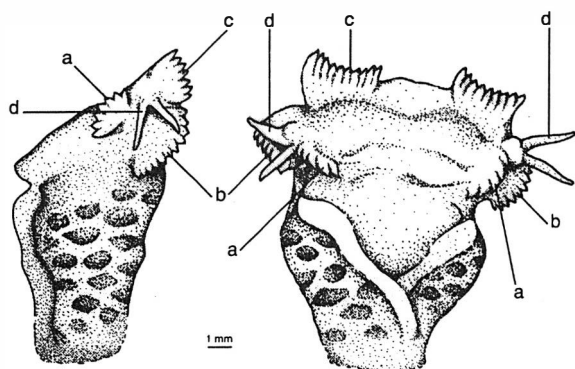


FIG. 8. Hemipenis morphology of *Calumma vatosoa* n. sp. (MRSN R1628, holotype): lateral view on the left, sulcal view on the right. Main ornamentations: sulcal rotulae (a); asulcal rotulae (b); large apical rotulae (c); pairs of papillae in latero-sulcal position (d).

Franco Andreone wishes to dedicate this new species to his daughter, Serena Crystal Vatosoa, with much love and hope of endless happiness.

Habitat and habits. At the place where the holotype was found (Tsararano, 665 m) the forest appears to be a mixture of typical rainforest with small patches of *Philippia* [= *Erica*] ericoid heathland. This vegetation is present here at a lower altitude than at other sites (e.g. at Marojejy it appears to be confined to altitudes higher than 1800 m: Nicoll & Langrand, 1988). *Calumma vatosoa* n. sp. seems to be a chameleon closely tied to this habitat. The holotype was found during the day about 110 cm from the ground.

JUSTIFICATION OF THE TWO NEW SPECIES AND OBSERVATIONS ON HEMIPENIS MORPHOLOGY

Calumma vencesi n. sp. shows general external morphological features that led us to include it in the *C. furcifer* group, which has until now comprised the following species: *C. furcifer*, *C. gastrotaenia*, *C. peyrierasi*, *C. guillaumeti*, *C. marojezensis*, *C. andringitraensis* and *C. glawi*. Nevertheless, remarkable differences allow identification of the new species, which differs from *C. furcifer* in the absence of the forked rostral appendage in males; from *C. peyrierasi* in terms of its larger size and the double longitudinal, whitish ventral lines; from *C. gastrotaenia* and *C. guillaumeti* in terms of the larger size of males, reduced or absent dorsal crest, nuchal fold and rings on

fingers; from *C. andringitraensis* by the larger size of males, nuchal fold, rings on fingers; from *C. glawi* by the larger size of males and reduced dorsal crest; from *C. marojezensis* in terms of the nuchal fold and markedly oblique parietal profile (subhorizontal in *C. marojezensis*). The obvious differences from *C. vatosoa* n. sp. are discussed at the end of this section.

Moreover, in accordance with Klaver & Böhme (1986, 1997), Böhme (1997) and Ziegler & Böhme (1997), we assume that the hemipenis morphology plays a fundamental role in specific recognition of chameleons, in particular within the *C. furcifer* group, in which morphological differences are less obvious than in other groups. The comparison of the hemipenis structure of *C. vencesi* n. sp. with that already described for the other taxa belonging to the *C. furcifer* group shows evidence for the presence of some ornamentation structures exclusive to this new species: (1) the papillary field on each sulcal rotula; (2) the double denticulated edge of each asulcal rotula; (3) the pair of pointed cylindrical papillae bearing a micropapillary field on top (Fig. 4). The double row of pointed papillae descending along the sulcal lips is not a feature exclusive to *C. vencesi*, since we observed the same ornamentation (Fig. 3) also in all the examined males of *C. marojezensis* (two from Marojejy and five from Masoala). This feature was overlooked by Brygoo *et al.* (1970a), when they described the peculiar hemipenis morphology of *C. marojezensis* in examining the

TABLE 1. Biometric measurements (in mm) of the type specimens of *Calumma vencesi* n. sp. and *C. vatosoa* n. sp. M, male; F, female; J, juvenile; SVL, snout-vent length; TL, tail length; HL, head length; HD, head depth; HW, head width; SD, socket diameter; AGD, axilla-groin distance.

Species	Status	Sex	Locality	SVL	TL	HL	HD	HW	SD	AGD
<i>Calumma vencesi</i> n. sp.										
MRSN R1690	Holotype	M	Ambolokopatrika	73.0	72.0	19.0	14.2	11.0	5.6	38.0
MRSN R1686.1	Paratype	M	Ambolokopatrika	70.0	64.0	18.0	13.0	9.6	5.8	39.0
MRSN R1686.2	Paratype	M	Ambolokopatrika	73.0	64.0	19.3	10.5	10.0	6.0	40.0
MRSN R1687.1	Paratype	M	Ambolokopatrika	68.0	67.0	18.0	12.0	10.5	5.6	38.0
MRSN R1687.2	Paratype	M	Ambolokopatrika	69.0	62.0	19.0	13.0	10.6	6.3	40.0
MRSN R1688	Paratype	M	Ambolokopatrika	70.0	68.0	19.8	12.0	10.6	5.2	38.0
MRSN R1689.2	Paratype	M	Ambolokopatrika	63.0	67.0	17.0	11.0	9.8	5.0	32.0
MRSN R1689.1	Paratype	F	Ambolokopatrika	60.0	56.0	17.3	10.0	9.4	5.4	30.0
MRSN R1689.3	Paratype	F	Ambolokopatrika	52.0	54.0	15.4	9.3	8.7	4.5	27.0
MRSN R1703.1	Paratype	M	Besariaka	67.0	73.0	21.5	11.5	9.9	6.0	33.0
MRSN R1703.2	Paratype	F	Besariaka	67.0	55.0	20.0	12.0	9.0	5.9	29.0
MRSN R1681	Paratype	F	Besariaka	71.0	63.0	19.5	11.0	10.0	6.0	36.0
MRSN R1682.1	Paratype	F	Besariaka	72.0	59.0	21.0	12.0	10.5	6.0	37.0
MRSN R1682.2	Paratype	J	Besariaka	45.0	30.0	13.5	8.5	7.5	4.0	21.0
MRSN R1685	Paratype	M	Tsararano	67.0	65.0	17.0	11.0	9.6	6.1	32.0
MRSN R1683.1	Paratype	F	Tsararano	56.0	55.0	16.8	10.2	9.0	5.0	27.0
MRSN R1683.2	Paratype	F	Tsararano	57.0	58.0	17.0	11.7	9.5	5.6	30.0
MRSN R1684	Paratype	F	Tsararano	68.0	54.0	17.0	10.7	9.4	5.5	42.0
<i>Calumma vatosoa</i> n. sp.										
MRSN R1628	Holotype	M	Tsararano	60.0	66.0	18.0	9.0	7.5	6.4	36.0

holotype (MNHN 1993.0160). We noticed the occurrence of this ornamentation both in the holotype and in the only paratype showing everted hemipenes (MNHN 1989.2873). In this respect, we consider it helpful to redescribe the hemipenis structure of this species using for the first time the terminology introduced by Klaver & Böhme (1986). The following description deals with the ornamentations observed in the specimen MRSN R1701: hemipenis (Fig. 3) clavate, calculated, capitate, sulcal lips divergent, caput ornamentation consists of: (1) a pair of sulcal rotulae; (2) a pair of asulcal rotulae; (3) a pair of rounded hypertrophic papillae in sulcal central position joined together to form a unique structure; (4) a pair of very long, pointed cylindrical papillae slightly enlarged on top, sited between the pair of sulcal rotulae and the pair of central papillae; (5) a double row of fifteen pointed, thin papillae of various sizes respectively starting on the left and the right of the pair of central papillae, and descending along the sulcal lips. Hemipenis length around 14 mm, i.e. 22% of SVL. Within the caption of Fig. 3, which compares hemipenis ornamentations of *C. vencesi* n. sp. and *C. marojezensis*, the identification of presumably homologous structures has been suggested following the guidelines already proposed by Klaver & Böhme (1986). In this context, we consider homologous the pair of hypertrophic papillae with the unique structure made by their fusion, and the respective pairs of sulcal rotulae, asulcal rotulae, and pointed cylindrical papillae. In terms of the double row of pointed papillae on the sulcal lips occurring in *C. vencesi* n. sp. and *C. marojezensis*, it appears that this is a structure maintained in a very conservative way in both species. It is difficult to establish whether all these characters might be considered as plesiomorphic, and whether the long and pointed papillae in *C. vencesi* n. sp. are apomorphic characters. Further studies and comparative analyses in this area are badly needed.

Whereas the absence of the rostral appendage in *Calumma vatosoa* n. sp. and the double, ventral white lines makes it unlikely that the species would be confused with *C. furcifer*, it is clearly different from *C. gastrotaenia*, *C. marojezensis*, *C. guillaumeti*, *C. andringitraensis* and *C. glawi* due to different head morphology and, again, the absence of the double ventral white line. The general morphology apparently shares some similarities with *C. peyrierasi*, this being confirmed by some affinities in hemipenis ornamentation (a pair of large apical rotulae; a pair of asulcal rotulae in lateral position; two pairs of papillae in latero-sulcal position, each of them showing the external one as shorter). The description and the drawings of the hemipenis structure of *C. peyrierasi* are reported by Brygoo *et al.* (1974). Nevertheless, *C. vatosoa* n. sp. reaches a larger size than *C. peyrierasi* (126 mm compared to 110 mm), and has a flattened helmet extending caudally (the occiput is heightened in *C. peyrierasi*), canthi rostrales which – even though joined at snout tip

– do not limit a depressed area, and no dorsal crest. Finally, a comparison with *C. vencesi* n. sp. reveals obvious differences: the holotype of *C. vatosoa*, besides lacking ventral lines, dorsal crest and rings on fingers, is in fact characterised by heterogeneous scalation and joined canthi rostrales. Further evidence for treating MRSN R1628 as a new taxon comes from the comparison of hemipenis ornamentation: the third pair of rotulae observed in this specimen has not been found in any other *Calumma* species so far described.

MORPHOMETRIC OBSERVATIONS

Within *Calumma vencesi* n. sp., males are in general larger than females (Table 1). The adult specimens of the typical series showed that males and females have a mean SVL \pm SD of 68.9 \pm 3.1 mm and 62.9 \pm 7.6 mm respectively. These values are significantly different ($t=2.19$; $df=15$, $P<0.05$). The same significance was found for other biometric parameters, such as tail length, head depth and axilla-groin distance. Conversely, we did not find any significant difference in biometric ratios, although these are usually higher in males. This suggests, at least according to the limited number of specimens examined, that in this species males differ from females mainly in general body size, rather than in development of the morphometric characters analysed. Most likely a different body size, associated with behaviour and coloration, are sufficient to ensure male-female recognition in the wild.

Calumma vencesi n. sp. appears to be the largest member of the *C. furcifer* group analysed by us, with a maximum SVL of 73.0 mm (Table 2). In terms of body length, *C. vencesi* n. sp. is followed by *C. marojezensis*, *C. gastrotaenia*, *C. andringitraensis* and *C. guillaumeti*. *Calumma furcifer* has been reported (Glaw & Vences, 1994) to reach a total length of 150 mm, which represents the highest value ever recorded in any species belonging to the *C. furcifer* group. *C. andringitraensis* and *C. guillaumeti*, as already stated, are typical high altitude taxa, therefore their small SVL may be related to their elevational preference. Almost nothing is known about the size range of either *C. vatosoa* n. sp. or *C. peyrierasi*, of which only two specimens are known.

