A multivariate analysis of the fringe-toed lizards of the *Acanthodactylus scutellatus* group (Squamata: Lacertidae): systematic and biogeographical implications

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The taxonomy of the fringe-toed lizards of the *Acanthodactylus scutellatus* group has long been unstable and no consensus exists on the systematic status of its various forms. A multivariate analysis of morphological characters, performed on over 1000 specimens from most of the African range of this group, allowed us to clarify the specific allocation of most of the Saharan populations included in this species group. Based on comparisons of morphology between allopatric and sympatric populations of this complex, we propose the recognition of six biological species. Our results confirm the specific status of *Acanthodactylus aureus*, *A. dumerili*, *A. scutellatus, A. longipes* and the recently described *A. taghitensis*. In addition, we re-validate *A. senegalensis* (occurring from Mauritania and Mali south to Senegal), which has been treated as a synonym of *A. dumerili* by previous authors. *Acanthodactylus longipes* is reported for the first time from coastal Mauritania, and *A. taghitensis* (previously known only from a very small region in Algeria) is reported from continental Mauritania. The systematic section of this paper includes a full list of examined material, diagnosis and known distribution of each species, in addition to some information on geographical variation and ecology. A key for specific identification is provided as an appendix.   © 2003 The Linnean Society of London, *Zoological Journal of the Linnean Society,* 2003, **137**, 117–155

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INTRODUCTION

The lizards of the genus *Acanthodactylus* constitute an important part of the vertebrate fauna in many arid and desert ecosystems in the Middle East and North Africa (e.g. Nouïra & Blanc, 1994; Shenbrot & Krasnov, 1997), where they are often the most conspicuous diurnal reptiles. As such, they have been the subjects of many ecological (e.g. Aljohany & Spellerberg, 1989; Mellado & Olmedo, 1991; Pérez Mellado, 1992; Perry & Dmi'el, 1994; Belliure & Carrascal, 1996) and behavioural (e.g. Perry *et al.*, 1990; Day *et al.*, 1999;

Sword *et al.*, 2000) studies. Following the confirmation than the long-recognized genus *Lacerta* actually consists of several genera (e.g. Fu, 1998; Harris *et al.*, 1998; Arribas, 1999), the genus *Acanthodactylus* is now the most specious one in the Lacertidae family, with as many as 36 species listed in the EMBL Reptile Database (http://www.embl-heidelberg.de/~uetz/ LivingReptiles.html). Most of these species live on the southern side of the Mediterranean basin and in the Arabian Peninsula, one of them reaching Europe (Iberian Peninsula), and the genus has spread east to western India and south to the Sahel zone in Africa (Salvador, 1982).

Given this remarkable diversity, it is hardly surprising that a large number of species are poorly known

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and that many systematic questions remain unresolved. As many as nine species listed in the EMBL Reptile Database were described after 1980. This systematic uncertainty does not only concern poorly studied taxa. Even the Israeli populations intensively studied under the name *Acanthodactylus scutellatus* (Audouin, 1827) were recently discovered to actually include two species (Y. L. Werner, pers. com., pers. obs.), a fact that stresses the need for a careful systematic analysis of any study population.

Several species groups have been recognized in the genus *Acanthodactylus* (Salvador, 1982; Arnold, 1983). The *scutellatus* species group has been defined by the following external characters: four rows of scales around toes and fingers; subocular plate not bordering the lip; fourth toe strongly pectinated; ventral scales in more or less oblique series; acuminate snout; and pale, often weakly contrasted coloration (Salvador, 1982; Arnold, 1983). Arnold (1983) added a set of additional characters which he considered derived: premaxillary most often with five teeth and ending abruptly; generally 23 or 24 presacral vertebrae with only slight variation between the sexes; fifth sternal rib interrupted in most specimens; the medial lobe of the hemipenis, medial branch of the sulcus, and medial side of the armature absent or greatly reduced; and the clavula ⊃-shaped in cross-section.

The *Acanthodactylus* of the *scutellatus* species group also share similar habitat requirements. All species are found exclusively in sandy habitats, from moving dunes in the erg areas to sand banks on hard or rocky substratum, with different habitat preferences between species. They are widespread over the Sahara (from the Senegal coast to Egypt), and east to Israel, the North of the Arabian Peninsula and Iraq. Although dealing with all the species of the *scutellatus* group, this study will focus on the situation in western Saharan Africa, especially in the country of Mauritania.

As many as three (Arnold, 1983) or four (Bons & Girot, 1964; Salvador, 1982) species have been assigned to the *Acanthodactylus scutellatus* species group. If all authors agree on the limits of the group, the systematic ranking of its various taxa differs between all revisions.

The *Acanthodactylus scutellatus* species group was first recognized, although not as a species group, by Boulenger (1921) in his 'Monograph of the Lacertidae', where he included the taxa *scutellatus*, *longipes* Boulenger, 1918; *audouini* Boulenger, 1918; *aureus* Günther, 1903; *inornatus* (Gray, 1838) and *dumerili* (Milne Edwards, 1829) as 'varieties' of *A. scutellatus*.

Bons & Girot (1964) recognized four species among the varieties of Boulenger: *Acanthodactylus scutellatus*, *A. inornatus*, *A. dumerili* and *A. longipes*. They maintained *audouini* as a subspecies of *A. scutellatus*,

along with the recently described *hardyi* Haas, 1957; AND treated *aureus* as a subspecies of *A. inornatus*. They described a new subspecies of *A. longipes* from south-eastern Morocco: *A. l. panousei* Bons & Girot, 1964.

Salvador (1982) also recognized four species within the *Acanthodactylus scutellatus* group, but they do not correspond exactly to the species established by Bons & Girot (1964). Salvador lumped all the populations treated as *A. inornatus* and *A. dumerili* by Bons & Girot under *A. dumerili*, with two subspecies (*A. d. dumerili* [corresponding to *A. dumerili*] and *A. d. exiguus* Lataste, 1885 [corresponding to *A. inornatus*]), and placed *A. inornatus* in the synonymy of *A. scutellatus*. He treated *A. aureus* as a distinct species, and recognized only two subspecies within *A. scutellatus* (*A. s. scutellatus* and *A. s. hardyi*), treating *audouini* as a synonym of *scutellatus*. Last, he treated *A. longipes* as a monotypic species; with *panousei* a synonym of *longipes*.

Arnold's (1983) treatment differs from Salvador's (1982) treatment in lumping into one taxon, called *Acanthodactylus scutellatus scutellatus*, all the populations included by Salvador in *A. dumerili* and *A. scutellatus*. Arguing that the variability was too high in these taxa and the distribution patterns too complex to recognize *dumerili* as a valid taxon, he placed *dumerili* and *exiguus*, as well as *audouini* and *inornatus*, in the synonymy of *scutellatus*. Arnold (1983) thus recognized three species within the *scutellatus* group: *A. scutellatus* (*A. s. scutellatus* and *A. s. hardyi*), *A. longipes* (monotypic) and *A. aureus* (monotypic).

Whereas Salvador (1982) and Arnold (1983) agreed on the recognition of *Acanthodactylus longipes*, Mellado & Olmedo (1990) had difficulty separating it from *A. scutellatus-dumerili*. Consequently, they included *A. longipes* in *A. scutellatus*, and only recognized *A. scutellatus* and *A. aureus* in Morocco, although they commented that *A. dumerili* may be distinct from *A. scutellatus*. Similarly, Blanc & Ineich (1985), in a study of southern Tunisian populations of the *scutellatus* group, reported a north–south continuum in several morphological traits from lizards similar to *A. inornatus* – a taxon considered by Salvador (1982) as a synonym of *A. scutellatus* – to others similar to *A. longipes*. They noted a high morphological variability within most of the populations studied, and concluded that the characters used to separate *A. longipes* from the others members of the *scutellatus* group, such as the length of the hind leg, are of limited use.

More recently, Baha El Din (1994) reported the discovery of *Acanthodactylus longipes* in Egypt, and insisted that it could be safely differentiated from *A. scutellatus*. Similarly, Bons & Geniez (1996) distinguished *A. longipes* from *A. dumerili* in Morocco, and

considered *A. scutellatus* to be absent from this country. Nouïra (1996), based on a detailed analysis of morphological characters, recognized three species of the *A. scutellatus* group in Tunisia: *A. scutellatus*, *A. dumerili* and *A. longipes*.

Last, Geniez & Foucart (1995) described a new species of the *scutellatus* group from Algeria, *A. taghitensis*, which is rather similar to *A. aureus* but has a completely allopatric inland distribution. Unfortunately, this description was based on only two specimens, one of which was not collected but photographed alive in the field.

One of the last contributions to the study of the genus *Acanthodactylus*, a partial molecular phylogeny based on mitochondrial DNA sequencing (Harris & Arnold, 2000), confirms the monophyly of the *scutellatus* species-group. Although the main subject of this work is not the species-level systematics, it also includes some information on the genetic distinctiveness of *A. aureus*, which fully supports the specific status of this taxon. *Acanthodactylus longipes* also appears as well differentiated from *A. scutellatus* (*sensu* Arnold, 1983, i.e. including all the populations classified in *A. dumerili* by Salvador). In fact, this comparison rests on one specimen of *A. longipes* from Egypt and one specimen of *A. dumerili* (following Bons & Geniez, 1996) from Morocco, and thus has a limited value when it comes to assess the status of these taxa. Last, the authors recommend in their introduction that *hardyi* be treated as a distinct species, *A. hardyi*, a proposition that they unfortunately do not explain.

The lack of consensus between the various authors having recently dealt with the systematics of the *Acanthodactylus scutellatus* group thus primarily concerns: (1) the validity of *A. longipes* and (2) the number of valid species in the populations included in *A. scutellatus* by Arnold (1983), and their name. These questions have never been addressed using rigorous morphological analyses of a large number of widely distributed specimens. Fortunately, we have at our disposal a large sample recently collected by one of us from the coastal region of Mauritania (I. Ineich; Projet C.C.E. DG VIII B7-5040, Biodiversité du littoral mauritanien, F. Colas [CIRAD] dir.). According to Salvador (1982) and Arnold (1983), two species of the *scutellatus* group occur in this area: *A. aureus* and *A. dumerili* (for Salvador, 1982) or *A. scutellatus* (for Arnold, 1983). When analysing these newly collected specimens, we became convinced that more than two forms occur within this area, and that some of these forms are sympatric in several locations (Ineich, 1996, 1997). We have thus undertaken a morphological analysis of our Mauritanian sample, comparing it with material from other areas in the Sahara, particularly Senegal, Western Sahara, Morocco and Tunisia, representing all of the previously or currently recognized species

within the *scutellatus* group. The aims of this study are to allocate taxonomically the material we have collected in Mauritania and to provide systematic and nomenclatural conclusions for populations of the *scutellatus* group occurring in the western part of the Sahara (east to Libya). We did not include in the present work enough material from further east (from Egypt to Israel and Arabia). Consequently, we do not discuss the validity of the various subspecies of *A. scutellatus* (*A. s. scutellatus*, *A. s. audouini* and *A. [s]. hardyi*) and their relationships although, based on a preliminary examination of a limited number of specimens from Egypt and Israel, we agree with Boulenger (1921) and Bons & Girot (1964) that *scutellatus* and *audouini* are distinct taxa. Only *A. s. audouini* will be included in the present study.

MATERIALS AND METHODS

MATERIAL EXAMINED, SPECIMEN IDENTIFICATION

The 1084 specimens of the *scutellatus* group analysed in this study (see Appendix 1) include 349 specimens collected from 50 Mauritanian localities situated along the coast. These localities extend from the extreme north point of the Cap Blanc peninsula to the southern Sahelian town of Dar es Salam, thus covering nearly the entire Mauritanian coastline (cf. Fig. 1). This sample was increased by 735 specimens from various Saharan or Sahelian localities (Niger, Senegal, Morocco, Algeria, Tunisia, Libya, Egypt and Israel) borrowed from museums or private collections. We also used our personal colour photograph collection to document some specific occurrences and gain additional information on the species's appearance in life.

As our aim was mainly to check the validity of taxa already recognized by several authors, we identified a priori most of our specimens using the most specious classification at hand. Specimens were thus initially classified into six taxonomic categories following the systematic hypotheses and characters of Salvador (1982): *Acanthodactylus dumerili dumerili*, 'intermediate populations between *A. d. dumerili* and *A. d. exiguus*', *A. d. exiguus*, *A. scutellatus scutellatus*, *A. longipes* and *A. aureus*. A seventh taxonomic unit, *A. taghitensis*, was only marginally present in our samples. These identifications were refined as we discovered additional diagnostic features. Some of the features used for identification were not included in our analyses because they only concern a small number of specimens (some features separating the three *A. taghitensis* from *A. aureus*) or are difficult to transcribe (head shape, skin aspect, general impression). They are mentioned in the Discussion (interpretation of the analyses) and Systematic review sections. For the multivariate analyses, we did not create operational taxonomic units (OTUs) by grouping a priori
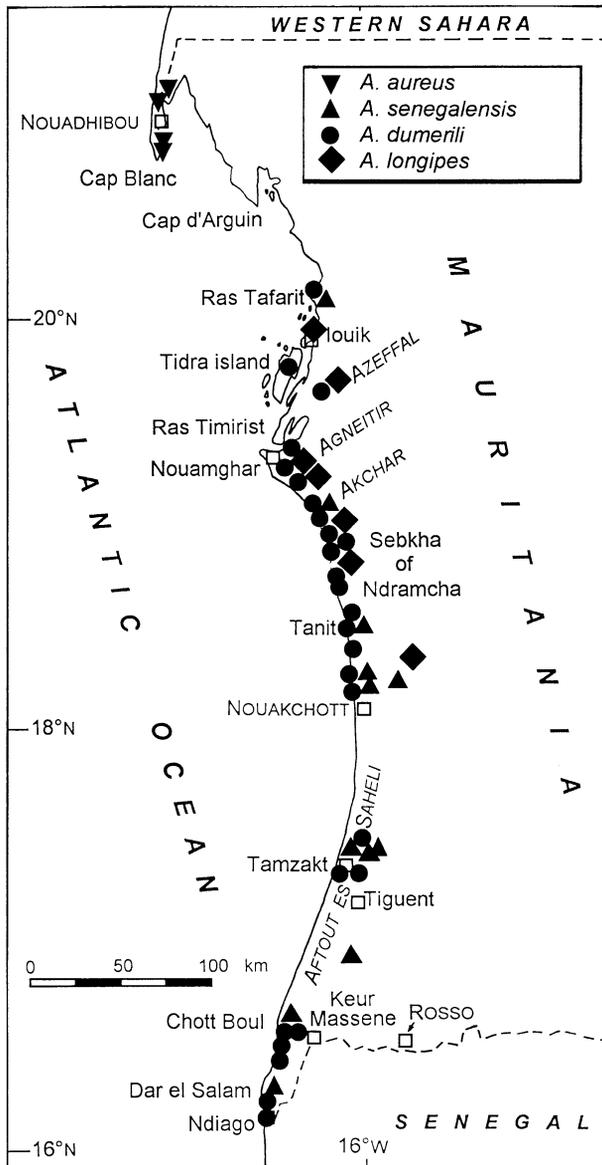
Figure 1. Locality of the stations where specimens of *Acanthodactylus* group *scutellatus* were collected in coastal Mauritania.

specimens originating from the same area because this procedure can mix several taxa in the same OTU. Each specimen was instead treated individually, and its position on the resulting scatter plots examined according to our hypothetical identification.

CHARACTERS STUDIED

Twenty-two characters were studied in this work (see Table 1). They came from scalation, body proportions and colour pattern. We counted the number of dorsal scale rows at mid-body (DORS) roughly at mid-distance between the insertion of forelimbs and hindlimbs. For the number of longitudinal rows of ventral plates (VENT), we counted the row bearing the highest number of plates (generally situated on the anterior third of the ventral side). The number of supraciliary granule rows (GRAN) is the number of granule rows running along the third supraocular plate. When the second row was incomplete, stopping somewhere along the edge of the third supraocular, we counted one and a half rows. Tail length (LOQU) was only measured on unbroken and non-regenerated tails. For the number of supralabials in front of the subocular (SUPR) and the number of supralabials in contact with the subocular (SUBO), we used the highest values when asymmetry was present. All specimens were examined, and all characters were recorded, by the same observer (P.G.).

For most multivariate analyses, only 12 of these 22 variables were used (DORS, VENT, VENL, GRAN, SUPL, SUBO, PORF, CARE, SVL, LOPI, COUL, CLAB, see Table 1). The variables discarded were either available for only a subset of animals, or were ratios (such as %LPI), which are useful to record shape differences but are entirely redundant when the original variables are entered in the analysis. No variable was transformed prior to the analyses. Classical transformations such as log-transformation can enhance the power of PCAs when there is a strong size effect with allometry. In our analyses, size is usually not a very strong component of the total variance. Strongly correlated variables (such as body length, SVL, and pileus length, LOPI) were used as such because PCAs are especially powerful in separating common (size) effects and shape effects (differences in slopes of relationships of pileus length on body length).

STATISTICAL ANALYSES – SYSTEMATIC INTERPRETATION

Means, standard deviations and ranges for quantitative characters can be found in Table 2, and the frequency of occurrence of each state of semiquantitative or qualitative variables in each sample is given in Tables 3 and 4.

The main multivariate method used in this paper is principal component analysis (PCA). Results of PCAs do not depend on a priori specimen classification. Several PCAs were run on various subsamples according to the questions outlined (see below). All characters were standardized (to zero mean and unit variance) prior to PCAs. In addition, one discriminant-function analysis (DFA) was used. With DFA, results depend on the a priori classification of the specimens, as the discriminant functions computed by the method are the linear combination of the original variables that maximize differences between given groups. It thus depends on which individuals are attributed to each group before the computation and is less parsimonious

Table 1. List of the morphological variables used in this study and their coding rules

Variable	Character	Numerical codes
DORS	Number of dorsal scales at midbody	x
VENT	Number of longitudinal rows of ventral plates	x
VENL	Number of transversal rows of ventral plates	x
GRAN	1 row of supraciliary granules	1
	1.5 rows of supraciliary granules	2
	2 rows of supraciliary granules	3
	2.5 rows of supraciliary granules	4
	3 rows of supraciliary granules	5
SUBO	Subocular in contact with 2 supralabials	2
	Subocular in contact with 3 supralabials	3
	Subocular in contact with 4 supralabials	4
SUPR	3 supralabials in front of subocular	3
	4 supralabials in front of subocular	4
	5 supralabials in front of subocular	5
PORF	Number of femoral pores right and left (average of both sides)	x
CARE	Dorsals smooth	1
	Dorsals weakly carinate on the vertebral area only	2
	Dorsals weakly carinate	3
	Dorsals well carinate	4
	Dorsals strongly carinate	5
	Dorsals flat and very strongly carinate	6
SVL	Snout-vent length of adults	x
LOQU*	Tail length (unregenerated tail only)	x
LTOT*	Total length of adults (with unregenerated tail only)	x
%LQU*	Percent ratio of tail length over total length	x
LOPI	Pileus length	x
%LPI*	Percent ratio of pileus length over snout-vent length	x
COUL	One colour in the dorsal pattern	1
	Two colours in the dorsal pattern, no dark elements	2
	Three colours in the dorsal pattern	3
	Two colours in the dorsal pattern, no pale spotting	4
CLAB	White labials	1
	Labials uniformly pale greyish	2
	Labials with light grey markings	3
	Labials with medium grey markings	4
	Labials with dark grey markings	5
	Labials with black markings	6
CGOR*	White throat	1
	Dark-coloured throat (grey to black)	2
CQUE*	Ventral tail side without reddish colouration	1
	Ventral tail side reddish or red coloured	2
SO1 (used in one DFA only)	First subocular (SO1) in full contact with the second subocular (SO2)	1
	SO1 and SO2 in partial contact	2
	No contact between SO1 and SO2	3
SO4 (used in one DFA only)	Fourth subocular (SO4) entire	1
	SO4 partially fragmented	2
	SO4 completely fragmented	3
GPRO (used in one DFA only)	Number of proximal granules between SO1 and SO2 (highest value when different on both sides)	x

*Not used in multivariate analyses.

Table 2. Means, standard deviations (in parentheses) and ranges of the quantitative variables used in this study. See Table 1 for variable definitions

Taxa	Variables		
	DORS	VENT	VENL
A. senegalensis	34–41.28 (3.50)–53 (*n* = 187)	10–11.99 (0.68)–14 (*n* = 188)	26–29.61 (1.26)–33 (*n* = 188)
A. dumerili (Mauritania)	40–46.94 (3.28)–58 (*n* = 256)	11–12.82 (0.91)–15 (*n* = 258)	27–31.03 (1.35)–36 (*n* = 256)
A. dumerili (Sahara)	39–51.74 (6.59)–69 (*n* = 184)	12–14.04 (0.71)–17 (*n* = 182)	28–32.06 (1.66)–38 (*n* = 183)
A. scutellatus audouini	39–53.40 (6.02)–69 (*n* = 92)	12–13.88 (0.70)–16 (*n* = 92)	29–32.03 (1.74)–36 (*n* = 91)
A. longipes	55–66.37 (5.49)–77 (*n* = 65)	13–16.14 (1.09)–19 (*n* = 65)	28–32.09 (1.78)–37 (*n* = 65)
A. aureus	38–46.74 (4.64)–59 (*n* = 86)	12–13.93 (0.82)–17 (*n* = 86)	28–30.51 (1.14)–34 (*n* = 86)
A. taghitensis	43–44.00 (0.82)–45 (*n* = 3)	13–13.67 (0.47)–14 (*n* = 3)	30–30.67 (0.47)–31 (*n* = 3)
	PORF left	PORF right	SVL
A. senegalensis	11–15.62 (1.75)–21 (*n* = 172)	11–15.65 (1.62)–20 (*n* = 178)	33.0–49.14 (3.40)–60.0 (*n* = 152)
A. dumerili (Mauritania)	15–18.73 (1.62)–23 (*n* = 236)	15–18.82 (1.57)–23 (*n* = 241)	39.0–47.70 (3.48)–55.0 (*n* = 151)
A. dumerili (Sahara)	16–20.02 (1.87)–26 (*n* = 170)	15–20.09 (1.80)–25 (*n* = 174)	39.5–50.23 (4.05)–63.0 (*n* = 159)
A. scutellatus audouini	16–21.04 (1.89)–26 (*n* = 90)	18–21.19 (1.68)–26 (*n* = 89)	43.5–58.24 (6.75)–72.5 (*n* = 75)
A. longipes	17–21.52 (2.28)–28 (*n* = 60)	17–21.40 (2.19)–28 (*n* = 63)	41.0–49.23 (4.46)–61.0 (*n* = 55)
A. aureus	17–21.27 (1.82)–26 (*n* = 83)	17–21.12 (1.79)–26 (*n* = 83)	36.5–49.21 (5.68)–65.0 (*n* = 85)
A. taghitensis	20–22.00 (2.16)–25 (*n* = 3)	21–21.67 (0.94)–23 (*n* = 3)	53.0–54.00 (1.00)–55.0 (*n* = 3)
	LOQU	LTOT	%LQU
A. senegalensis	73.0–91.50 (8.54)–111.0 (*n* = 61)	117.5–140.20 (9.94)–165.0 (*n* = 61)	60.5–65.23 (1.93)–70.6 (*n* = 61)
A. dumerili (Mauritania)	71.0–93.09 (11.18)–123.0 (*n* = 49)	112.5–140.19 (14.36)–178.0 (*n* = 49)	62.5–66.30 (1.60)–69.2 (*n* = 49)
A. dumerili (Sahara)	77.0–94.30 (10.13)–118.0 (*n* = 61)	123.0–143.80 (13.41)–173.0 (*n* = 61)	62.3–65.51 (1.55)–69.8 (*n* = 61)
A. scutellatus audouini	82.0–107.76 (17.47)–149.0 (*n* = 37)	127.5–165.50 (24.59)–217.0 (*n* = 37)	61.9–65.00 (1.34)–68.7 (*n* = 37)
A. longipes	75.0–91.71 (9.97)–115.0 (*n* = 28)	116.0–140.51 (13.65)–173.5 (*n* = 28)	62.7–65.21 (1.24)–68.1 (*n* = 28)
A. aureus	63.0–92.30 (14.07)–132.0 (*n* = 31)	102.0–142.20 (18.77)–192.0 (*n* = 31)	61.0–64.79 (1.81)–68.7 (*n* = 31)
A. taghitensis	103.0 (*n* = 1)	157.0 (*n* = 1)	65.6 (*n* = 1)
	LOPI	%LPI	
A. senegalensis	8.65–11.54 (0.70)–13.70 (*n* = 151)	19.70–23.50 (1.37)–28.30 (*n* = 151)	
A. dumerili (Mauritania)	10.00–11.73 (0.86)–14.00 (*n* = 162)	22.22–24.81 (1.04)–30.43 (*n* = 162)	
A. dumerili (Sahara)	8.00–12.29 (0.91)–14.30 (*n* = 164)	16.16–24.49 (1.22)–28.02 (*n* = 164)	
A. scutellatus audouini	11.00–13.82 (1.53)–17.50 (*n* = 78)	19.59–23.68 (1.05)–25.98 (*n* = 78)	
A. longipes	10.85–12.37 (0.93)–14.80 (*n* = 58)	23.00–25.32 (1.03)–27.96 (*n* = 58)	
A. aureus	9.90–12.40 (1.21)–16.00 (*n* = 84)	22.68–25.40 (1.05)–27.42 (*n* = 84)	
A. taghitensis	13.10–13.22 (0.10)–13.35 (*n* = 3)	23.82–24.48 (0.48)–24.91 (*n* = 3)	