Differences between the males of *C. vencesi* n. sp. and *C. marojezensis* concern the SVL, which is significantly different ($t=3.29$, $df=16$, $P<0.01$) and the head depth/head length ratio ($t=2.16$, $df=16$, $P<0.05$). *C. vencesi* n. sp. is also larger than *C. gastrotaenia* (68.9 \pm 3.1 versus 60.4 \pm 8.5 mm; $t=2.77$, $df=14$, $P<0.05$), while no other significant differences are found for the other parameters. The comparison between *C. vencesi* n. sp. and *C. guillaumeti* (three measured specimens) shows significant differences regarding all the lengths, which seems obvious taking into account the remarkable diversity between these two taxa (*C. guillaumeti* has a mean SVL which more or less corresponds to 77% of *C. vencesi* n. sp.).

Females of *C. gastrotænia* are smaller in SVL (49.0 ± 4.35 mm) than females of *C. vencesi* n. sp. (62.9 ± 7.6 mm; $t=2.94$, $df=15$, $P<0.05$), which differ also for the socket diameter / SVL ratio (0.10 ± 0.01 versus 0.09 ± 0.01 ; $t=3.25$, $df=9$, $P<0.01$). Conversely, female *C. marojezensis* and *C. vencesi* n. sp. do not differ in general lengths, while they show significant differences in the axilla-groin distance (37.6 ± 2.8 mm versus 32.3 ± 5.5 mm; $t=2.56$, $df=15$, $P=0.05$) and in axilla-groin / SVL ratio (0.58 ± 0.03 versus 0.51 ± 0.05 ; $t=3.45$, $df=15$, $P=0.01$).

It therefore appears that, with a few exceptions, differences between sexes and species lie mainly in size. The group appears to be extremely conservative in terms of coloration, ecology and morphology, and – for this reason – identification in the field is somewhat difficult. Thus, we can reasonably hypothesize that other undescribed taxa remain to be discovered within the *C. furcifer* group, especially in the territories of central and south-eastern Madagascar.

KEY TO THE MALES OF THE *CALUMMA* *FURCIFER* GROUP

Here we provide an identification key to the males of the *Calumma furcifer* group, based mainly on the external morphology (thus excluding hemipenial characters), coloration, and provenience. The females of this groups are substantially similar, and it is extremely difficult to identify diagnostic characters. Furthermore for many species they are still unknown.

1. Bifid rostral appendage..... *Calumma furcifer*
No rostral appendage..... 2
2. One longitudinal stripe or no stripes at all at mid-venter.....3
Two parallel white longitudinal stripes at mid-venter5
3. Nuchal fold..... *C. glawi*
No nuchal fold.....4
4. Dorsal crest well developed.....*C. peyrierasi*
No dorsal crest.....*C. vatosoa* n. sp.
5. Dorsal crest well developed at least on the anterior two-thirds of the body.....6
Dorsal crest absent, or if present, slightly developed and not exceeding the anterior two-thirds of the body.....7
6. Helmet well developed and swollen on the occiput, white spots on the flanks usually arranged in one row, under 1100 m altitude, probably central-eastern Madagascar.....*C. gastrotænia*
Helmet normally developed and flattened on the occiput, white spots on the flanks usually arranged in two or more rows, between 1200 and 1700 m altitude, likely only in N. Madagascar (complex Tsaratanana-Marojejy-Anjanaharibe-Sud).....
.....*C. guillaumeti*
7. Very distinct mid-ventral white stripes starting at the tip of the chin (Andringitra Massif, 1500 m).....
.....*C. andringitraensis*

- Mid-ventral white stripes slightly distinct anteriorly to the insertion of forelegs, well distinct posteriorly to it.....8
8. Nuchal fold present, body comparatively well-developed vertically; oblique parietal profile.....*C. vencesi* n. sp.

No nuchal fold, body comparatively slender, sub-horizontal parietal profile..... *C. marojezensis*

DISCUSSION

The description of two new species of *Calumma* chameleon emphasizes, once again, how the Madagascan herpetofauna, although considerably diverse in species (182 amphibians and 333 reptiles according to Glaw & Vences, 2000) is still poorly known. Indeed, other species await discovery: producing descriptions is therefore a race against time, as species are habitat-specific, and the implacable deforestation affecting Madagascar makes it likely that many species will disappear before they are known to science.

The biogeographical importance of northern Madagascar is also confirmed by several other findings, including some dwarf *Brookesia* chameleons (Raxworthy & Nussbaum, 1995), skinks of the genus *Mabuya* (Nussbaum & Raxworthy, 1998), treefrogs of the genus *Boophis* (Andreone, 1996), a new *Pseudoxyrhopus* snake (Nussbaum *et al.*, 1998), and the second known specimen of the colubrid *Brygophis coulangesi* (Andreone & Raxworthy, 1998). This richness in species diversity is most likely due to several different causes, including (1) presence of many ecosystems, including rainforests and dry deciduous areas; (2) presence of many massifs (such as Anjanaharibe-Sud, Marojejy, Manongarivo, Tsaratanana, Montagne d'Ambre) which act as biogeographic refuges; and (3) the active survey work carried out by several teams in the last years.

The two new chameleons have been included in the *Calumma furcifer* group, which appears to be composed of two different phenetic clusters. The first is represented by the "*Calumma gastrotænia*-like" species, which include the former subspecies of *C. gastrotænia* (*C. gastrotænia*, *C. guillaumeti*, *C. marojezensis*, *C. andringitraensis*), *C. glawi*, *C. vencesi* n. sp., and possibly, *C. furcifer*. All these chameleons are green coloured, live mainly in primary rainforests (or in mature secondary rainforests), and generally show limited capacities to adapt to disturbed environments. The only possible exception to this ecological preference is represented by *C. gastrotænia*, which has sometimes recorded even on shrubby vegetation along asphalted roads and in areas in where selective logging has taken place (L. Brady, pers. comm.; F. Andreone pers. obs.). Moreover, with the exception of *C. furcifer*, these species do not have dermal appendages, and possess a body almost flattened laterally yet rather well-developed vertically. All the species exhibit overall similar ecological preferences, and occupy apparently analogous spatial, temporal, and trophic niches. They are often vicariant, either in terms of geo-



FIG. 5. Holotype (MRSN R1690, male) of *Calumma vencesi* n. sp. from Ambolokopatrika, N.E. Madagascar.

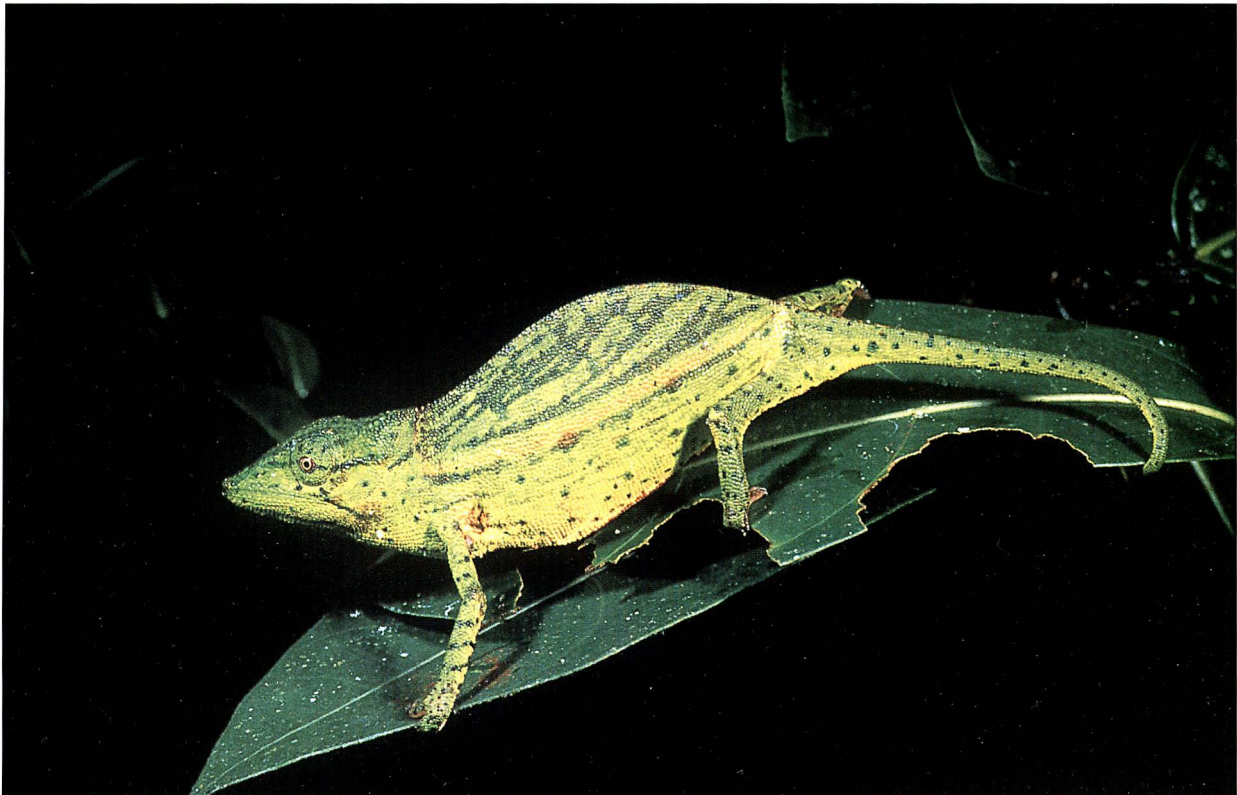


FIG. 6. *Calumma vencesi* n. sp. (PBZT-FN 6690, female) from Ambolokopatrika, N.E. Madagascar.



FIG. 9. Holotype (MRSN R1628, male) of *Calumma vatosoa* n. sp. from Tsararano, N.E. Madagascar.

graphical distribution or elevation. According to our knowledge, *C. gastrotaenia* is present in the central eastern rainforests, at low and mid-altitudes (Andreone, 1991a,b; Glaw & Vences, 1994; Brady & Griffiths, 1999). It is possible, on the other hand, that some *C. gastrotaenia* records belong to other taxa that yet have to be described. As an example, the recent works by Nussbaum *et al.* (1999) at Andohahela (S.E. Madagascar) provided evidence for the presence of *C. gastrotaenia*. Anyhow, it is not clear whether these authors follow Böhme's (1997) suggestion to consider former subspecies of *C. gastrotaenia* as full species. If this was the case, the *C. gastrotaenia* from Andohahela would correspond to the "old" *C. g. gastrotaenia*.

Apart from *C. gastrotaenia* (which has a wide distribution), the other members of this group from central-eastern Madagascar are *C. andringitraensis*, which is known for Andringitra Massif (Rasolonandrasana & Goodman, 2000), and *C. glawi*, from the Ranomafana area (Böhme, 1997). *C. glawi* is the only taxon known to occur in sympatry (likely in syntopy) with another species of the same group (namely *C. gastrotaenia*: L. Brady, pers. comm.). Observations of *C. glawi* at Ranomafana indicate that it is generally allotopic with *C. gastrotaenia*. Brady and co-workers (pers. comm.) observed both species at several locations within this national park. At Vatoharanana (the study area detailed by Jenkins *et al.*, 1999), only *C. glawi* was observed. However, at nearby Vohiparara both species occur together and are therefore syntopic.