Table 3. Frequency of occurrence of each class of the qualitative and semiquantitative variables except SO1, SO4 and GPRO. Variable definitions and coding as in Table 1. Bottom line indicates sample size for each character

	GRAN		SUPR		SUBO		CARE		COUL		CLAB		CGOR		CQUE	
A. senegalensis	1	45.7	3	0.0	2	0.0	1	0.0	1	0.0	1	6.6	1	100.0	1	100.0
	1.5	13.3	4	87.8	3	87.2	2	0.0	2	0.7	2	0.0	2	0.0	2	0.0
	2	39.4	5	12.2	4	12.8	3	0.0	3	99.3	3	10.6				
	2.5	0.5					4	5.9	4	0.0	4	13.9				
	3	1.1					5	5.3			5	5.3				
							6	88.8			6	63.6				
	n	188	*n*	186	*n*	188	*n*	188	*n*	152	*n*	151	*n*	151	*n*	188
A. dumerili	1	61.9	3	0.4	2	0.0	1	0.0	1	0.0	1	12.4	1	100.0	1	100.0
from	1.5	15.2	4	87.9	3	90.3	2	0.4	2	32.3	2	0.0	2	0.0	2	0.0
Mauritania	2	23.0	5	11.7	4	9.7	3	1.9	3	67.7	3	26.8				
and	2.5	0.0					4	69.5	4	0.0	4	20.3				
Western Sahara	3	0.0					5	17.8			5	7.8				
							6	10.4			6	32.7				
	n	257	*n*	257	*n*	257	*n*	259	*n*	155	*n*	153	*n*	259	*n*	259
A. dumerili	1	55.7	3	0.0	2	0.5	1	0.5	1	0.6	1	4.3	1	69.8	1	100.0
from	1.5	16.2	4	97.3	3	94.0	2	1.1	2	10.6	2	0.0	2	30.2	2	0.0
continental	2	27.0	5	2.7	4	5.5	3	10.8	3	82.6	3	19.6				
Sahara	2.5	1.1					4	61.4	4	6.2	4	15.3				
	3	0.0					5	26.4			5	9.8				
							6	0.0			6	50.9				
	n	185	*n*	184	*n*	184	*n*	185	*n*	161	*n*	163	*n*	106	*n*	184
A. scutellatus	1	51.1	3	0.0	2	1.1	1	1.1	1	0.0	1	5.1	1	50.9	1	79.3
audouini	1.5	18.5	4	92.5	3	90.3	2	0.0	2	1.3	2	2.5	2	49.1	2	20.7
	2	28.3	5	7.5	4	8.6	3	13.0	3	72.2	3	12.7				
	2.5	1.1					4	45.7	4	26.6	4	7.6				
	3	1.1					5	40.2			5	7.6				
							6	0.0			6	64.6				
	n	92	*n*	93	*n*	93	*n*	92	*n*	79	*n*	79	*n*	53	*n*	92
A. longipes	1	7.8	3	0.0	2	0.0	1	4.7	1	0.0	1	23.6	1	100.0	1	00.0
	1.5	6.3	4	85.7	3	88.9	2	79.7	2	45.5	2	0.0	2	0.0	2	0.0
	2	62.5	5	14.3	4	11.1	3	12.5	3	54.5	3	23.6				
	2.5	10.9					4	3.1	4	0.0	4	14.5				
	3	12.5					5	0.0			5	5.5				
							6	0.0			6	32.7				
	n	64	*n*	63	*n*	63	*n*	64	*n*	55	*n*	55	*n*	55	*n*	64
A. aureus	1	87.0	3	0.0	2	98.7	1	0.0	1	0.0	1	21.1	1	100.0	1	100.0
	1.5	10.4	4	87.0	3	1.3	2	0.0	2	6.6	2	23.7	2	0.0	2	0.0
	2	2.6	5	13.0	4	0.0	3	10.4	3	63.2	3	7.9				
	2.5	0.0					4	88.3	4	30.3	4	21.1				
	3	0.0					5	1.3			5	18.4				
							6	0.0			6	7.9				
	n	77	*n*	77	*n*	77	*n*	77	*n*	76	*n*	76	*n*	77	*n*	77
A. taghitensis	1	100.0	2	0.0	3	100.0	1	0.0	1	0.0	1	50.0	1	100.0	1	100.0
	1.5	0.0	3	100.0	4	0.0	2	0.0	2	0.0	2	0.0	2	0.0	2	0.0
	2	0.0	4	0.0	5	0.0	3	0.0	3	100.0	3	50.0				
	2.5	0.0					4	0.0	4	0.0	4	0.0				
	3	0.0					5	0.0			5	0.0				
							6	100.0			6	0.0				
	n	4	*n*	4	*n*	4	*n*	4	*n*	4	*n*	4	*n*	4	*n*	4

Table 4. Frequency of occurrence of each class of the variables SO1, SO4 and GPRO in a subsample of *Acanthodactylus dumerili* (mainly Tunisia) and *A. scutellatus* and sample size of each species for each variable (*n*)

Variable	Species	
GPRO	*A. dumerili*	*A. scutellatus*
0	58.4	13.8
1	7.7	8.6
2	20.5	19.8
3	4.4	7.8
4	3.4	8.6
5	1.7	4.3
6	2.3	10.3
7	1	6
8	0	5.2
9	0.3	3.4
10	0.3	5.2
11	0	1.7
12	0	0.9
13	0	1.7
14	0	1.7
16	0	0.9
n	298	116
SO1	*A. dumerili*	*A. scutellatus*
1	93.3	51.7
2	6.7	30.2
3	0	18.1
n	298	116
SO4	*A. dumerili*	*A. scutellatus*
1	48.7	30.2
2	37.6	32.8
3	13.8	37.1
n	298	116

than PCA. It has nevertheless a better discriminatory power and was used when PCA did not give conclusive results.

All these analyses were run on the computer program packages BIOMECO 4.2 (Lebreton *et al.*, 1990), PRAXIS 2.0 (Reboulet *et al.* 1995) and STATISTICA (Stat-Soft, Inc., Tulsa, USA). Only adult specimens were used in the multivariate analyses because strong ontogenic modifications in colour patterns were evident. Specimens of uncertain determination were not removed from the analyses because it would clearly remove specimens with intermediate morphology. Both sexes were usually treated separately, as preliminary analyses have shown that there are highly significant differences among sexes for most or all variables in every species (results not shown). The 12 variables used in multivariate analyses are listed in Table 1.

Our main concern in this study is to identify valid species within the *Acanthodactylus scutellatus* species group. We apply the Biological Species Concept, and thus look for evidence of reproductive isolation among sympatric taxa, that is for discontinuous – discreet or strongly bimodal – patterns of morphological variation. Multivariate analyses are powerful tools for this because they combine the information derived from several characters simultaneously. Whereas discreet patterns of variation for one character can be due to intraspecific polymorphism, the sympatric occurrence of more than one type of animals which simultaneously differ in several independent characters demonstrates reproductive isolation. In this paper, a clearly different distribution of individual scores along one or several multivariate axes (i.e. different distribution on bivariate plots) among sympatric individuals is interpreted as evidence of reproductive isolation. For allopatric taxa, use of the reproductive isolation criteria is not possible without experimental work. In the absence of any molecular phylogeny allowing to reconstruct history, we use amount of morphological differences between allopatric taxa as an indication of distinctiveness. We treat allopatric taxa that differ morphologically as much as sympatric species and are not linked by populations with intermediate sets of characters as valid species.

In addition to classical univariate statistics, the following multivariate analyses were done:
1 A PCA run on all specimens for males and females separately. It aims at investigating the morphological distinctiveness of *Acanthodactylus aureus*. This species is distinguished from all other members of the *scutellatus* group except *A. taghitensis* by the disposition of the supralabials (see systematic account), and the genetic data of Harris & Arnold (2000) indicate that *A. aureus* is specifically distinct from *A. longipes* and *A. dumerili* (*sensu* Salvador, 1982; synonymised with *A. scutellatus* by these authors). This analyses can thus provide a 'yardstick' to evaluate the power of the multivariate analyses we performed in retrieving patterns of morphological variation.
2 A PCA run on all specimens (males and females separately) of the *scutellatus* group except *A. aureus* and *A. taghitensis* because these taxa are clearly distinct from the other members of the *scutellatus* group (see above and results of the first PCA). This second analysis deals with the status of *Acanthodactylus longipes*.
3 A PCA on the North African populations of the *scutellatus* group attributed to *Acanthodactylus dumerili* and *A. scutellatus* by Salvador (1982), i.e. the following four categories: '*A. dumerili dumerili*', 'intermediate populations between *A. d. dumerili* and *A. d. exiguus*', '*A. dumerili exiguus*' and '*A. scutellatus scutellatus*'. Both sexes were analysed separately.
4 A DFA run on specimens of *Acanthodactylus dumerili* and *A. scutellatus* (males and females together) except specimens of '*A. dumerili dumerili*', as the pre-

vious analysis has shown this category to be a species distinct from both *A. dumerili* and *A. scutellatus*. Mauritanian populations of *A. dumerili* were also excluded because they differ significantly from the Saharan populations of the species in many of the characters used (see below). In addition to the 12 variables used in all PCAs, we used three variables provided by Nouïra (1996). This DFA was thus based on 15 variables. We used specimens from allopatric areas as references to tentatively identify the specimens coming for the proposed area of sympatry between the two forms prior to the DFA. The groups entered in the DFA were '*A. scutellatus*' and '*A. dumerili*', based on this initial tentative identification. Both males and females were treated together in this analysis, as results of DFA are sensitive to the number of specimens used. If the number of specimens is too low compared to the number of variables, DFA might be able to separate the groups even if they do not differ statistically in any of the characters used. As a rule of thumb, the number of specimens should be at least 10 times the number of variables. This was achieved in our case by pooling sexes. This might cause a loss of power but not provide misleading results because proportions of males and females are similar in each group.

5 A PCA dealing with geographical variation among populations of *A. dumerili* (excluding populations treated in previous analyses, i.e. using only populations classified by Salvador (1982) as *A. dumerili exiguus* and 'intermediate between *A. d. dumerili* and *A. d. exiguus*'). Both sexes were analysed together as some samples are small and would have been hardly usable if males and females were treated separately. Furthermore, PCA separates the variation among individuals due to differences among sexes and due to other factors such as specimen origin, so that in the worst case using both sexes together would only result in a loss of sensitivity. For the purpose of this analysis, *A. dumerili exiguus* specimens were grouped into seven geographical units: Mauritania, Western Sahara, Southern Morocco, South-eastern Morocco, Western Algeria, Central Algeria and Tunisia. Differences in PC scores among geographical samples were analysed using analysis of variance (ANOVA).

6 A PCA comparing the three available specimens of *Acanthodactylus taghitensis* to *A. aureus*. As for the previous analysis, both sexes were used together, as only three specimens of *A. taghitensis* (two males and a female) are available.

RESULTS

1. Acanthodactylus aureus

According to previous works, *Acanthodactylus aureus* can be distinguished from all other members of the *scutellatus* group except *A. taghitensis* by a peculiar head scalation: in this species two supralabials only are in contact with the subocular, as a result of the fusion of the third and fourth (rarely the fourth and fifth) supralabials. This character was absent in only one of the *A. aureus* in our sample ($n = 77$), and was present in only one *A. scutellatus* and one *A. dumerili* (out of 746 specimens that do not belong to *A. aureus* or *A. taghitensis*). In addition, we found other diagnostic characters in colour pattern and habitus (see systematic account below). *Acanthodactylus aureus*, based on our sample, is thus a clearly diagnosable and easy to identify taxon.

The PCAs for males ($n = 409$) and females ($n = 267$) of all taxa resulted in a separation of *Acanthodactylus aureus* from the other taxa along the third principal component (PC). The eigenvalue, percent of explained variance, and cumulated percent of explained variance for the first three PCs are given in Table 5 with the contribution of each variable to the PCs. The variables contributing most to the first PC are the same for both sexes: DORS, VENT and PORF on the positive side, and CARE on the negative side. The first PC thus separates, on the positive side, the specimens with a high number of dorsal scales, transversal rows of ventral scales, of femoral pores, and weekly keeled dorsals, and on the negative side, the specimens with low number of scales and femoral pores and strongly keeled dorsals. The second axis is essentially a size axis, with SVL and LOPI (body length and pileus length) having the highest contribution. The third axis, which separates the *A. aureus*/*A. taghitensis* specimens from the other species, is mainly explained by variation in SUBO. It separates the specimens with two supralabials in contact with the subocular (*A. aureus*/*A. taghitensis*, cf. supra) from the specimens with three supralabials in contact with the subocular (the other species).

The third PC neatly separates *Acanthodactylus aureus* (and *A. taghitensis*) from the other taxa. The bivariate plots of the PC2 and PC3 scores look very similar for males and females (Fig. 2). Specimens of *A. aureus* − *A. taghitensis* form a distinct cluster that shows very little overlap with the other taxa. As shown by the contributions of the variables to PC3 (Table 5), this separation is mainly due to differences in the character SUBO. The other two characters contributing to this axis are GRAN and CLAB (both with a positive correlation), indicating that *A. aureus* has also a higher number of supraciliary granules and darker labials than the other taxa. One male specimen clearly falls outside the cluster of its group: an *A. aureus* with three supralabials in contact with the subocular on one side only (specimen MNHN 1980.1519).

Table 5. Eigenvalues, percent of explained variance, cumulative percent of explained variance, and contributions of the variables to the factors for the first three principal components of a PCA run on specimens of all taxa (males and females separately)

		CP1	CP2	CP3
Males (*n* = 409)				
Eigenvalue		3.76	1.80	1.44
Percent of explained variance		31.2	15.0	12.0
Cumulated percent of explained variance		31.2	46.3	58.3
Contributions of the variables to the factors	DORS	**0.83**	−0.26	0.16
	VENT	**0.81**	−0.24	−0.02
	VENL	0.64	−0.13	0.16
	GRAN	0.13	−0.47	0.44
	SUPL	0.01	−0.05	−0.11
	SUBO	−0.10	−0.19	**0.84**
	PORF	**0.81**	−0.08	−0.19
	CARE	**−0.79**	0.34	0.17
	SVL	0.47	**0.73**	0.29
	LOPI	0.62	0.67	0.13
	COUL	0.02	0.52	−0.04
	CLAB	−0.19	0.17	0.56
Females (*n* = 267)				
Eigenvalue		3.23	2.04	1.47
Percent of explained variance		27.0	17.0	12.2
Cumulated percent of explained variance		27.0	43.9	56.2
Contributions of the variables to the factors	DORS	**0.83**	0.02	0.26
	VENT	**0.82**	0.14	−0.06
	VENL	0.50	0.01	0.33
	GRAN	0.23	−0.02	0.49
	SUPL	−0.12	0.04	−0.08
	SUBO	−0.14	0.03	**0.78**
	PORF	**0.79**	0.07	−0.25
	CARE	**−0.78**	−0.32	0.07
	SVL	0.18	**−0.87**	0.05
	LOPI	0.47	**−0.78**	−0.06
	COUL	−0.05	−0.67	−0.26
	CLAB	−0.16	−0.29	0.53

2. Acanthodactylus longipes

We could not find a single character that would alone unambiguously separate *Acanthodactylus longipes* from the other taxa of the *scutellatus* group. Nevertheless, a combination of several scale counts and a distinct habitus allowed a tentative identification of most individuals prior to multivariate analyses. When a PCA is run on each sex of all specimens excluding *A. aureus* and *A. taghitensis*, the bivariate plot of PC1 and PC2 clearly separates most specimens identified as *A. longipes* from the remaining animals (Fig. 3). Most of this separation is due to differences along the first axis, which account for about a third of the total variance in both sexes (see Table 6). This first axis is most correlated to the variables DORS, VENT, VENL and PORF on the positive side, and CARE on the neg- ative side (Table 6). Size also contributes somewhat to this axis (see contribution of SVL and LOPI in Table 6). The *A. longipes* specimens are thus charac- terized by high counts of dorsal and ventral scales, high number of femoral pores and weakly keeled dor- sal scales, in both males and females. Some non-*longipes* specimens share some of these characters, as they have about the same position along the first PC but most are separated from *A. longipes* by the second PC. This PC2 is mainly a size effect, but other vari- ables contribute to it, especially GRAN on the positive side and COUL, CLAB and CARE on the negative side. The specimens that fall close to *A. longipes* along the first axis are thus larger than this species, with more keeled dorsals, more colours on the back, darker labials and less supraciliary granules. A number of

○ *A. aureus + A. taghitensis*

▪ other taxa of the *scutellatus* group
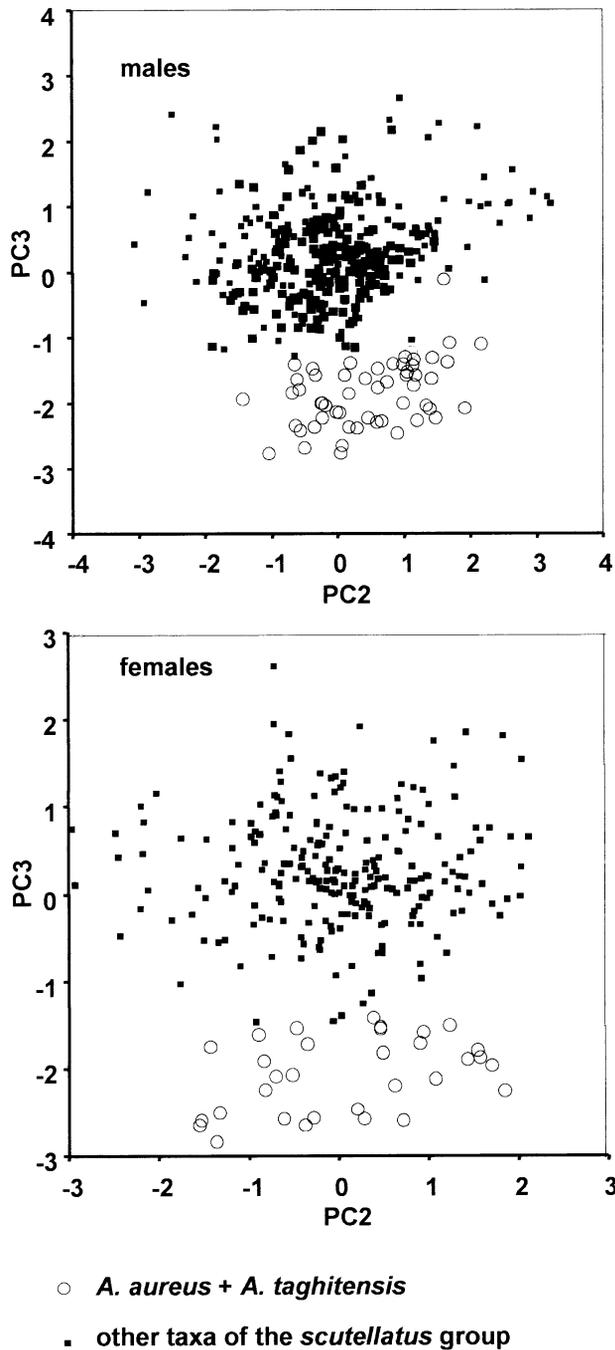
Figure 2. Bivariate plot of PC2 and PC3 scores generated by a PCA run on all adult specimens (males and females separately) using the 12 morphological variables (see Methods).

○ *A. longipes* from outside Mauritania

⊗ *A. longipes* from Mauritania

▪ *A. scutellatus + A. dumerili* sensu Salvador (1982)

Figure 3. Bivariate plot of PC1 and PC2 scores generated by a PCA run on all adult specimens except *Acanthodactylus aureus* and *A. taghitensis* (males and females separately) using the same 12 variables as in the previous analysis. Arrows indicate *A. longipes* syntypes.

individuals do not fall in the cluster where they would be expected according to their initial identification, but despite this limited overlap the *A. longipes* cluster is well distinct from the cluster of the other animals.

3. Acanthodactylus dumerili dumerili sensu Salvador, 1982

The PCA run on all specimens of the populations attributed to *Acanthodactylus dumerili* and *A. scutellatus* by Salvador (1982) neatly separates the specimens of *A. dumerili dumerili sensu* Salvador (1982) from specimens of all other populations. Most of the

Table 6. Eigenvalues, percent of explained variance, cumulative percent of explained variance, and contributions of the variables to the factors for the first three principal components of a PCA run on specimens of all taxa except *Acanthodactylus aureus* and *A. taghitensis* (males and females separately)

		CP1	CP2	CP3
Males (*n* = 366)				
Eigenvalue		3.90	1.93	1.20
Percent of explained variance		32.5	16.1	10.0
Cumulated percent of explained variance		32.5	48.6	58.5
Contributions of the variables to the factors	DORS	**0.87**	0.2	−0.13
	VENT	**0.82**	0.22	−0.14
	VENL	0.68	0.05	−0.02
	GRAN	0.20	0.44	−0.41
	SUPL	−0.02	0.11	0.10
	SUBO	0.03	−0.03	−0.57
	PORF	**0.83**	−0.10	0.08
	CARE	**−0.79**	−0.36	0.03
	SVL	0.47	**−0.77**	0.16
	LOPI	0.62	−0.68	0.19
	COUL	−0.05	−0.55	−0.48
	CLAB	−0.16	−0.37	−0.60
Females (*n* = 247)				
Eigenvalue		3.39	2.14	1.13
Percent of explained variance		28.3	17.8	9.4
Cumulated percent of explained variance		28.3	46.1	55.5
Contributions of the variables to the factors	DORS	**0.87**	0.03	−0.05
	VENT	**0.84**	0.10	−0.01
	VENL	0.52	0.03	0.01
	GRAN	0.28	0.01	−0.38
	SUPL	−0.12	0.04	−0.69
	SUBO	−0.17	0.05	0.64
	PORF	**0.79**	0.03	0.03
	CARE	**−0.80**	−0.28	−0.09
	SVL	0.16	**−0.86**	0.11
	LOPI	0.46	**−0.76**	0.10
	COUL	−0.12	**−0.72**	0.04
	CLAB	−0.12	−0.42	−0.26

separation is due to differences in PC1 scores, for both males and females (see Fig. 4). The variables contributing most to this separation are (see Table 7): DORS, VENT, VENL, PORF, LOPI and SVL on one side and CARE on the other. The first axis thus separates smaller animals with lower number of dorsal scales, ventral plates, femoral pores, and more keeled dorsals (*A. dumerili dumerili*) from the other specimens. The second axis separates, although not very well, the 'intermediate populations between *A. d. dumerili* and *A. d. exiguus*' (*sensu* Salvador, 1982) from the other animals. The 'intermediate' specimens are larger animals (negative loading of SVL and LOPI), with fewer colours on the back (negative loading of COUL), paler labials (negative loading of CLAB) and less keeled dorsals (negative loading of CARE) when compared to the other specimens.