All the other species are apparently restricted to N. Madagascar. According to current information,

Calumma guillaumeti is a high altitude species, which was found at 1200-1675 m on three massifs: Marojejy (Brygoo *et al.*, 1974; Raselimanana *et al.*, 2000), Anjanaharibe-Sud (Raxworthy *et al.*, 1998) and Tsaratanana (Jesu *et al.*, 1998; Mattioli, 1998). These findings suggest that the current distribution is due to the restriction of this species to refuge massifs. The hemipenis morphology of *C. guillaumeti* is different from that observed in the other taxa closely related to *C. gastrotaenia*. Interestingly, another species, *C. andringitraensis*, exhibits morphological and hemipenial characters which appear to make these two species very similar (Glaw & Vences, 1994; Mattioli, 1998). Like *C. guillaumeti*, *C. andringitraensis* has been found only at rather high altitudes (up to 1680 m on the Andringitra mountains; Raxworthy & Nussbaum, 1996). We are inclined to consider *C. guillaumeti* and *C. andringitraensis* as sister species, with a north-south vicariant distribution. In this sense they are similar to other taxa having this kind of distribution, such as the snakes *Pseudoxyrhopus sokosoko* and *P. heterurus* (Raxworthy & Nussbaum, 1994), the green treefrogs *Boophis jaegeri* and *B. andohahela*, the dwarf chameleons *Brookesia lolontany* and *B. nasus* (Raxworthy & Nussbaum, 1995).

Another species of this group, *C. marojezensis*, is restricted to northern Madagascar, but appears to be a lowland taxon. Up to now it has been recorded at Marojejy, Masoala, Anandrivola and, possibly, Anjanaharibe-Sud. Actually the last record, reported by Raxworthy *et al.* (1998), needs confirmation, since the re-examined specimens currently conserved at Torino

TABLE 2. Biometric measurements (precision at 0.1 mm) of adult males and females (juveniles are excluded) of the species belonging to the *Calumma furcifer* group, including the newly described *C. vencesi* n. sp. and *C. vatosoa* n. sp. For each taxon the mean± SD (1st row), and range (minimum and maximum values, 2nd row, in parentheses) are given. Abbreviations are given in Table 1.

Taxon	Number	SVL	TaL	HL	HD	HW	SD	AGD
<i>C. andringitraensis</i>	2MM	56.0±8.5 (50.0-62.0)	65.0±12.7 (56.0-74.0)	16.1±3.8 (13.4-18.7)	11.7±3.0 (9.5-13.8)	8.6±1.8 (7.3-9.8)	5.7±1.6 (4.5-6.8)	29.5±5.0 (26.0-33.0)
<i>C. furcifer</i>	1M	72.0	76.0	23.1	11.7	10	5.5	37.0
<i>C. gastrotaenia</i>	7MM	60.4±8.5 (46.0-73.0)	63.1±8.4 (48.0-74.0)	17.9±1.1 (16.6-19.4)	12.2±2.8 (7.5-15.0)	9.3±1.4 (6.6-10.5)	5.4±4.5 (4.8-6.0)	32.4±6.0 (22.0-42.0)
	3FF	49.0±4.4 (46.0-54.0)	46.0±1.0 (45.0-47.0)	14.7±1.5 (13.0-15.6)	9.3±1.3 (8.0-10.6)	7.1±0.8 (6.4-7.9)	5.0±0.6 (4.3-5.4)	28.0±5.3 (24.0-34.0)
<i>C. glawi</i>	1F	56.0	59.0	15.5	9.3	7.9	4.6	29.0
<i>C. guillaumeti</i>	3MM	53.3±4.2 (50.0-58.0)	53.7±5.9 (47.0-58.0)	15.9±2.2 (13.7-18.0)	10.1±1.5 (8.4-11.4)	8.0±0.8 (7.1-8.6)	4.6±0.3 (4.3-4.8)	27.0±2.6 (24.0-29.0)
	1F	56.0	52.0	16.0	10.5	8.0	4.5	25.0
<i>C. marojezensis</i>	9MM	63.6±3.7 (60.0-71.0)	63.0±5.8 (55.0-72.0)	16.9±1.7 (15.0-20.5)	9.6±0.7 (9.0-10.7)	9.1±4.5 (8.5-9.7)	5.8±0.9 (5.0-7.2)	35.1±4.1 (29.0-42.0)
	8FF	64.4±5.3 (55.0-72.0)	55.8±5.2 (47.0-61.0)	17.6±0.9 (16.5-19.0)	10.9±1.0 (9.2-12.5)	9.6±0.6 (8.8-10.7)	5.6±0.9 (4.7-7.4)	37.6±2.8 (33.0-41.0)
<i>C. vencesi</i> n. sp.	9MM	68.9±3.1 (63.0-73.0)	66.9±3.7 (62.0-73.0)	18.7±1.4 (17.0-21.5)	12.0±1.2 (10.5-14.2)	10.2±0.5 (9.6-11.0)	5.7±0.4 (5.0-6.3)	37.1±3.8 (32.0-42.0)
	8FF	62.9±7.6 (52.0-72.0)	56.8±3.1 (54.0-63.0)	18.0±1.9 (15.4-21.0)	10.9±1.0 (9.3-12.0)	9.4±0.6 (8.7-10.5)	5.5±0.5 (4.5-6.0)	32.3±5.4 (27.0-42.0)
<i>C. vatosoa</i> n. sp.	1M	60.0	66.0	18.0	9.0	7.5	6.4	36.0
<i>C. peyrierasi</i>	1M	49.0	61.0	15.0	11.4	7.0	4.9	24.0
	1F	50.0	37.0	14.3	10.2	8.0	5.0	29.0

actually all belong to *C. guillaumeti*, while specimens from lower altitudes are missing. Also the designation of *C. marojezensis* for Anandrivola (475-625 m) given by Raxworthy (1988) needs careful investigation, since this record apparently occurs within the distribution area of *C. gastrotaenia*.

The finding of a new species, *C. vencesi*, in the mountainous area around Andapa deserves more detailed comments. According to our data it is a mid-elevation taxon, present at Ambolokopatrika, Besariaka, and Tsararano. Since Anjanaharibe-Sud lies just midway between Ambolokopatrika and Besariaka, it is likely that the low altitude areas of this massif are inhabited by this species. Recent data for Marojejy by Raselimanana *et al.* (2000) indicate the presence of *C. marojezensis* at two lower transects (below 850 m), with *C. guillaumeti* from 1250 to 1675 m. In their survey there is a gap between 850 and 1250 m, due to the absence of study sites.

It is not unlikely, therefore, that the rainforests within this mid-altitude elevational range are occupied by *C. vencesi* n. sp. An alternative explanation could interpret this as a real absence, and in this case we may hypothesize that it might be due to a barrier effect

played by the Marojejy Massif. Indeed, this is similar to the case observed by Vences *et al.* (1999) and Andreone *et al.* (2000) for the dwarf *Zonosaurus* species: these authors found *Z. brygooi* in forests west of Marojejy – this species seems to be absent at Marojejy, where it is apparently replaced by *Z. rufipes* and *Z. subunicolor*. Further surveys are badly needed to confirm this hypothesis, especially with respect to the western slopes of Marojejy.

The second species cluster within the *C. furcifer* group is represented by *C. peyrierasi* (an apparently rare taxon endemic to Marojejy) and *C. vatosoa* n. sp. They are two obviously related species, yet rather different from the *C. gastrotaenia* cluster. In particular, *C. peyrierasi* and *C. vatosoa* n. sp. differ from these species in: (1) being not predominantly greenish in coloration; (2) having a body profile not particularly high; (3) being almost exclusive to the ericoid bush habitat of mid-high altitudes; (4) lacking a clearly defined double white belly line; (5) showing a very peculiar hemipenis morphology (especially *C. vatosoa*, which represents the only *Calumma* species exhibiting three pairs of rotulae). Although more detailed analyses are needed, we believe that *C. peyrierasi* and *C.*

vatosoa n. sp. are not so closely related to the species of the *C. gastrotaenia* complex, and possibly they should be included in a different phenetic group.

In terms of conservation, it is worth stressing that the presence of three species of the *C. gastrotaenia* complex, and of *C. peyrierasi*/*C. vatosoa* n. sp., in the massifs surrounding Andapa makes the north-east of Madagascar one of the most important geographic areas in terms of chameleon biodiversity. Parts of Anjanaharibe-Sud and Marojejy massifs are currently managed as protected areas (see Berner, 1995), and therefore this fact should assure some degree of protection to *C. guillaumeti*, *C. marojezensis* and *C. peyrierasi*. On the other hand, the two newly described species were found only outside these protected forests. As has already been suggested by Andreone *et al.* (2000), some protection should be given to Ambolokopatrika, Besariaka, and Tsararano forests. In particular, Ambolokopatrika appears to still retain good habitat (although "tavy" - i.e. "slash and burn" agricultural practice seems to be widespread), and it would be advisable to include it in the Anjanaharibe-Sud/Marojejy complex as the natural bridge between these massifs. This would give some protection to some of the *C. vencesi* n. sp. populations. Moreover, the importance of the Besariaka and Tsararano complex is due to the fact that, apart from the presence of both *C. vatosoa* n. sp. and *C. vencesi* n. sp. at Tsararano, these forests are also part of the important corridor which connects the Marojejy and the Anjanaharibe-Sud massifs to the large Masoala Forest. Conservation of these forests would also ensure the survivorship of the diverse faunas, floras and biotopes of the largest rainforest complex in Madagascar.

ACKNOWLEDGEMENTS

This survey work has been carried out within a project supported by WWF/ETP (Antananarivo), WCS (Antananarivo), MRSN (Torino), and Gondwana Research (Torino), aimed at monitoring some rainforest areas in N.E. Madagascar. Thanks to WWF and WCS staffs, Antananarivo, especially to S. M. Goodman, M. Hatchwell, O. Langrand, S. O'Connor, J.-P. Paddock, H. Rabetaliana, L. Ramarojaona, and to all the people in WWF at Andapa and WCS at Maroantsetra. We are also grateful to M. Madoglio, G. Fino, P. Lehmann, and A. Andriamanalina, who assisted in the production of the drawings and the map; to S. Ivaldi who translated some papers from German; and to G. Schimmenti who made valuable comments on the identification key. G. Aprea and G. Schimmenti accompanied us during our field surveys. W. Böhme, L. D. Brady, B. T. Clarke, G. Doria, A. Dubois, F. Glaw, A. Ohler, R. Poggi, and M. Vences were of help in loaning the specimens held in their institutions and in providing literature. C. Cummins and two anonymous referees reviewed a first draft of this paper and made useful criticisms. L. D. Brady, beside acting as a referee, was extremely kind in providing published and unpublished information. The

field work in Madagascar was possible due to the agreement of MEF and ANGAP, which provided the requested authorizations.

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Accepted: 11.12.00

APPENDIX: Specimens Examined

Calumma andringitraensis (Brygoo, Blanc and Domergue, 1972): MNHN 1993.0330-1 (626-7 C; A 330-1), holotype and paratype (MM), Ampanasana, 1530 m, Andringitra Massif, Fianarantsoa Faritany (Province), 17 January 1971, leg. C. P. Blanc.