These 'intermediate' specimens (called as such by Salvador, 1982) are in fact clearly not intermediate morphologically between *Acanthodactylus dumerili dumerili* and *A. d. exiguus* because they do not occupy an intermediate position in the PC1 × PC2 plan (see Fig. 4). They are much closer to the *A. d. exiguus* – *A. scutellatus* cluster, and largely overlap with it. Furthermore, on the second axis these 'intermediate' specimens are opposed to both *A. d. dumerili* and many *A. d. exiguus*, showing that they have their own characters and not a mixture of *A. d. dumerili* and *A. d. exiguus* characters.

4. Acanthodactylus dumerili exiguus (including the 'intermediate populations' of Salvador (1982) and Acanthodactylus scutellatus

Acanthodactylus dumerili (*sensu* Salvador, 1982) is

Table 7. Eigenvalues, percent of explained variance, cumulative percent of explained variance, and contributions of the variables to the factors for the first three principal components of a PCA run on specimens classified as *Acanthodactylus dumerili* and *A. scutellatus* following Salvador (1982) (males and females separately)

		CP1	CP2	CP3
Males (*n* = 330)				
Eigenvalue		3.93	1.65	1.22
Percent of explained variance		32.7	13.8	10.1
Cumulated percent of explained variance		32.7	46.5	56.6
Contributions of the variables to the factors	DORS	**−0.81**	0.18	−0.20
	VENT	**−0.76**	0.18	−0.15
	VENL	**−0.71**	0.24	−0.15
	GRAN	0.20	0.02	−0.62
	SUPL	0.10	0.13	0.31
	SUBO	−0.00	−0.22	−0.53
	PORF	**−0.84**	0.09	−0.02
	CARE	0.70	−0.42	0.11
	SVL	−0.62	−0.60	0.31
	LOPI	**−0.74**	−0.48	0.31
	COUL	−0.16	−0.61	−0.27
	CLAB	0.02	−0.55	−0.30
Females (*n* = 226)				
Eigenvalue		3.35	2.00	1.14
Percent of explained variance		28.0	6.6	9.5
Cumulated percent of explained variance		28.0	44.6	54.1
Contributions of the variables to the factors	DORS	**0.82**	0.10	−0.06
	VENT	**0.76**	0.17	−0.01
	VENL	0.56	0.29	0.21
	GRAN	0.05	−0.27	0.38
	SUPL	−0.18	−0.04	0.66
	SUBO	−0.22	0.08	0.66
	PORF	**0.77**	0.27	0.04
	CARE	−0.67	−0.41	0.13
	SVL	0.45	**−0.73**	−0.12
	LOPI	0.65	−0.59	−0.09
	COUL	0.19	−0.67	−0.13
	CLAB	−0.00	−0.45	0.15

not clearly separated from *A. scutellatus* by the characters used in our PCAs. On average, *A. scutellatus* is larger but the individual PC scores of both forms widely overlap (results not shown). There is a large overlap in dorsal scales number, an important character to separate these two forms according to Salvador (1982). However, animals from the eastern and southern Sahara (*A. scutellatus sensu* Salvador, 1982) clearly differ from the animals inhabiting central and western North Africa (*A. dumerili sensu* Salvador, 1982) in habitus and pileus coloration (see systematic account below). Based on our examination of the specimens we had, we gained the impression that the 'eastern' (= *scutellatus*) type and 'western' (= *dumerili*) type co-exist in Tunisia, a fact already recognized by Nouïra (1996). In addition to the characters outlined above, Nouïra (1996) suggests that differences in the head scalation separate these two forms (SO1, SO4, GPRO, see Tables 1 and 4).

We performed a DFA using these three characters, in addition to the 12 used in the PCAs, on a large sample of specimens of the *scutellatus* and *dumerili* types, originating from the areas of allopatry and from southern Tunisia where these two types meet. Our aims were to confirm the existence of differences between the eastern and western forms (placed in synonymy by Arnold, 1983) and to check whether these differences are maintained in areas of sympatry (southern Tunisia).

The result of the DFA on 206 specimens (51 *A. dumerili* and 24 *A. scutellatus* from allopatric areas and 97 *A. dumerili* and 34 *A. scutellatus* from sympatric areas) using the 15 variables detailed above is shown in Fig. 5. Both forms are morphologically dis-
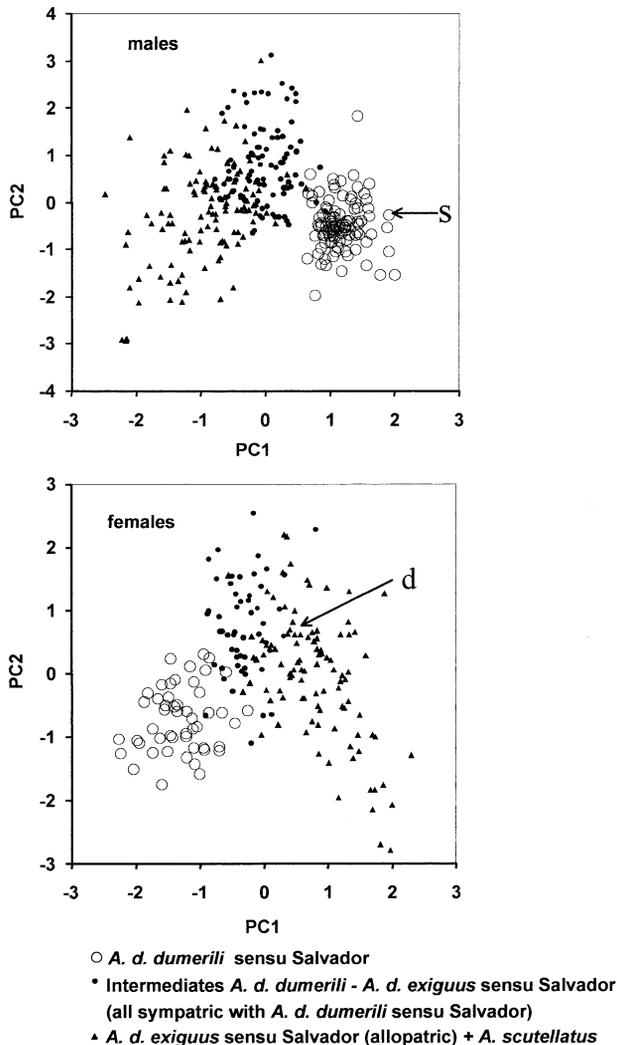
Figure 4. Bivariate plot of PC1 and PC2 scores generated by a PCA run on all adult specimens of (following Salvador's 1982 classification) *Acanthodactylus dumerili* and *Acanthodactylus scutellatus*. The specimen marked 'd' is the holotype of *dumerili*, the specimen marked 's' the holotype of *senegalensis*.

Figure 5. Box plots of the discriminant function scores for *Acanthodactylus dumerili* and *A. scutellatus* (both sexes together) in allopatric and sympatric situation. The DFA was run using the 12 variables included in the PCAs and the variables SO1, SO4 and GPRO (see Table 1).

tinct, as specimens from the allopatric areas have significantly different discriminant function scores (see below). Specimens from the area of sympatry also differ clearly. Discriminant function scores overlap in both sympatric and allopatric situation, but there is more overlap in the area of sympatry. An ANOVA on the discriminant function values identified significant effects of the initial determination ($P < 0.001$), of the sample origin (from sympatric or allopatric range) ($P = 0.047$) and of the interaction between these two factors ($P = 0.002$). A Student *t*-test on the discriminant function values showed that *scutellatus* from the

sympatric area have significantly lower scores compared to specimens from the allopatry zone ($P = 0.023$), whereas *dumerili* do not show significant differences between sympatric and allopatric specimens.

5. Geographical variation in Acanthodactylus dumerili exiguus (including the 'intermediate populations' of Salvador, 1982)

As apparent from Fig. 4, Mauritanian populations of *Acanthodactylus dumerili* (i.e. the 'intermediate' specimens of Salvador, 1982) display morphological differences from the other populations of the species. This led us to investigate further the extent of morphological variation among geographical populations of *A. dumerili exiguus*. There was a significant effect of specimen origin on their position along the axis for the first principal component (PC1; one-way ANOVA, $F = 36.16$; $P < 0.001$), the second (PC2; $F = 19.69$; $P < 0.001$) and the third (PC3; $F = 2.54$; $P = 0.02$) but not for the remaining axes. PC1 and PC2 thus explain most of the differences between populations (cumulated percent of explained variance: 36%, see Table 8). PC1 mainly separates populations from Mauritania from all the other populations of *A. dumerili* (see Fig. 6). This indicates that the main source of varia-

Table 8. Eigenvalues, percent of explained variance, cumulative percent of explained variance, and contributions of the variables to the factors for the first three principal components of a PCA run on specimens of *Acanthodactylus dumerili*, following our definition of the species, i.e. excluding *A. d. dumerili* of Salvador (1982) = *A. senegalensis* (males and females together)

		CP1	CP2	CP3
Males and females (*n* = 313)				
Eigenvalue		2.48	1.87	1.22
Percent of explained variance		20.7	15.6	10.2
Cumulated percent of explained variance		20.7	36.3	46.5
Contributions of the variables to the factors	DORS	−0.46	0.68	0.09
	VENT	−0.54	0.30	0.14
	VENL	−0.41	0.57	0.05
	GRAN	−0.03	0.40	0.06
	SUPL	0.06	−0.12	−0.05
	SUBO	0.10	0.14	0.04
	PORF	−0.60	0.03	−0.21
	CARE	0.01	−0.64	0.14
	SVL	**−0.76**	−0.43	−0.23
	LOPI	**−0.77**	−0.42	−0.21
	COUL	−0.41	−0.14	0.66
	CLAB	−0.27	−0.11	**0.76**
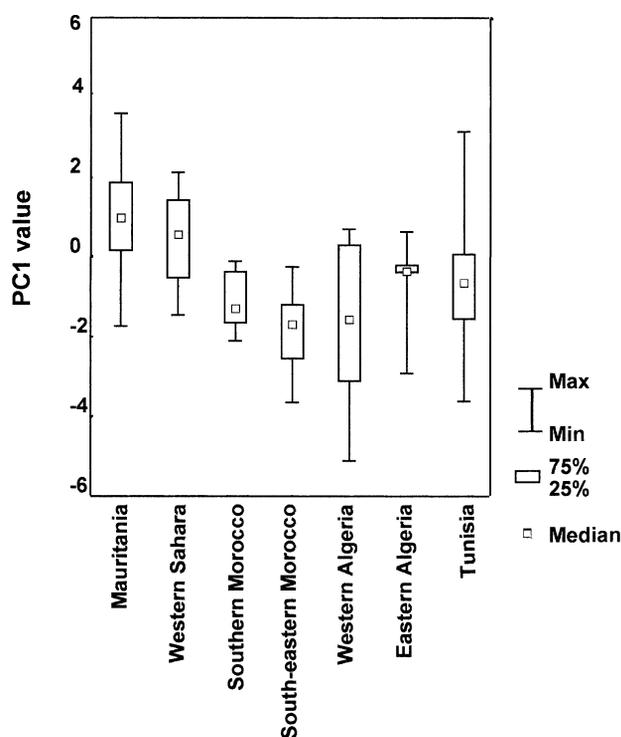
Figure 6. Box plots of the PC1 scores for different geographical samples of *Acanthodactylus dumerili* (our new acceptance of the species, corresponding to *A. d. exiguus* and 'specimens intermediate between *dumerili* and *exiguus*' in Salvador, 1982). The PCA was run on both sexes together using the 12 morphological characters employed in the other PCAs.

tion in morphological characters between our *dumerili* specimens is due to geographical differentiation between Mauritania and the rest of the species range. Western Saharan populations, which are geographically situated between the Mauritanian and Saharan populations, also have an intermediate position between these populations on the first axis. This suggests that morphological intergradation occurs between Mauritanian and Saharan samples and supports the idea that they are conspecific. The variables contributing most to PC1 are (in decreasing order) LOPI and SVL (extremely correlated), PORF, VENT, DORS, VENL, COUL and CLAB, all of which are negatively correlated with PC1 (see Table 8). The Mauritanian populations of *A. dumerili* are thus characterized by their smaller size, reduced number of femoral pores, ventral scales (see Fig. 7), dorsal scales (see Fig. 8), a different colour pattern and less strongly marked labial plates (see systematic account below).

The PC2 mainly separates the animals from the centre of the species range (from Southern Morocco to Western Algeria) from the western (Mauritania) and eastern (Central Algeria to Tunisia) specimens (see Fig. 9). The Central Sahara animals are characterized by higher number of dorsal scales (Fig. 7), ventral scales (no specimen with fewer than 14 longitudinal rows of ventrals, Fig. 8), superciliary granules, less keeled dorsal scales and small size. The PC3 (not shown) weekly separate the Moroccan samples, which are the most strongly patterned animals (highest values of COUL and CLAB).
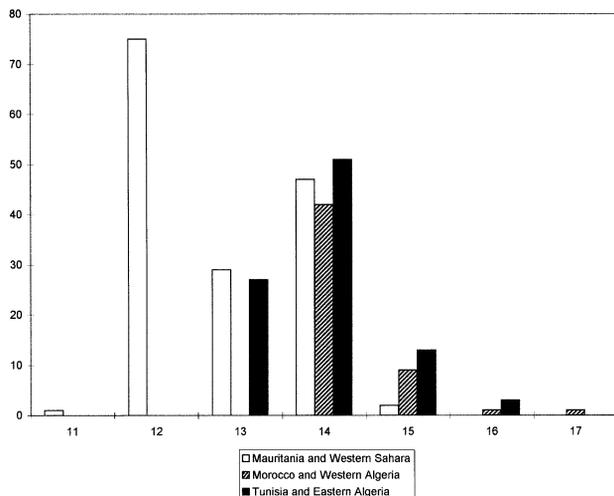
Figure 7. Number of longitudinal rows of ventral scales for different geographical samples of *Acanthodactylus dumerili*.

6. Acanthodactylus taghitensis

Only one specimen of *Acanthodactylus taghitensis* was previously available for examination in scientific collections (female holotype, MNHN 1995.1201 from the Beni Abbes area, see Geniez & Foucart, 1995), in addition to another specimen photographed in the field from the same region. We located two additional male specimens of this species in the British Museum (Natural History) collections (BMNH 1982.292-293) originating from Fort Gouraud (= Fderik), Mauritania. Fderik is situated 1300 km south-west of the two previously known localities and thus constitutes a remarkable range extension for the species.

We performed a PCA on males and females of *Acanthodactylus aureus* and *A. taghitensis*. Most of the diagnostic characters of *A. taghitensis* compared to *A. aureus* (scales on the back larger than on the flanks, raised nostrils, different head shape and colour pattern, see systematic account below) were not taken into account in the variables used for the PCAs. Nevertheless, the fourth PC neatly separates the two species (Fig. 10). The variables contributing most to this axis are (Table 9) GRAN on the positive side and CARE on the negative side of the axis, indicating that *A. taghitensis* has more supraciliary granules and less carinate dorsals than *A. aureus*. The new specimens of *A. taghitensis*, although being much closer to the range of *A. aureus*, do not differ from the type specimen in any diagnostic characters, and are indeed morphologically very similar to it (see Fig. 10). They had been tentatively assigned to *A. aureus* by Arnold (1983), whereas Salvador (1982) found them too different from this species to include them in *A. aureus* and did not identify them specifically.

SYSTEMATIC INTERPRETATIONS OF THE RESULTS – DISCUSSION

1. Acanthodactylus aureus

Acanthodactylus aureus is sympatric with *Acanthodactylus senegalensis* in coastal Senegal (this work, see also Böhme, 1978) and is widely parapatric with *A. dumerili* (*sensu* Salvador, 1982) in Western Sahara (Bons & Geniez, 1996). No intermediate specimens between *A. aureus* and other species of the *scutellatus* group were found in the material that we examined. We found only one *A. aureus* specimen with head scalation differing from the typical scalation of this species, but in all other aspects it was a typical *A. aureus*. As can be seen from the systematic account below, *A. aureus* is morphologically characterized by a set of original characters, and based on our experience it is the most distinctive form in the *scutellatus* group. The genetic data of Harris & Arnold (2000) clearly support the species status that has long been adopted for this taxon. We fully agree with this position, in accordance with the recent systematic treatments of the *scutellatus* group (Salvador, 1982; Arnold, 1983; Mellado & Olmedo, 1990).

2. Acanthodactylus longipes

Despite the fact that some specimens have morphological characters overlapping those of other species, *Acanthodactylus longipes* constitute a well differentiated taxon on the basis of the morphological characters used in the multivariate analyses, as shown by the separation of most specimens on the scatterplots (see Fig. 3). As it is completely sympatric with other members of the *scutellatus* group, this morphological distinctiveness indicates that it is a valid species, in accordance with the opinion of Salvador (1982), Arnold (1983) and Baha El Din (1994). The fact that the specimens' clusters overlap can result from misidentification of a few specimens, from occasional hybridization or, more likely, from intraspecific variability in all the studied taxa, resulting in overlapping sets of morphological characters.

Our new specimens from coastal Mauritania do not differ from those in the rest of the range (see Fig. 3), with the exception of a tendency to have a lower number of longitudinal rows of ventral scales (15 rows of ventral scales on 30% of the specimens examined). This confirms the range extension for this species that we initially suspected based on the examination of the Mauritanian samples. The new localities are situated along, or near, the coast from Iouik to 50 km northeast of Nouakchott (see Fig. 1), and are the only ones known along the Atlantic coast of Africa for these species. The closest locality was previously Choum (Mauritania; MNHN. 1967.553, Salvador, 1982),
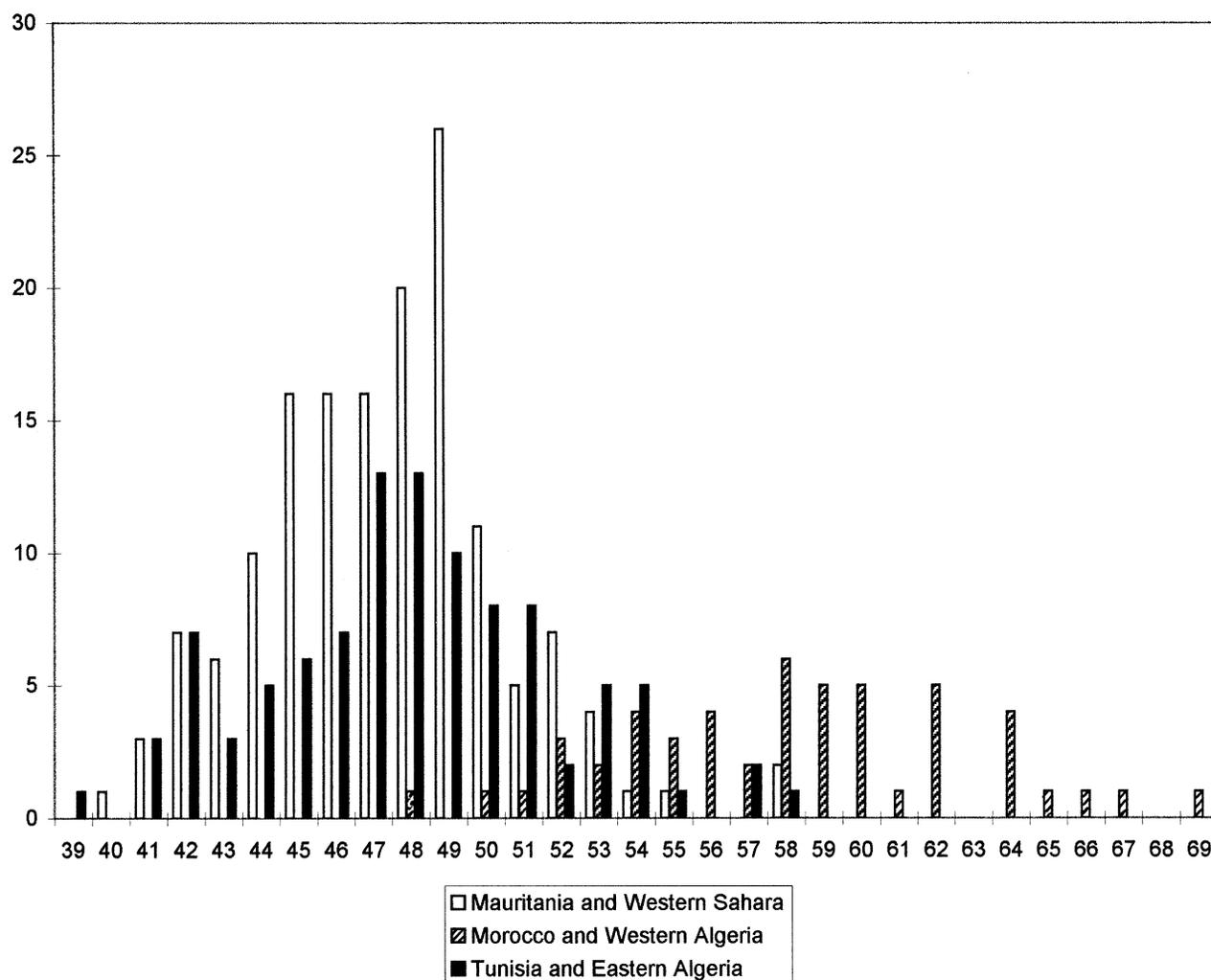
Figure 8. Number of longitudinal rows of dorsal scales at mid-body for different geographical samples of *Acanthodactylus dumerili*.

some 450 km to the north-east of the Nouakchott locality.

3. *Acanthodactylys dumerili dumerili sensu Salvador, 1982*

The initial impression gained in the field in several coastal localities in Mauritania was that two types of *Acanthodactylus* occur in sympatry, although not usually in syntopy. Examination of the specimens showed that one form corresponds to the intermediate specimens between *A. dumerili dumerili* and *A. dumerili exiguus* of Salvador (1982; called ADX hereafter), the other to *A. d. dumerili* (ADD) *sensu* Salvador (1982). The fact that these two forms are widely sympatric in Mauritania contradicts Salvador's systematic position about them.

Our PCA confirms that two morphologically distinct forms of *Acanthodactylus* co-exist in Mauritania (see Fig. 4). One includes the ADD specimens (from Senegal to Mauritania), the other includes the ADX specimens and is more similar to the *A. d. exiguus* (*sensu* Salvador, 1982) specimens from the rest of the species range (from Morocco to Tunisia, called ADE hereafter). The ADD specimens from Mauritania and Senegal are morphologically indistinguishable by the characters used in our analyses, and we were unable to find any trait that differs between them. The forms called *A. dumerili dumerili* (= ADD, southern populations from Senegal to Mauritania) and 'intermediate populations between *A. dumerili dumerili* and *A. dumerili exiguus*' (= ADX, northern populations, Mauritania) by Salvador (1982) are thus morphologically distinct and widely sympatric. They also have distinct

Table 9. Eigenvalues, percent of explained variance, cumulative percent of explained variance, and contributions of the variables to the factors for the third and fourth principal components of a PCA run on specimens of *Acanthodactylus aureus* and *A. taghitensis* (males and females separately)