Calumma furcifer (Vaillant & Grandidier, 1880): MNHN 1992.4410, Andekaleka, Toamasina (Tamatave) Faritany (Province), leg. F. Leberre; ZSM 314 2000, Vohidrazana, Toamasina (Tamatave) Faritany (Province), 10 April 2000, leg. F. Glaw; ZSM 315 2000, Vohidrazana, Toamasina (Tamatave) Faritany (Province), 10 April 2000, leg. F. Glaw.

Calumma gastrotaenia (Boulenger, 1888): MNHN 1899.0416, next to Suberbievilla, Boina, 23 October 1899, leg. J. L. Guillaumet and M. A. Grandidier; MNHN 1970.0382, Madagascar, leg. J. Arnould; MNHN 1974 1081, Natural Reserve XII, West Marojejy, 1140 m, Sambava, Antsiranana (Diégo Suarez) Faritany (Province), leg. P. Soga; MNHN 1996.0007, don. F. Girard; MRSN R1191, Périnet-Analamazoatra, 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), 1 May 1990, leg. F. Andreone and J. E. Randrianirina; MRSN R1702, Périnet-Analamazoatra, 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), 21 July 1998 leg. F. Andreone and J. E. Randrianirina. MZUT R660.1-2, "Umbi Valley", Andrangoloaka, 47°55'S, 19°02'E, 1386 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), leg. G. Pittarelli (?), don. M.G. Peracca; ZFMK 59810, (M), RS d'Ambositantely, Ankazobe Fivondronana, about 1500 m, Antananarivo (Tananarive) Faritany (Province), 7 April 1995, leg. F. Glaw and D. Vallan; ZFMK 60143 (F), RS d'Ambositantely, Ankazobe Fivondronana, Antananarivo (Tananarive) Faritany (Province), 7 April 1995, leg. F. Glaw and D. Vallan; ZFMK 50634,

Andasibe (likely Périnet-Analamazoatra), 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), leg. F. W. Henkel, W. Schmidt & V. Müller, May 1989; ZFMK 48190, Andasibe (likely Périnet-Analamazoatra), 18°56'S, 48°25'E, about 900 m, Fivondronana Moramanga, Toamasina (Tamatave) Faritany (Province), leg. F. W. Henkel & R. Seipp, April 1988; ZFMK 69998, Andraha (likely Mandraka);

Calumma marojezensis (Brygoo, Blanc and Domergue, 1970): MNHN 1989.2873 (529 C, 713), paratype (M), 14°26'S, 49°45' 40'E, about 700 m, Marojejy Massif, Sambava Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 30 December 1968, leg. C.P. Blanc; MNHN 1993.0160-2 (531 C, 712 and 714; A 160-2), holotype (M) and two paratypes (M and F), 14°26'S, 49°45' 40'E, about 700 m, Marojejy Massif, Sambava Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 30 December 1968, leg. C. P. Blanc; MRSN R1693.1-3, Forêt de Beanjada, 15°16.8'S, 49°59.8'E, 620 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 22 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1694, Forêt d'Andasin'i Gouvernera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 9 December 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1695, Forêt d'Andasin'i Gouvernera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 3 December 1998 leg. F. Andreone and J. E. Randrianirina; MRSN R1696, Forêt d'Andasin'i Gouvernera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 2 December 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1700, Forêt de Beanjada, 15°16.8'S, 49°59.8'E, 620 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 22 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1697, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 450 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 16 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1698, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 450 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 17 November 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1699, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 450 m, PN de Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 19.XI.1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1701, Forêt d'Andasin'i Gouvernera, 15°18.5'S, 50°01.4'E, 620 m, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 2 December 1998, leg. F. Andreone and J. E. Randrianirina; MRSN R1704.1-2, Corridor d'Ambatoledama, 15°17.00'S, 50°01.3'E, 500 m, PN de

Masoala, Antalaha Fivondronana, Antsiranana (Diégo Suarez) Faritany (Province), 3-9 September 1998, leg. J. E. Randrianirina; ZFMK 59795 (F), Marojejy above Camp 1 (about 300 m), Antsiranana (Diégo Suarez) Faritany (Province), 1 March 1995, leg. F. Glaw and O. Ramilison.

Calumma guillaumeti (Brygoo, Blanc and Domergue, 1974): MRSN R1691, Anjanaharibe-Sud, Campsite W1, 14°44'S, 49°25'E, 1000-1100 m, Befandriana Fivondronana, Mahajunga (Majunga) Faritany (Province), 25 January – 3 February 1996, leg. F. Andreone, J. E. Randrianirina and H. Randriamahazo; MRSN 1692.1-2, Anjanaharibe-Sud, Campsite W2, 14°46'S, 49°30'E, 1200-1600 m, Befandriana Fivondronana, Mahajunga (Majunga) Faritany (Province), 5-11 February 1996, leg. F. Andreone, J. E. Randrianirina and H. Randriamahazo;

MSNG 49104, Manarikoba Forest, WP 14, 14°02.4'S, 48°47.3'E, 1,300 m, RNI de Tsaratanana, Antsiranana (Diégo Suarez) Faritany (Province), 22 February 1997, leg. R. Jesu and G. Schimmenti.

Calumma peyrierasi (Brygoo, Blanc and Domergue, 1974): MNHN 1973.0440 (689 C), holotype (M), 1900-2000 m, Marojejy Massif, Antsiranana (Diégo Suarez) Faritany (Province), 30 November 1972, leg. C. P. Blanc; MNHN 1973.0441 (699 C), paratype (F), 1900-2000 m, Marojejy Massif, Antsiranana (Diégo Suarez) Faritany (Province), 30 November 1972, leg. C. P. Blanc.

Calumma glawi (Böhme, 1997): ZFMK 62882, paratype (F), Vohiparara, about 1000 m, Ambohimahasoa Fivondronana, Fianarantsoa Faritany (Province), 27 February 1996, leg. F. Glaw, D. Rakotomalala and F. Ranaivojaona.

EFFECTS OF AGE AND GROUP SIZE ON HABITAT SELECTION AND ACTIVITY LEVEL IN *RANA PIPIENS* TADPOLES

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Amphibian larvae may use both intrinsic cues – such as their own age, size or developmental stage – and extrinsic cues – such as chemical cues and group size – to make behavioural decisions. We performed a laboratory experiment to study habitat selection and activity level of *Rana pipiens* tadpoles at different ages and in groups of different sizes. Two ages of tadpoles were used: early (2 weeks after hatching; Gosner stage 25) and late (8 weeks after hatching; Gosner stages 36-38). Three group sizes were used: one, two and six. Tadpoles in pairs or groups tended to be more active and to occur in the open water column more than lone tadpoles. Younger tadpoles tended to use the open water column less and to be less active than older tadpoles, but there was no effect on the use of the vegetated habitat. Our results indicate that the determinants of amphibian larval behaviour include responses to both intrinsic (body size, age) and extrinsic (group size) cues.

Key words: activity, age, group size, habitat selection, *Rana pipiens*, tadpoles

INTRODUCTION

Amphibians appear to use cues (direct and indirect) to determine the appropriate behaviour for any given situation. The possibility exists that amphibian larvae use both intrinsic cues (e.g. their own age, size or developmental stage) and extrinsic cues (e.g. chemical cues and group size) to make behavioural decisions. For example, the presence of predators affects the behaviour of amphibian larvae in numerous ways (e.g. Anholt & Werner, 1995; Kupferberg, 1998; Lefcort, 1998). However, changes in age, size or developmental stage, or changes in the number of larvae in a given area, could alter the perception of predation risk, thus altering the behaviour of the larvae. Other factors potentially affecting tadpole activity and habitat selection include oxygen concentration, population density, water temperature, water depth, vegetation density, predators, time of day, and substrate type or pattern (Noland & Ultsch, 1981; Waringer-Löschenkohl, 1988; Johnson, 1991; Peterson, Bull & Wheeler, 1992; Kiesecker & Blaustein, 1998; Schley, Griffiths & Román, 1998; Nie, Crim & Ultsch, 1999). Understanding how behaviour (e.g. habitat selection, activity level) is determined, and what cues or factors influence this determination, is important for understanding the link between an individual's behaviour and the consequences of that behaviour on individual performance, population dynamics or community processes.

We performed an experiment to assess the effect of age and group size on habitat selection and activity level of northern leopard frog (*Rana pipiens*) tadpoles. Since amphibian larvae often respond to predator cues in such a way as to reduce predation risk (e.g. Anholt &

Werner, 1995; Kupferberg, 1998; Lefcort, 1998; including the southern leopard frog, *Rana utricularia*, Lefcort, 1996), we hypothesized that tadpoles may alter their behaviour in response to an intrinsic cue – age/body size – and an extrinsic cue – group size – in a manner consistent with adaptive anti-predator responses. The susceptibility of anuran larvae to predation often decreases with size (e.g. Semlitsch, 1990), thus we expected younger, smaller tadpoles to use habitats that may be perceived as less risky (e.g. increased use of a vegetated habitat, decreased use of the open water column) and to lower their activity level, decreasing predation risk (e.g. Skelly, 1994; Kupferberg, 1998). We predicted that tadpoles alone or in small groups would use less risky habitats and have lower activity levels when compared to tadpoles in larger groups, since the size of the group may influence the perception of predation risk – the larger the group the lower the individual's risk (e.g. Watt, Nottingham, & Young, 1997). We also expected that the effect of group size would decrease in older, larger tadpoles since the perception of risk would be lower; thus group size may not have any additional effect (i.e. we predicted a significant interaction term).

Younger and smaller tadpoles might also be predicted to swim less and use the open water column less simply because they may be less skilled or powerful swimmers than older and larger tadpoles (e.g. Chovanec, 1992; Brown & Taylor, 1995; Jung & Jagoe, 1995; McCollum & Leimberger, 1997). However, if this were the case we would expect no interaction term between group size and age class (i.e. young tadpoles are poor swimmers regardless of what size group they are in). Our controlled experimental design allows us to ignore possible explanations based on food distribution, temperature variability and oxygen availability.

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TABLE 1. MANOVA table for the effects of age/developmental stage and group size on the behavior of *Rana pipiens* tadpoles. For univariate tests, $\alpha=0.017$.

(1) MULTIVARIATE TEST				
	Wilks' Lambda	df	F	P
Age class	0.13	3,16	35.70	<0.0001
Group size	0.22	6,32	6.12	0.0002
Age class x group size	0.45	6,32	2.62	0.04

(2) UNIVARIATE TESTS			
	df	F	P
<i>Use of open water column</i>			
Age class	1	72.05	<0.0001
Group size	2	9.12	0.002
Age class x group size	2	9.12	0.002
Error	18		
<i>Use of vegetated habitat</i>			
Age class	1	0.01	0.93
Group size	2	1.88	0.18
Age class x group size	2	0.03	0.97
Error	18		
<i>High activity level</i>			
Age class	1	8.75	0.01
Group size	2	8.87	0.003
Age class x group size	2	0.002	1.00
Error	18		

MATERIALS AND METHODS

Rana pipiens range across the northern part of the United States and the southern half of Canada (Conant & Collins, 1991). They do not appear to form aggregations in the field or the laboratory (Wassersug, 1973). *Rana pipiens* is also apparently palatable to fish (Kruse & Francis, 1977). Other likely predators include macroinvertebrates such as immature odonates.