		CP3	CP4
Males and females ($n = 87$)			
Eigenvalue		1.37	1.18
Percent of explained variance		11.4	9.9
Cumulated percent of explained variance		47.6	57.4
Contributions of the variables to the factors	DORS	0.33	0.29
	VENT	−0.39	−0.22
	VENL	0.46	−0.17
	GRAN	−0.22	**0.73**
	SUPL	−0.59	0.16
	SUBO	0.15	0.13
	PORF	−0.22	0.11
	CARE	−0.12	−0.65
	SVL	−0.05	−0.07
	LOPI	−0.11	−0.06
	COUL	0.61	0.10
	CLAB	−0.17	−0.06
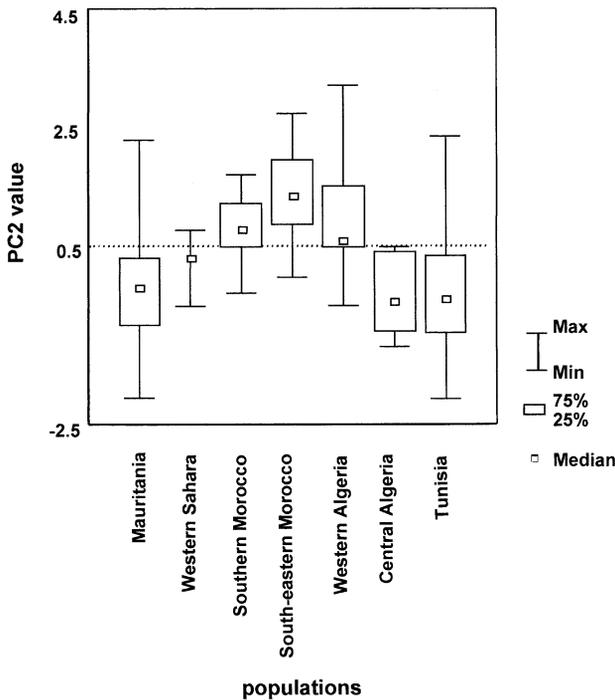
Figure 9. Box plots of the PC2 scores for different geographical samples of *Acanthodactylus dumerili*. Same analysis as in Figure 6.
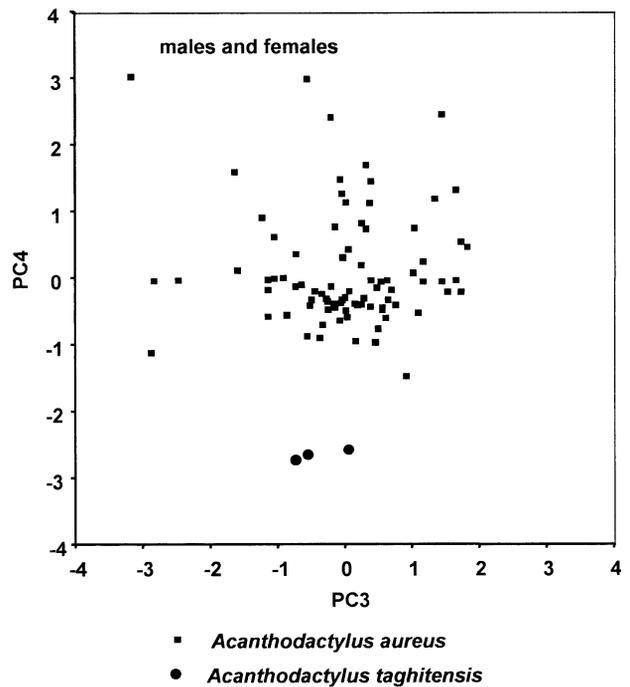
Figure 10. Bivariate plot of PC3 and PC4 scores generated by a PCA run on all adult specimens of *Acanthodactylus aureus* and *A. taghitensis* (males and females together) using the same 12 variables as in the other PCAs.
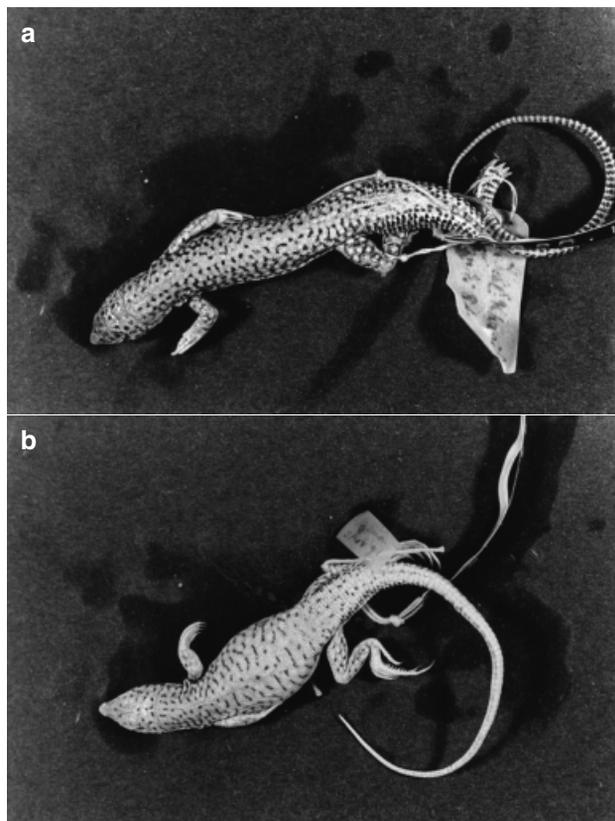
Figure 11. (a) *Acanthodactylus scutellatus audouini*, male, lectotype, BMNH 1923.1.20.3006, Wadi El Kreil (Tunisia), dorsal view of specimen. (b) *A. s. audouini*, female, paralectotype of *Acanthodactylus scutellatus* var. *audouini*, BMNH 97.10.28.319, Wadi Halfa (Sudan).

habitat requirements over their sympatric area (see systematic account and ecological requirements below). They thus constitute two reproductively isolated species.

Which name should apply to each of these species? When we examined the type of *A. dumerili* (MNHN 2759, a female labelled 'Sénégal'), we found clear differences from the southern species (= ADD) in scalation and colour pattern: 55 longitudinal rows of dorsal scales which are weakly but distinctly keeled, and of the same size on the dorsum and flanks (34–53 rows of dorsals in the southern species, with scales on the back strongly carinate and about twice as large as the flank scales), 14 longitudinal rows of ventral scales (10–12 in the southern species, exceptionally 14), 20 and 19 femoral pores on the left and right side, respectively (fewer than 18 usually in the southern species), no vertebral line (females of the southern species have a lineated pattern with a dark vertebral line, see systematic account below for the characters of the southern species). This specimen is, on the other hand,

typical of the northern populations (ADX and ADE specimens, Tunisia to Mauritania). In the bivariate plot of PC scores for the females, this specimen falls within the ADX + ADE cluster and far from the ADD cluster (Fig. 4). Given that 'Sénégal' referred in the early 19th century to a large area of western Africa, including a fair proportion of the Sahara, we consider that the type of *A. dumerili* is a typical specimen of the northern populations referred by Salvador as *A. dumerili exiguus*.

The southern species (ADD), therefore, should not be called *Acanthodactylus dumerili*. The name *Acanthodactylus senegalensis* Chabanaud (1918) is available for this species. *Acanthodactylus senegalensis* was considered as a synonym of *A. d. dumerili* by Salvador (1982: 128). The unique specimen of the description of *A. senegalensis*, an adult male (MNHN 1918.43), has morphological characters typical of the southern species (see Fig. 4). Its locality (Sangaléam, near Rufisque) is situated on the coast of Senegal, within the range of the southern species. In light of this, the southern species of the '*A. dumerili*' populations (*A. dumerili dumerili sensu* Salvador, 1982) should be called *A. senegalensis* (= ADD in this analysis). The northern forms (*Acanthodactylus dumerili exiguus* and specimens intermediate between *exiguus* and *dumerili sensu* Salvador, 1982) should therefore be called *A. dumerili*.

4. Acanthodactylus dumerili exiguus (including the 'intermediate populations' of Salvador, 1982) and Acanthodactylus scutellatus

Our results indicate that these two taxa are morphologically distinct, even if no single character permits a clear separation. Furthermore, *Acanthodactylus dumerili* remains as distinct in the area of sympatry as in the area of allopatry, which demonstrates the lack of extensive intergradation between these two taxa. Although *A. scutellatus* specimens from the area of sympatry are slightly more similar to *A. dumerili* than allopatric specimens, they remain distinct. This is explained by geographical variation in *A. scutellatus*, with the possibility that the Tunisian populations are closer to *A. dumerili* in morphology because of common environmental factors such as climate (for effects of climatic conditions on scalation see, e.g. Schmidtler, 1986). The higher dispersion of the discriminant function scores in sympatric areas suggests that some misidentifications must have occurred. This is not surprising, given the close similarity of *A. scutellatus* and *A. dumerili*. Large adult specimens (males especially) are distinctive (compare Fig. 11 with Figs 12c and d), but females and younger specimens can be very difficult to identify and the error rate of our initial classification can be quite high. Although
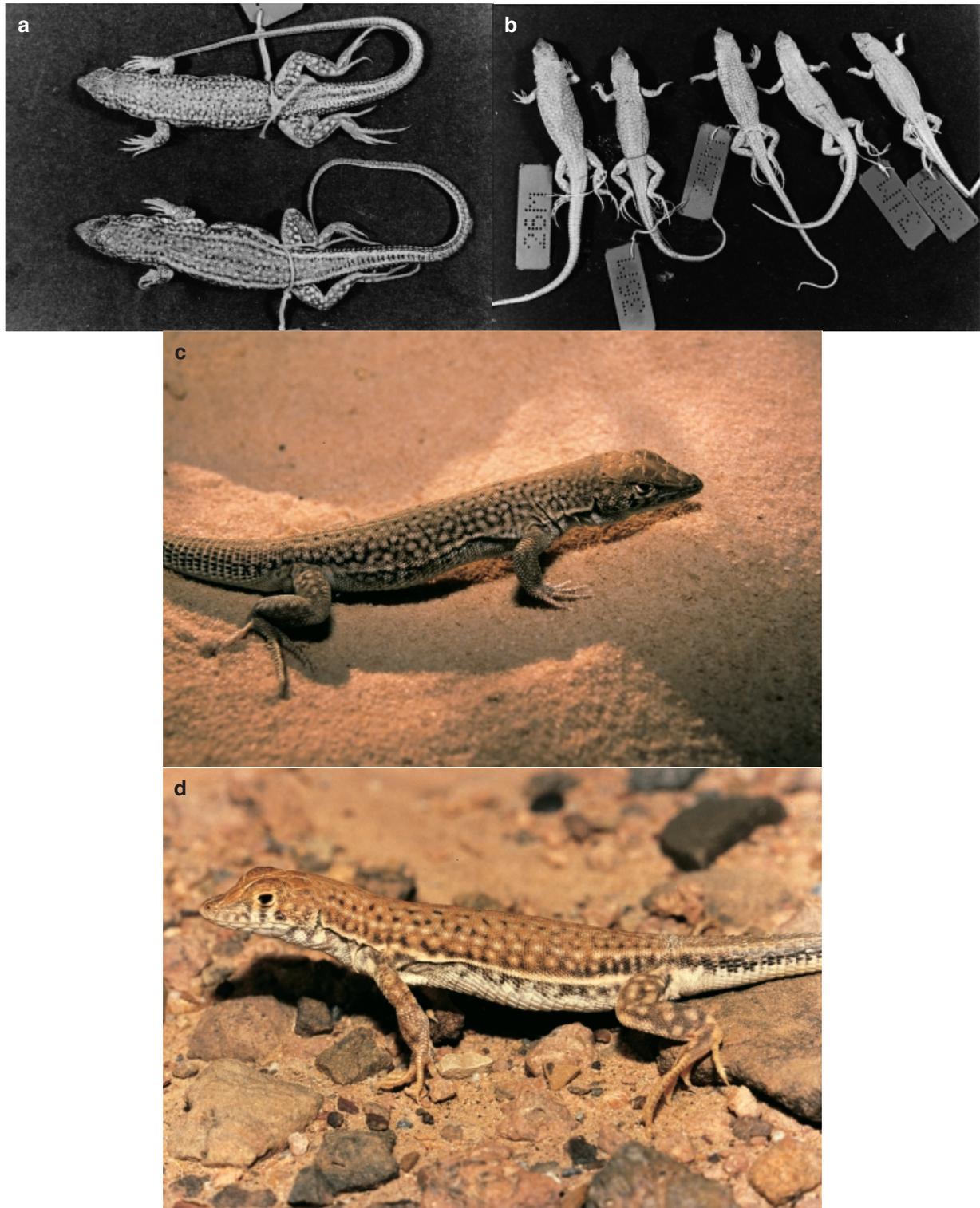
Figure 12. (a) *Acanthodactylus senegalensis*, male (above), MNHN 1997.4688, female (below), MNHN 1997.4659. Both from Tamzakt camp (Mauritania). (b) *A. dumerili*, from left to right male, MNHN 1997.3764, male MNHN 1997.3774, male MNHN 1997.3763, female MNHN 1997.3769, female MNHN 1997.3777, all from Blaouakh (Mauritania). (c) *A. dumerili*, male, PHG 48, Douz (Tunisia), picture by V. Rufray. (d) *A. dumerili*, female, PHG 3, 12 km from Mecissi toward Rissani (Morocco), picture by P. Geniez.

the characters used in our multivariate analyses do not allow a clear separation of these two forms, as shown by the widely overlapping discriminant scores, use of habitus and coloration characters allow identification of most adult specimens. We found that adult males are especially distinct and clearly fall into two discreet morphological groups in sympatric areas (e.g. southern Tunisia).