Rana pipiens eggs were obtained from the Carolina Biological Supply Company. Eggs were incubated at room temperature (19°C). Eggs hatched after 10 days of incubation. After hatching, tadpoles were kept in opaque plastic tubs in aerated, filtered, non-chlorinated water in a room maintained at around 19°C and on a 12L:12D photoperiod. Tadpoles were fed and containers cleaned daily.

Test arenas (3) were 19 litre aquaria each with a shallow bed of pebbles covering the bottom, with two larger rocks (20 - 30 cm in diameter, 2 - 4 cm thick) at one end of the tank to provide potential shelter and contrast with the gravel, and artificial vegetation (a mix of standard plastic aquarium plants; three "plants" per arena) placed at the other end of the tank; leaving an open area in the centre. The test arenas were filled half-full (9 litres) with filtered, non-chlorinated water (at room temperature c. 19°C). Lighting of the test arenas was achieved by hanging fluorescent lights about 20

cm above the tops of the aquaria. These lights were longer than the aquaria thus giving equal light to the entire test arena. After each trial, test arenas were emptied, cleaned and refilled to eliminate any potential chemical cues from previous tadpole(s).

The first set of trials (early) occurred two weeks after hatching (8-12 December 1997) when all tadpoles were free swimming (stage 25; Gosner, 1960). The second set of trials (late) occurred six weeks after the completion of the first set of trials (eight weeks post-hatching; 22-29 January 1998). Tadpoles in the second set of trials were stages 36-38 (Gosner, 1960). Tadpoles differed substantially in size between trials. Within each set of trials tadpoles were matched for size, and any tadpole that differed from the others in size or developmental stage was not used. Individual tadpoles were used only once in the entire study.

Each trial was begun by carefully placing the appropriate number of tadpoles (one, two or six) in the middle of the test arena and allowing 15 min for tadpoles to acclimate to the arena. Following the acclimation period, the position and activity level for each tadpole were noted at one minute intervals for 15 min (i.e. 15 observations per trial). Specific information collected included: (1) location in the tank (bottom = resting on the substrate or against walls of the aquarium, open = floating or swimming in water column); (2) habitat (rock, neutral, vegetated); and (3)

activity level (low = no movement, medium = some tail movement, high = actively swimming). Four replicates were performed for each tadpole density. Trials were typically run in the afternoon. Tadpoles were not fed during the trials; however, they did have constant access to food in their holding containers prior to a trial.

To analyse the data, we generated a mean proportion of tadpoles observed in each location, habitat, or at each activity level for a given trial, by averaging the proportions of tadpoles from each of the 15 observations per trial. For example, if all tadpoles were in the vegetation for 10 of the 15 observations and in the neutral area for the remaining five observations, the mean proportion in the vegetation would be 0.67, and the mean proportion in the neutral area would be 0.33. Thus for each trial we had a mean proportion for each location (bottom, open), habitat (rock, neutral, vegetated) and activity level (low, medium, high). Prior to analysis we transformed all proportion data with an arcsin square-root transformation.

Since the mean proportions within a behavioural category (e.g. location, habitat and activity) are not independent, we chose to use only a single variable in each category in the statistical analyses. Variables analysed were (1) use of open water column, (2) use of vegetated habitats, and (3) high activity levels (analyses with the other variables gave qualitatively similar results). These variables were chosen for analysis because they closely reflect our predictions: increased use of open water column and high activity levels would suggest increased use of risky habitats, whereas increased use of the vegetated area would suggest decreased use of risky habitat. We used a MANOVA to determine if any overall effect of the independent variables existed, and then univariate ANOVAs to test each behavioral category if the MANOVA indicated significant effects (see Scheiner, 1993).

RESULTS

Overall, there was a significant effect ($\alpha=0.05$) of age class and group size (MANOVA; Table 1). The interaction between age class and group size was also significant. Since there were significant multivariate effects we conducted univariate tests on each behavioral category (corrected $\alpha = 0.05/3 = 0.0167$).

Early tadpoles never used the open water column (Table 1; Fig. 1A). Lone tadpoles were less likely to be in the open water column than tadpoles in pairs or groups (Table 1; Fig. 1A). The difference between early and late tadpoles' use of the open area increased between single and multiple individuals (Table 1; Fig. 1A). The proportion of lone individuals using the open water column was similar for both early and late stage tadpoles, whereas for pairs and groups of six, late stage tadpoles used the open water column more than early stage tadpoles.

Age class and group size did not affect tadpole use of the vegetated habitat (Table 1). The interaction term was also not significant.

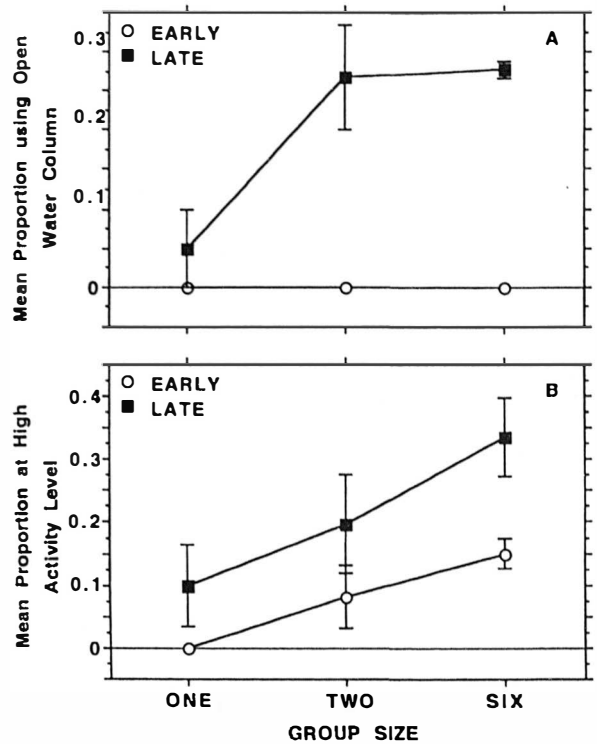


FIG. 1. The effect of age class and group size on mean (± 1 SE) proportion of observations of *Rana pipiens* tadpoles (A) in the open water column of the test arena, and (B) at high activity levels (actively swimming). Values are untransformed means.

Late tadpoles showed high activity levels more often than early tadpoles (Table 1; Fig. 1B). The proportion of time tadpoles spent at high activity level increased with group size for both early and late tadpoles (Table 1; Fig. 1B). The interaction between age and group size was not significant.

DISCUSSION

In our experiment, *R. pipiens* tadpoles altered their behaviour in response to extrinsic (group size) and intrinsic (age, stage or size) cues. Tadpoles in pairs or groups were more likely to be active and in the open water column than lone tadpoles that tended to be inactive and resting on the bottom.

Early tadpoles tended to stay at the bottom of the test arena and be less active than late tadpoles. However, early and late tadpoles did not differ in their use of vegetated habitats. Our results are similar to those from other studies. Puttlitz *et al.* (1999) found that *Hyla regilla* tadpoles changed their response to predators as they grew: tadpoles increased activity in the presence of a predator as they got bigger. Warkentin (1999) also found changes in antipredator responses with age in *Agalychnis callidryas* tadpoles, including microhabitat use and activity. Other studies have shown that responses to predator cues change with age in some anuran larvae (e.g. Brown & Taylor, 1995; Bridges & Gutzke, 1997). Large tadpoles may reach a size where they are no longer able to be eaten by a gape-limited predator (see Caldwell, Thorp, & Jervey, 1980;

Semlitsch, 1990); thus larger tadpoles may use riskier, more rewarding habitats or behaviours.

Our results might also be explained by differences in swimming performance between the early and late tadpoles. The younger tadpoles may be weaker swimmers (e.g. Chovanec, 1992; Brown & Taylor, 1995; Jung & Jagoe, 1995; McCollum & Leimberger, 1997), and thus swim less and use the open water less than older tadpoles. Indeed, the early tadpoles in our experiment had just become free swimming and may have avoided or not been able to exploit as well, habitats requiring active swimming – such as the open water column. This does not, however, explain the difference in the use of the open water column of older tadpoles in pairs and groups of six, and lone tadpoles (see Fig. 1A), nor does it explain the increase in high activity with group size in both early and late tadpoles (see Fig. 1B).

Single tadpoles avoided more risky habitats and behaviours, such as the open water column and high activity levels. Our results are similar to those of other researchers investigating anuran larvae. *Phrynomantis microps* tadpoles in a natural pond use vegetated habitats more when in small groups, whereas they use open water more when in large groups (Rödel & Linsenmair, 1997). Increasing group size increases activity level in some anuran larvae, both in the presence (Lefcort, 1998) and absence (Griffiths & Foster, 1998) of predator cues. Our results appear to be consistent with what would be expected if such behavioural shifts were selected to avoid predation. Larger groups may afford some degree of protection for individuals from predation (e.g. Watt *et al.*, 1997). Thus, individuals in larger groups may be more active, which is often beneficial as it facilitates foraging and may ultimately increase growth (e.g. Skelly & Werner, 1990; Kupferberg, 1998). Another explanation is that tadpoles in larger groups perceive the possibility of increased competition and increase activity and swimming (and thus also use the open water column) to increase foraging. Higher tadpole activity levels appear to be a characteristic of superior competitors (e.g. Werner, 1992, 1994), and activity level increases in low food situations where competition might be expected (e.g. Anholt & Werner, 1995).

ACKNOWLEDGMENTS

This paper constitutes a portion of the requirements for the senior author's Senior Thesis. We thank D. Hews, A. Laurila, and an anonymous reviewer for providing helpful comments on earlier versions of this manuscript.

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Accepted: 6.12.00

SHORT NOTES

HERPETOLOGICAL JOURNAL, Vol. 11, pp. 75-77 (2001)

EVIDENCE FOR DIURNALITY FROM AN EYE LENS CRYSTALLIN IN *CNEMASPIS* (REPTILIA, GEKKONIDAE)

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Key words: lizard vision, diurnal behaviour, eye lens crystallin

Geckos are small to moderate-sized, agile lizards occurring worldwide in tropical and subtropical regions (Gekkonidae *sensu* Kluge, 1967). The majority of gekkonid lizards are nocturnal; however, members of some genera are diurnal. Between the categories “nocturnal” and “diurnal” there are several intermediate conditions, e.g. crepusculo-diurnal geckos like the members of the genus *Sphaerodactylus* or the nocturno-diurnal species *Phelsuma guentheri* or the otherwise strictly diurnal genus *Phelsuma* (Langebaek, 1982).

According to Walls (1942), nocturnal geckos are supposed to have descended from primarily diurnal lizard ancestors whose visual cells had been cones, generally with coloured oil droplets. If so, the rod-like visual cells of extant nocturnal geckos have transmuted from cones. Regarding nocturnality as a derived character, Walls designated geckos as “secondarily” nocturnal. With few exceptions, their visual cells lack oil droplets (Walls, 1942; Underwood, 1970; Röhl, 2000a). Furthermore, Walls suggested that those gekkonid species which are now diurnal have reverted from nocturnal gecko ancestors and thus are “tertiarily” diurnal. Their visual cells have undergone a second transmutation from rod-like cells back to cones, most of which also lack oil droplets (Walls, 1942; Underwood, 1970; Röhl, 2000a). In those species that still have oil droplets in some of their visual cells, the oil droplets are transparent. There are no extant “primarily” diurnal geckos (Röhl, 2000b).

Yellow ocular filters, e.g. yellow oil droplets, are typically associated with diurnality (Lythgoe, 1979). They absorb potentially harmful ultraviolet and shortwave blue radiation. Walls (1942) suggested yellow lenses of some “tertiarily” diurnal geckos to be a substitute for coloured oil droplets. The yellow colour

of these lenses is caused by γ -crystallin, a water-soluble eye lens protein which is composed of the retinol-binding protein type 1 (CRBP 1) and the unusual chromophore 3,4-didehydroretinol (Röhl, Amons & de Jong, 1996; Röhl & Schwemer, 1999). γ -Crystallin occurs exclusively in lenses of diurnal geckos. Neither the retinol-binding protein nor the chromophore 3,4-didehydroretinol, also known as vitamin A₂, have been reported in lenses of other vertebrates.

On the other hand, nocturnal animals (including nocturnal geckos) have colourless eye lenses as it is essential to capture as many photons as possible under dim light conditions. In the daytime, e.g. when basking in the sun, nocturnal geckos close their movable iris, which then forms a characteristic slit pupil. However, diurnal geckos generally have a round pupil, and its diameter is virtually constant.

The gekkonid genus *Cnemaspis* comprises about 35 species which occur in equatorial Africa and from India to south-east Asia. Most species of *Cnemaspis* inhabit rain forests and are found on trees or on rocks near waterfalls or streams (Loveridge, 1947; Manthey & Großmann, 1997). Specimens have been observed basking during the day. When disturbed they quietly slipped into their retreats, which were usually close by (Loveridge, 1947).

When *Cnemaspis* has been described as a diurnal genus, this has often been based simply upon its round pupil, but not verified by behavioural observations, as criticized already by Smith (1935). Nevertheless, at least the Asian species *C. siamensis* appears to be partly diurnal (Taylor, 1963). On the other hand, Loveridge (1947) considered African forms of *Cnemaspis* to be crepuscular or nocturnal. Joger (1981) also reported the West African species *C. occidentalis* and *C. spinicollis* – despite their round pupils – to be nocturnal. However, more recent behavioural observations on Asian species of *Cnemaspis* suggest that these are predominantly diurnal or crepuscular (Denzer, 1996; Manthey & Großmann, 1997).

These contradictory descriptions of the activity cycle of *Cnemaspis* are probably due to the secretive habits of several species. Under laboratory conditions with a 12 hr light/dark cycle, *C. africana* remains extremely shy and hides most of the time in a hollow branch from where it watches for passing prey. When undisturbed during the day, it may sit outside its retreat – especially in the morning – but it will disappear immediately when slightly aroused. This extremely secretive behaviour is in marked contrast with that of members of other diurnal genera, e.g. *Lygodactylus*, *Phelsuma* or *Pristurus*. However, the behaviour of *C. africana* is quite different from a “typical” nocturnal gecko just basking in the sun. The pupil of *C. africana* is circular – as it is in its congeners and in typical diurnal geckos as well – and it is fully dilated during daytime (Fig. 1). Its narrow iris is light brown with a golden reflection.

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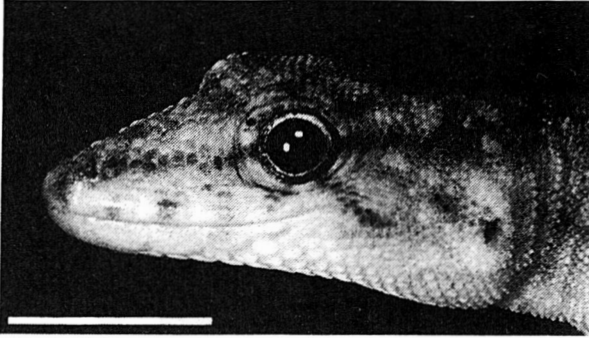


FIG. 1. Portrait of *Cnemaspis africana*. Note the large round pupil. The narrow iris is of golden-brown colour. Scale bar = 0.5 cm.

Nocturnal and diurnal gekkonid species differ in the biochemical compositions of their eye lenses. Nocturnal species have uniform crystallin compositions made up of the ubiquitous α -, β - and γ -crystallins and the taxon-specific δ - and τ -crystallins (the latter occur in all lizards). Further taxon-specific crystallins have been utilized by diurnal genera, e.g. π -crystallin by *Phelsuma*, *Rhoptropella* and *Rhoptropus*, ϵ -crystallin by *Phelsuma* and ι -crystallin by e.g. *Lygodactylus*, *Pristurus* and *Quedenfeldtia* (Röll, 1995; Röll & de Jong, 1996; Röll & Schwemer, 1999). The latter crystallin is especially interesting because of its physiological role as yellow ocular filter (see introductory paragraphs). A screening of the lenses of *Cnemaspis* for its crystallin composition in general and especially for the presence of any of the just mentioned taxon-specific crystallins seemed promising.

For examination, two eye lenses of *C. africana* were available. The eye lenses are definitely yellow, comparable with lenses of *Lygodactylus* and *Pristurus*. This colouring of the lens immediately suggests diurnal habits (see above).

For examination of the crystallin composition, lenses were homogenized in distilled water. Insoluble fractions were removed by centrifugation at 4 °C for 15 min at 15 000 \times g. Samples for gel electrophoresis were prepared in 50 mM Tris-HCl buffer, pH 8.8. After determination of the protein concentration, the samples were denatured in a solution containing 5% SDS, 2% mercaptoethanol and 10% glycerol with bromphenol blue and boiled for 3–5 min. Aliquots were run on 14% polyacrylamide gels containing 0.1% SDS. Protein bands were stained with Coomassie Brilliant Blue R-250 and scanned densitometrically. They were compared with those of species of the diurnal genera *Gonatodes*, *Lygodactylus* and *Pristurus* (Fig. 2). Additionally, Western blots of lens extracts were performed as described in Röll & Schwemer (1999). For identification of ι -crystallin, the blots were incubated with a monoclonal antibody against CRBP I.

The most abundant proteins in the lens of *C. africana* are δ -, τ - and β -crystallins (Fig. 2A). The subunits of the tetrameric δ -crystallin and the dimeric

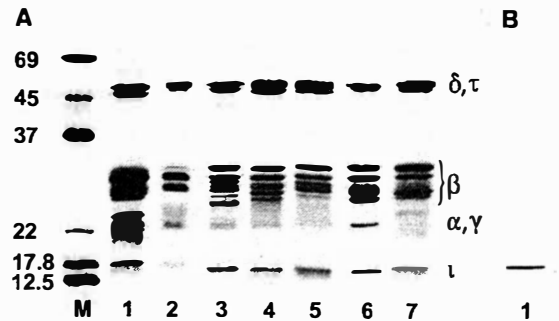


FIG. 2. A, Crystallin compositions of crude lens extracts of *Cnemaspis africana* and of other gekkos with yellow lenses. SDS gel electrophoresis (14% polyacrylamide) of water-soluble proteins (about 10 μ g per lane). Lane M: marker proteins (molecular weights in kDa); lanes 1–7: lens extracts of *Cnemaspis africana* (1), *Gonatodes albogularis* (2), *Lygodactylus capensis* (3), *L. chobiensis* (4), *L. tuberosus* (5), *Pristurus celerimus* (6), *P. sokotranus* (7). Composite of lanes from different gels. Greek letters mark the crystallins.

B, Western Blot stained with peroxidase using a monoclonal antibody against CRBP I. Lane 1: lens extract of *C. africana*, lane 2: lens extract of *L. chobiensis* (positive control).

or monomeric τ -crystallin have molecular weights of about 52 and 50 kDa, respectively. β -Crystallin consists of 4 different subunits in the range of 30–25 kDa. The monomeric γ -crystallin and the two subunits of α -crystallin cannot be recognized as clearly separated protein bands because of their similar molecular weights in the range of 19 to 22 kDa. These five crystallins are typical for nocturnal gekkonid and other squamate lizards (Röll, 1995). As in other diurnal gekkos the expression of α - and γ -crystallin is reduced.

In addition to these typical crystallins, the lens extract of *C. africana* contains ι -crystallin which induces the yellow colour of the lens (Fig. 2B). Depending on genus, ι -crystallin has an apparent molecular weight between 17 and 16 kDa. The different mobilities on the gel seem to be due to different amino acid compositions; e.g., the crystallin of *Gonatodes vittatus* deviates from that of *Lygodactylus picturatus* in seven amino acids out of 58 residues which have been sequenced (nearly one half of the whole protein) (Werten, Röll, van Aalten & de Jong, 2000).

In lenses of *C. africana* the content of ι -crystallin reaches about 6% of the total amount of crystallins. This is comparable with the amount of ι -crystallin in lenses of most species of *Lygodactylus* (Röll & Schwemer, 1999). In lenses of *Gonatodes* the amount of ι -crystallin reaches only 2–4% (Röll & Schwemer, 1999), but because of the high absorption coefficient of CRBP I this amount is sufficient to cause a yellow lenticular colour.

The yellow colour of the lens of *C. africana*, which is caused by the taxon-specific ι -crystallin, definitely points to *C. africana* being diurnal. This is based on two

lines of argument: all other genera possessing ι -crystallin are diurnal, and it has been argued that ι -crystallin is an autapomorphy of this group of genera because of its complex structure (Röll & Schwemer, 1999). Secondly, yellow ocular filters are characteristic for diurnal vertebrates and should be selected against in nocturnal animals.

So far, the crystallin compositions of eye lenses within a given gekkonid genus have proved to be very uniform (Röll, 1995; Röll & de Jong, 1996; Röll & Schwemer, 1999). Therefore, it is predicted that other species of *Cnemaspis* will also possess yellow lenses with ι -crystallin. Thus, the genus *Cnemaspis* as a whole is regarded as diurnal.

On the other hand, the monophyly of the genus is sometimes doubted because of the disjunct distribution of its members. Therefore, it would be interesting to examine Asian members of *Cnemaspis* for their lens crystallin compositions.

ACKNOWLEDGEMENTS

I would like to thank F.-W. Henkel for providing a specimen of *Cnemaspis africana* and Prof. Dr J. C. Saari for the gift of the monoclonal antibody against CRBP I.

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Accepted: 16.1.01

OBSERVATIONS ON THE NATURAL HISTORY AND MORPHOMETRICS OF THE MONTEPELLIER SNAKE, *MALPOLON MONSPESSULANUS*, ON LAMPEDUSA ISLAND (MEDITERRANEAN SEA)

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Keywords: snake, diet, morphology, conservation

Lampedusa is an offshore island of Sicily, approximately 20.2 km² in surface area (Fig. 1). From a geological point of view it is part of the African platform. Once covered by Mediterranean woodlands, the whole surface of this island is now entirely deforested, and characterized by stony and rocky formations (either man-made or natural) on grasslands, and uncultivated land (mainly degraded Mediterranean maquis). This small island is very important in ecological terms because of its rare and diverse wildlife (Meschini & Frugis, 1993), including several endemics (Massa, 1995 and literature cited therein). With regard to herpetofauna, Lampedusa is noteworthy because of some important peculiarities, including the fact that it is (1) an important reproduction site for marine chelonians (Bruno, 1986; Jesu, 1995); (2) one of the few Mediterranean islands without any representative of the family Lacertidae (Corti, Lo Cascio, Vanni, Turrisi & Vaccaro, 1997); and (3) is inhabited by only two species of snakes, i.e. the colubrids *Macroprotodon cucullatus* and *Malpolon monspessulanus* (Bruno & Maugeri, 1990; Corti *et al.*, 1997).

Natural history information on Lampedusa snake populations is very limited (Bruno & Maugeri, 1990). The presence of one species with a lizard-based diet, i.e. *Macroprotodon cucullatus* (e.g. see Bruno & Maugeri, 1990), and one with an ontogenetic shift from a lizard-based diet to a bird and mammal-based diet, i.e.

Malpolon monspessulanus (Pleguezuelos, 1997), on an island without lacertids and with introduced rat populations, may be of interest. It provides an excellent opportunity to test for the ecological adaptations of colubrids to Mediterranean environments characterized by a relatively small surface area and limited food resources. Therefore, we decided to start an ecological project on the snakes of Lampedusa, also in consideration of the fact that this island is currently under heavy pressure from tourism for the whole of the summer season, and its snake populations may likely be exposed to serious conservation threats (Corti & Luiselli, 2001).

In this report we offer (1) a preliminary morphometric analysis of Lampedusa specimens of the Montpellier snake (*Malpolon monspessulanus*) with comparisons with museum vouchers from other geographic regions; and (2) some notes on this species' natural history.

Detailed morphometric data on *M. monspessulanus* specimens from Lampedusa are not available in the literature, given also the extreme rarity of such specimens in museum collections (but see Lanza & Bruzzone, 1960). Consequently we measured all the specimens stored in the collections of the Zoological Museum "La Specola", Florence (MZUF), which is likely to store the highest number of Lampedusa specimens available in the world's public collections. In addition, we examined specimens in the collections of MSNG (Museo Civico Storia Naturale, Genoa) and of ZFMK (Zoologisches Forschungsinstitut und Museum A. Koenig Bonn). The specimens examined were labelled as follows: MZUF 585, 11352, 11353, 32640, 35108, 36591, 38063, 38066, 38067 (all from Lampedusa); MZUF 128, 7935, ZFMK 48836, 48839, 48840 (all from Cyprus); MZUF 1328, 1330, 6983, 6984, 10563, MSNG 48613 (all from France or north-western Italy); MZUF 9054, 23876, 33026, 36577, 38068 (all from the Iberian peninsula); MZUF 1249, 1250, 11337, 11338, 31677, 31678, 38064 (all from Croatia and north-eastern Italy); MZUF 1254, 2614, 12483, 19935, 29754; MSNG 30619, 30620, 31582, 36538, 37852, ZFMK 23042, 23044, 23047 (all from Tunisia, Egypt, and Israel).

Every museum specimen was measured (to ± 0.1 cm) for snout-vent-length (SVL), tail length (TL), head length (HL), head width (HW), interorbital length (INT-ORB), and number of ventrals.

Field research was conducted throughout several short-term survey periods by Massimo Capula, Giovanni Di Claudio, Lorenzo Rugiero (who kindly provided us with their unpublished observations) and Luca Luiselli between spring 1984 and autumn 1989; and by Claudia Corti and Stefano Vanni during spring 1991. These periods ranged from three to seven days each, from March to October, and involved searching for snakes along randomly selected paths.

Free-living specimens were individually marked by scale-clipping, measured for SVL (to ± 0.5 cm) and processed to determine their diet. The snakes were pal-

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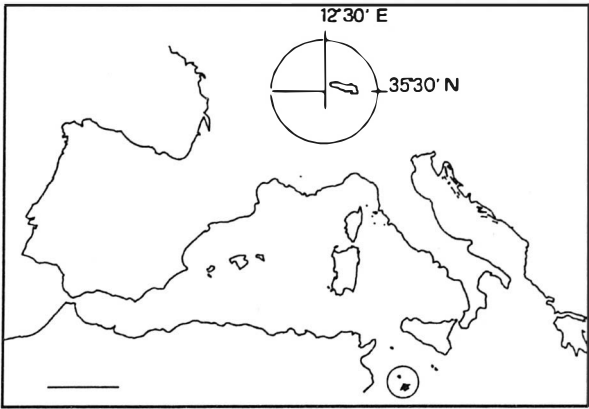


FIG. 1. Position of Lampedusa island in the western Mediterranean area. The line represents 500 km; the enlarged circle represents geographic co-ordinates of the studied island, from the small circle.

pated in the abdomen until regurgitation of the ingested food or defecation occurred. The prey items were identified to the lowest taxon possible. The snakes were then forced to reingest the disgorged prey. However, vouchers of some of the disgorged prey items are deposited in the herpetological collections of M. Capula and L. Rugiero (both collections in Rome).

Dorsal coloration of Lampedusa specimens >1000 mm SVL was normally uniform green or grey-green, whereas smaller specimens had many dark spots on a grey-greenish background. Moreover, females tended to be more spotted than males. These colour patterns were consistent in both the living ($n=17$) and preserved ($n=9$) specimens examined by us.

For morphometric analyses, museum voucher specimens were grouped into six geographical groups: (1) Lampedusa, (2) Cyprus, (3) France + NW Italy, (4) Iberian peninsula, (5) Croatia + NE Italy, (6) north Africa. SVL's of museum vouchers were not significantly different between sexes (Kruskal-Wallis ANOVA: $F=0.30$, $df=1,45$, $P=0.586$) or among geographical groups (Kruskal-Wallis ANOVA: $F=1.61$, $df=1,41$, $P=0.177$). Since SVL was significantly correlated with TL, HL, HW, and INT-ORB (in all cases at least Spearman's $r>0.6$, $P<0.0001$), residual scores from the general regressions of these parameters to SVL were used to test for size-corrected intergroup differences.

TABLE 1. Mean number of ventral scales of museum vouchers of *Malpolon monspessulanus* in relation to geographic area. Standard Deviations and sample sizes are also indicated. For statistical details, see text.

Locality	Mean± SD	Sample Size
Croatia + NE Italy	161.6±5.29	$n=7$
Cyprus	162.6±1.95	$n=5$
North Africa	168.5±2.74	$n=14$
Lampedusa	172.5±4.82	$n=9$
France + NW Italy	174.0±1.67	$n=6$
Iberian Peninsula	175.5±2.43	$n=6$

General MANOVA models indicated no effects on the regression of TL against SVL (independent variable) of both sex and locality (sex: $F=3.97$, $df=3,31$, $P=0.140$; locality: $F=3.19$, $df=3,31$, $P=0.185$). This means that males and females do not differ in terms of body proportions (i.e. tail length relative to body length), contrary to most snake species studied to date (e.g. cf. Shine, 1994). Neither is there any specific geographic variation in this general pattern. In this respect, our results fully agree with literature data (e.g. see Pleguezuelos, 1997, and literature cited therein).

However, there were important geographical variations in other morphometric and meristic traits. For instance, both sex and locality had significant effects on the regression of HL against SVL (general MANOVA - sex: $F=8.37$, $df=3,40$, $P=0.050$; locality: $F=36.66$, $df=3,40$, $P=0.0062$), and Tukey honestly significant *post-hoc* test (Sokal and Rohlf, 1981) indicated that (1) males had larger heads than females for the same body length, and (2) there were differences between areas in relative head size. Nevertheless, Lampedusa specimens were not distinctive (relatively to the average of the whole sample examined) in terms of head size patterns.

With regard to the number of ventral scales, there was no significant correlation between SVL and number of ventrals (Spearman's $r=0.226$, ANOVA: $F=2.42$, $df=1,45$, $P=0.126$). The mean number of ventrals in relation to geographic area is presented in Table 1. There was a very strong effect of locality on the numbers of ventrals (ANOVA: $F=17.84$, $df=5, 41$, $P<0.0001$), and general MANOVA models indicated that both locality and sex (as the covariates) significantly affected the regression of numbers of ventrals against SVL (locality: $F=48.53$, $df=3,42$, $P=0.0040$; sex: $F=113.36$, $df=3,42$, $P=0.0011$), with the interaction effect between sex and locality being also statistically significant ($F=77.58$, $df=2,42$, $P=0.012$). A Tukey honestly significant *post-hoc* test indicated that specimens from Spain, France and Lampedusa had significantly higher ventral counts for the same body length than specimens from North Africa, Cyprus and Croatia. The number of ventral scales is generally assumed to be an indirect way of counting vertebrae number, in both viperid (Saint Girons, 1978; Luiselli & Zuffi, 2001; Zuffi unpubl.), and colubrid species (Corti, Zuffi & Luiselli, 2000; Zuffi, 2000; Zuffi *et al.*, unpubl.). Significant differences may well lead to the critical re-evaluation of the taxonomic position of the involved taxon (Zuffi & Bonnet, 1999; Luiselli & Zuffi, 2001; Zuffi *et al.*, unpubl.). According to some authorities, *M. monspessulanus* should be divided into three subspecies (e.g. Bruno, 1986), or according to other authorities, into two subspecies (e.g. Pleguezuelos, 1997), but in both cases the Lampedusa population should be assigned to the same subspecies as the populations from North Africa, Sinai, and Palestine (ssp. *insignitus* Geoffroy Saint-Hilaire, 1827; Lanza & Bruzzone, 1960). Our data, even if preliminary, offer a quite heterogeneous, but furthermore

stimulating scenario throughout the whole species distribution range, and suggest that additional morphometrics and genetic research is needed before accepting the current taxonomic views on *M. monspessulanus*.

It is possible that natural colonization of wild *M. monspessulanus* on Lampedusa occurred well after the separation of the island from the African coastline, even though the open question remains about the migration route that *M. monspessulanus* could have followed. Alternatively, the Lampedusa population is the result of introduction(s) by man. Available data on non-flying terrestrial vertebrates, from which the zoogeography of the circum-Sicilian islands have been reconstructed, indicate a gradual orientation of corological categories in a north-west to south direction. The presence of southern European species decreases along this gradient, while western Mediterranean species increase in the same direction (Corti *et al.*, 1997). This set of results makes the presence of south-western species, such as *M. monspessulanus*, compatible with the faunistic composition of Lampedusa and the circum-Sicilian islands. On the other hand, even if compatible with the Lampedusa fauna, introduction by man can not be excluded for *M. monspessulanus*, as recently demonstrated for some other amphibian and reptilian taxa of this area (Böhme & Corti, 1993; Corti *et al.*, 1997).

Concerning Lampedusa specimens, faeces with identifiable prey items were removed from six specimens (five males and one female), and stomach contents from three additional males and three additional females. No identifiable food item was detected from juveniles. Faeces contained identifiable remains of rats (five specimens, one female and four males) and of an undetermined lizard (probably a *Chalcides ocellatus*). Stomach contents were all rats (five adults in five specimens, three females and two males; and newborns in another male snake). Although based on a small sample size, it is clear that Lampedusa *Malpolon* tend to prey almost exclusively upon small mammals, which represent an abundant resource in the environment (Corti *et al.*, unpublished observations). A rodent-based diet for *M. monspessulanus* is not surprising, as it is known in mainland regions. However, this species also consumes lizards, snakes, birds and mammals (e.g. see Naulleau, 1984; Pleguezuelos, 1997, and literature cited therein), which tends to confirm its status as an opportunistic species (Pleguezuelos, 1997).

In terms of conservation, our preliminary data suggest that *M. monspessulanus* is less uncommon in Lampedusa than *Macrotodon cucullatus* (Corti & Luiselli, 2001). However, an immediate monitoring project by the pertinent authorities is required to census the total population size on this Mediterranean island. We suggest that this project should work through some major research phases as already presented for Sardinian *Coluber hippocrepis* (Corti *et al.*, 2000). According to our own unpublished qualitative data, traffic

over busy roads, especially during the summer months, could affect the survival of large adult specimens. We believe that this could be the main threat to the populations of *Malpolon monspessulanus* on Lampedusa, as we have found some specimens squashed along the roads. Fortunately, this snake seems adaptable to altered habitats in Lampedusa, possibly as a result of its adaptation to a rat-based diet. Indeed, in Lampedusa rats are extremely abundant and are present virtually everywhere.

Given the small size of Lampedusa and its easily accessible environments, it is likely that it will be possible to obtain a good estimate of the whole population size of *M. monspessulanus* once this island is thoroughly surveyed.

Acknowledgements. We are indebted to W. Böhme (ZFMK), R. Poggi and G. Doria (MSNG), and M. Poggesi (MZUF), who permitted examination of specimens stored in the collections under their care, and to M. Capula, G. Di Claudio, L. Rugiero and S. Vanni for much unpublished data from their research. P. Lo Cascio helped with bibliographic citations. G. C. Akani, F. M. Angelici and M. Masseti critically commented on a previous draft. Trips to Lampedusa of C. Corti were supported by C.N.R. funds. Two anonymous referees critically revised and improved this paper.

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Accepted: 7.2.01

BOOK REVIEWS

The Lizards of Iran. Steven C. Anderson. (1999). vii+442 pp. Society for the Study of Amphibians and Reptiles, Ithaca, New York, USA. US \$65.00 (cloth).

This book is one of – if not the most – comprehensive disquisition of any group of reptiles from the middle or near east. It encompasses what is currently known about Iranian lizards and the biogeography of the region. It is long overdue since there is a great imbalance between, for example, the herpetological literature of Europe or North America and that of countries such as Iran and its neighbours. There are good reasons for this of course, the principal one being the exponential increase in herpetological activities in the Western Hemisphere in the last 20 years or so and the increasing political barriers between Iran and the West. Steven Anderson has gone some way to redress this situation with this first class treatise. It is the latest in a series of publications (volume 15) by The Society for the Study of Amphibians and Reptiles – a previous publication (volume 7) dealt with Iranian snakes (Latifi, 1991).

After an initial discourse on definitions and acknowledgements, the author gives a brief account of Iran's recent political history, a detailed account of its herpetological history and an introduction to the literature sources. On a point of pedantry, Samuel Gottlieb Gmelin is cited as the first European to have described the natural history of Iran in the 1770's but in fact Greek scientists in the service of the army of Alexander the Great had already surveyed the region in the fourth century BC. The botanical information from this expedition was incorporated into Theophrastus' *History of Plants* (Tarn & Griffith, 1966). However, since Gmelin's more recent survey a whole series of latter day field workers have provided detailed descriptions of the region's zoology and this chapter alone makes interesting reading. This is followed by an extensive and informative discussion on Iran's biogeography and ecology, particularly in the way that it is pertinent to lizards, in addition to a palaeographical history. Maps showing locations and illustrations of what Anderson defines as 'problematic specimens' accompany many of the species.

The lizard families covered are the *Agamidae*, *Anguidae*, *Eublepharidae*, *Gekkonidae*, *Lacertidae*, *Scincidae*, *Uromastycidae* and *Varanidae*. In his description of the *Uromastycidae* the author follows the classification of Moody (1987), who proposed that along with *Leiolepisis*, *Uromastyx* is a monophyletic group related to – but distinct from – all other agamid genera. Similarly the *Eublepharidae* are treated as a monophyletic subgroup of the Gekkota after Kluge (1987) and Grismer (1988). There is a description of each species, i.e. its maximum size, colour and general morphology followed by what is known of its natural history. This includes – at least when information is available – behaviour patterns, reproduction, feeding

habits and predators. Obviously there are gaps in this type of information for certain species, whilst in others there is good detail. Despite the variation in detail, however, I found all the information interesting and useful.

The final sections provide maps of the region (based on a satellite photograph); a series of photographs (143) on 18 plates showing lizards, and 38 photographs of their habitats on six plates. Not all the species described have accompanying photographs but the standard of the photography is generally high and all are in colour. However, some of the specimens shown appear to be either dead or are museum material. There is an extensive bibliography and three appendixes that deal with the abbreviations used in the text, the localities and sources of the material examined, and finally an index.

This book is written by a herpetologist for herpetologists; it is not one of those coffee table publications that are far to general to be really useful to the serious herpetologist. By bringing together information about Iranian lizards – many of which we still know relatively little about – in one volume makes this book especially valuable. The work is another in a succession of publications published by The Society for the Study of Amphibians and Reptiles, in its *Contributions To Herpetology* series. It certainly merits such a title since it is far more than a simple list of Iranian lizards. The information on climate, biogeography and historical aspects, in addition to the ecological background of the lizards, provides a valuable overview from a herpetological perspective. On a final note, I have to confess that I was unaware of the efforts of the Iranian Government in wildlife protection and conservation, and in sponsoring the field research of visiting scientists to Iran, particularly during the 1960s and 1970s.

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Der Kammolch. Ein Wasserdrache in Gefahr. Burkhard Thiesmeier and Alexander Kupfer (2000). 158 pp. Beiheft der Zeitschrift für Feldherpetologie 1. Laurenti-Verlag, Bochum. DM 44.00 (paper).

This monograph addresses the four crested newt super species: *Triturus cristatus*, the Northern crested newt, *T. dobrogicus*, the Danube crested newt, *T. karelinii*, the southern crested newt, and *T. carnifex*, the Italian crested newt. Emphasis is placed on the distribution, habitats and ecology of the Northern crested newt, the species occurring in Britain, Germany, and the main part of Northern and central Europe. Written by two experts on tailed amphibians (Thiesmeier is the publisher of Laurenti-Verlag and co-editor of the salamander volumes in the *Aula Handbuch* series of Amphibians and Reptiles of Europe; Kupfer contributes first hand information from fieldwork he has conducted in Germany), this little book is a well-researched summary of our knowledge of the natural history of the crested newt.

The first chapter describes the distribution of the species in some detail, including maps derived from more or less recent literature. It refers to the systematics and habitats of the four species and discusses questions regarding contact zones and regions where species overlap or hybridize. The chapter concludes with a description of aquatic and terrestrial habitats. The next chapter is devoted to the complex cycle of life in water and on land. Here a useful review is provided of the many studies of migration, orientation, site fidelity, aspects of life in water and on land, activity patterns, feeding, egg-laying, embryonic development and ecology of the larvae. Many examples are taken from case studies conducted in Germany, but ample reference is made to comparable studies from other countries, including Scandinavia, France, Great Britain and southern Europe. The following chapter on courtship and repro-

duction is somewhat shorter than the previous chapter, but again gives a readable, well-informed summary of what is known about the mating behaviour. The next chapter deals with aspects of population ecology, such as population size, sex ratio and growth. A separate chapter is devoted to the status of this newt, which is endangered in many areas, and refers to measures that are taken – or might be taken – to protect the species and its habitat. The book ends with a brief chapter on methods of recording the presence of the species and following its movements. A rich bibliography of thirteen pages and an index conclude the book.

Care and attention has been given to the production of the book: the colour photographs are of good quality; and the figures and maps are taken from the existing literature, including the illustration on the cover (which unfortunately makes for a cover that is not particularly eye-catching). Some minor errors, such as absence of a reference that is cited in the text but missing in the bibliography, are hardly worth mentioning. One might ask whether the authors are repeating in this volume the crested newt chapters in the forthcoming volume of the *Handbuch*. I expect, however, that the discussion of data in the present book is much more comprehensive than will be possible in the *Handbuch* and therefore assume that the latter will not compete with a monograph of this kind.

The text is well-written and on the whole well-balanced in terms of the information provided. The authors deserve our praise for compiling a wealth of data in this form. It would be very worthwhile to make an English translation of the book, for this treatise is attractive and informative enough to appeal to a wider readership of professionals and amateurs.

Max Sparreboom
The Hague

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised July 2000)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: *Full Papers* (no length limit); *Reviews* and *Mini-reviews* (generally solicited by a member of the editorial board); *Short Notes*; controversies, under *Forum* (details available from the Editor); and *Book Reviews*. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance. Authors should bear in mind that the *Herpetological Journal* is read by a wide range of herpetologists from different scientific disciplines. The work should therefore appeal to a general herpetological audience and have a solid grounding in natural history.
2. Three copies of all submissions, and illustrations, should be sent to the Scientific Editor. All papers will be subject to peer review by at least two referees. Authors are invited to suggest the names of up to three referees, although the editor may choose alternative referees to those suggested. Papers will be judged on the basis of the reports supplied by referees, scientific rigour, and the degree of general interest in the subject matter. The Editor's decision will be final.
3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer, and double-spaced with wide margins all round. The journal is typeset direct from the author's computer diskette, so all manuscripts should be prepared using a wordprocessor (preferably on a PC-compatible microcomputer). If figures are prepared using computer graphics, they should be supplied separately and NOT embedded in the text of the wordprocessor file. Preferred formats are MS Word for Windows (text) and MS Excel, Bitmap, TIFF, or JPEG files (graphics). It is not necessary to submit a computer diskette with the initial manuscript, but this will be required in the event of the manuscript being accepted for publication.
4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of five words or less, and the name and address of the corresponding author with (if available) an email address. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Keywords, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted. *Short Notes* (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text. A *sans serif* font (e.g. Universe or Helvetica) is preferred.
5. The usual rules of zoological nomenclature apply.
6. Tables are numbered in arabic numerals, e.g. TABLE 1; they should be typed double spaced on separate sheets with a title/short explanatory paragraph above the table. Horizontal and vertical lines should be avoided.
7. Line drawings and photographs are numbered in sequence in arabic numerals, e.g. FIG. 1. Colour photographs can only be included at cost to the author. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied camera-ready for uniform reduction of one-half on A4 size paper. Line drawings should be drawn and fully labelled in Indian ink, dry-print lettering or laser printed. Illustrations produced using other types of computer printer are not usually of suitable quality. A metric scale must be inserted in micrographs etc. Legends for illustrations should be typed on a separate sheet.
8. References in the text should be given as in the following examples: "Smith (1964) stated —"; "—as observed by Smith & Jones (1963)." "—as previously observed (Smith, 1963; Jones, 1964; Smith & Jones, 1965)". For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references the full title or standard abbreviations of the journal should be given. Articles 'submitted' or 'in prep' may not be cited in the text or reference list. The following examples will serve to illustrate the style and presentation used by the Journal.

Bellairs, A. d'A. (1957). *Reptiles*. London: Hutchinson.

Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* 2, 206–210.

Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83–101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* 216, 995–1002.
9. Final acceptance of a paper will depend upon the production by the author of a typescript, illustrations and computer diskette ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
10. Proofs should be returned to the Managing Editor by return of post. Alterations should be kept to the correction of errors; more extensive alterations will be charged to the author.
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