As there is no sign of intergradation between *A. scutellatus* and *A. dumerili* in the large overlapping portion of their range, these two taxa should be considered as distinct species. Our results thus support the specific status of *Acanthodactylus dumerili* and *A. scutellatus*, as suggested by Bons & Girot (1964) and Salvador (1982) and confirmed by Nouïra (1996).

Synonymy of these two species is still a bit confused. Many authors have in the past (e.g. Boulenger, 1921; Bons, 1959; Pasteur & Bons, 1960; Bons & Girot, 1964; Blanc & Ineich, 1985) used the name *Acanthodactylus inornatus* (Gray, 1838) for the species that we call *A. dumerili*. Later, Salvador (1982), following Lataste (1885), placed *A. inornatus* in the synonymy of *A. scutellatus*. We examined one type of *Scapteira inornata* (BMNH 1946.9.3.76; J. Ritchie coll.; Tripoli, Libya) and identified it instead as a specimen of *A. dumerili*. The syntypes of *Acanthodactylus scutellatus* var. *exiguus* that we could examine are also typical specimens of the Saharan populations of *Acanthodactylus dumerili*. We thus consider *inornatus* and *exiguus* as subjective junior synonyms of *A. dumerili*.

5. Geographical variation in Acanthodactylus dumerili exiguus (including the 'intermediate populations' of Salvador, 1982)

The multivariate analyses show some strongly significant variation in morphological characters among *Acanthodactylus dumerili* populations, with the Mauritanian samples being the most distinct. In spite of these statistical differences, no single character permits diagnosis of all the Mauritanian animals. A very distinct colour pattern (dark spots on the back absent) is present in only about 31% of the specimens. Multivariate scores show a wide overlap between Mauritanian and other samples, especially specimens from the east of the species range (see Fig. 6). Many Mauritanian animals appear indistinguishable from the specimens inhabiting the rest of the species range based on the results of our PCA. We thus refrain from naming the Mauritanian populations for the time being.

6. Acanthodactylus taghitensis

Based on the few additional specimens available, it is apparent that *Acanthodactylus taghitensis* is a widely distributed valid species that maintains its diagnostic character over its range.

CONCLUSION

Based on an analysis of morphological variation within the *Acanthodactylus scutellatus* species group, especially in overlap zones between the various morphotypes, we propose the recognition of six species in this group. Nevertheless, we acknowledge that, except for *A. aureus* and *A. taghitensis*, these species are not easily characterized by a diagnostic combination of colour and scalation features. Morphological variation within these taxa results in the occurrence of some specimens with intermediate morphology. We cannot exclude, based on the present data, that some of these intermediate specimens are hybrids, but only molecular studies would be likely to provide a definite answer. Nevertheless, our results clearly indicate that morphological variation is discontinuous, and that these species are on the whole reproductively isolated. A consequence of this intraspecific variability is that the identification of some specimens can be difficult or even impossible. Furthermore, non-adult specimens are more difficult to identify and complementary investigations would be required to define objective morphological characters on younger specimens. Despite this, most animals are easily classified.

Our conclusions are broadly similar to those of Bons & Girot (1964). These authors acknowledged that the small and mostly littoral members of the *scutellatus* group from Senegal and Mauritania constitute a separate species. They named it *Acanthodactylus dumerili*, probably because of the confusion over the type locality of *dumerili*, whereas we call it *A. senegalensis*. They recognized *A. longipes* as a distinct species. They restricted *A. scutellatus* to the large, eastern form found from Tunisia eastward, and called *A. inornatus* what we now call *A. dumerili*. The main difference between the present work and Bons & Girot (1964) is that they considered *A. aureus* as a subspecies of *inornatus* (= *dumerili*), whereas these species are widely parapatric (this study) or even sympatric (Salvador, 1982), without any trace of intergradation.

SYSTEMATIC REVIEW OF THE *ACANTHODACTYLUS SCUTELLATUS* GROUP

ACANTHODACTYLUS SCUTELLATUS (AUDOUIN, 1827)

Lacerta scutellata Audouin, 1827: 172, pl. i, fig. 7. Name-bearing type: the original description was clearly based on a single specimen (figured on the plate), which is thus the holotype. This specimen is not in the collections of the MNHN, and was perhaps never given to the MNHN collections (Brygoo, 1988: 44–45). It should be considered as lost. A neotype should be designated to stabilize the nomenclatural status of this taxon. We refrain from doing so here pending a more complete analysis of the populations

from the eastern part of the species range, including Egypt. Type locality: 'Egypte'.

Chresonyms. Acanthodactylus scutellatus (Audouin, 1827): Bons & Girot, 1964: 319; Salvador, 1982: 113; Arnold, 1983: 322 (part); Arnold, 1986: 425 (part).

Distribution (Fig. 13). In the Sahara, south-eastern Algeria, north-eastern Mali, northern Niger, northern Chad, northern Sudan, Egypt, Libya, and southern Tunisia (Salvador, 1982; Nouïra, 1996; Ch. P. Blanc, pers. com.; this study). The characters given above and a careful examination of the pictures published by Bons & Girot (1964) lead us to reject the occurrence of this species in Morocco (cf. Bons & Geniez, 1996), in opposition to the opinions of Bons & Girot (1964), Mellado & Olmedo (1990) and Pérez Mellado (1992). The species is also encountered in Israel, Arabia and Iraq (Salvador, 1982).

Diagnosis. (Remarks: the following diagnosis is based on specimens of *Acanthodactylus scutellatus audouini* only). The largest species of the group (reaching 72.5 mm snout-vent length, mean = 63.9; cf. Table 2, Figs 14 and 15). The subocular in contact with three or (rarely) four supralabials in 99% of the individuals (Table 3) distinguishes *A. s. audouini* from *A. aureus* and *A. taghitensis*. Dorsal scales usually small and rather numerous (in the Sahara, range: 39–69, mean: 53.4; Table 2, see remarks below under 'Geographical variation'), nearly equal in size between the dorsum and the flanks, and moderately to strongly carinate (codes 4 or 5 in 86% of our sample, no individual reaches code 6; Table 3, see Fig. 16). Fewer than two rows of supraciliary granules in 70% of the specimens, two rows in 28%, more than two rows in only 2% (Table 3). Generally 13 or 14 longitudinal rows of ventral scales (in 83% of the specimens, range: 12–16, mean: 13.9; Table 2). Femoral pores rather numerous (range: 16–26, mean: 21.1; Table 2). Adult males with a black, highly contrasting, dorsal reticulation. Females with isolated black spots at regular spaces on the back. Pale dorsal spots often lacking in adults, which have a dorsal coloration made of only two colours; most individuals have black spots on their pileus. For separation of *A. s. audouini* from *A. longipes* and *A. senegalensis*, see these species.
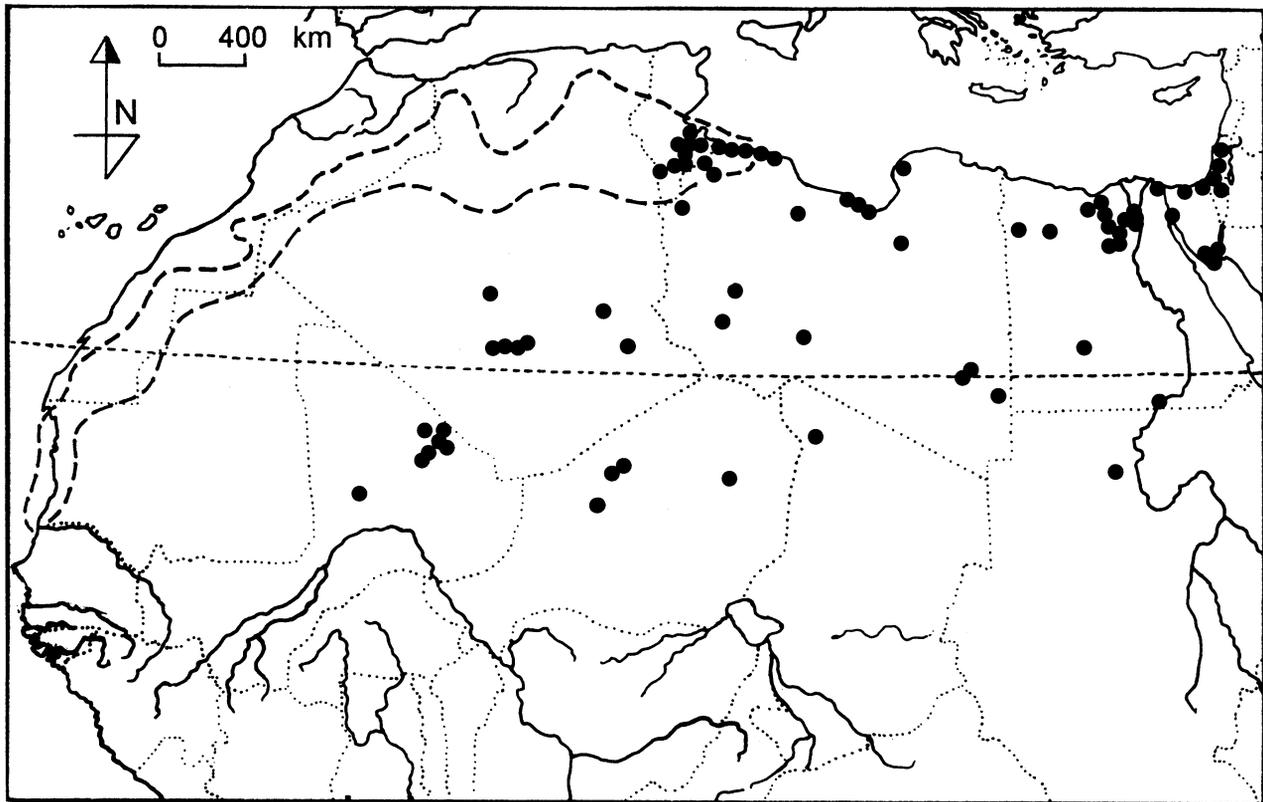
Figure 13. Geographic distribution of *Acanthodactylus scutellatus* in the Sahara (thus excluding part of the species range, see text). Dotted lines indicate the approximate limits of the distribution of *A. dumerili*. Data from Salvador (1982), Baha El Din (1994), Joger & Lambert (1996), Nouïra (1996), this study.
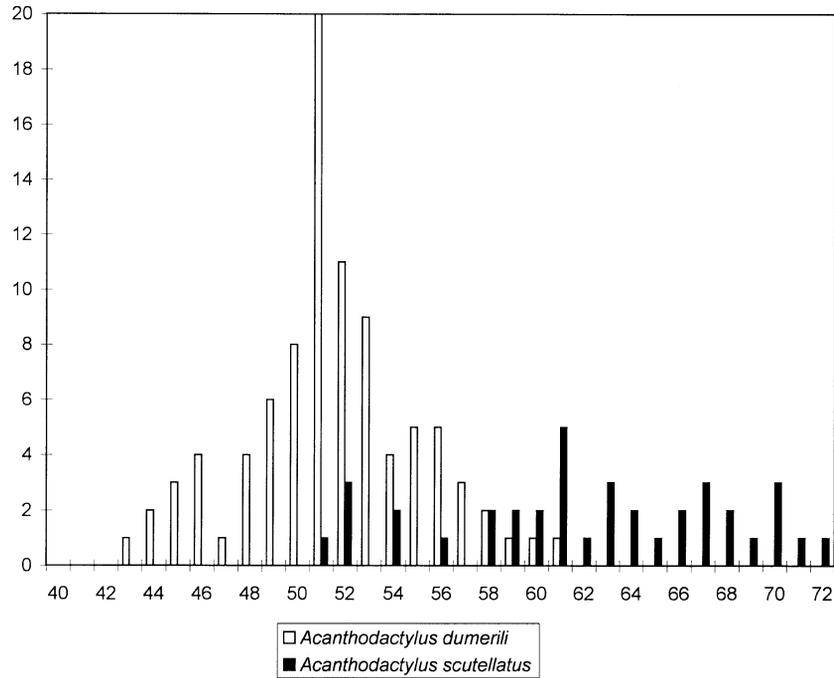
Figure 14. Snout-vent length of males in our samples of continental Sahara *Acanthodactylus dumerili* and *A. scutellatus audouini.*
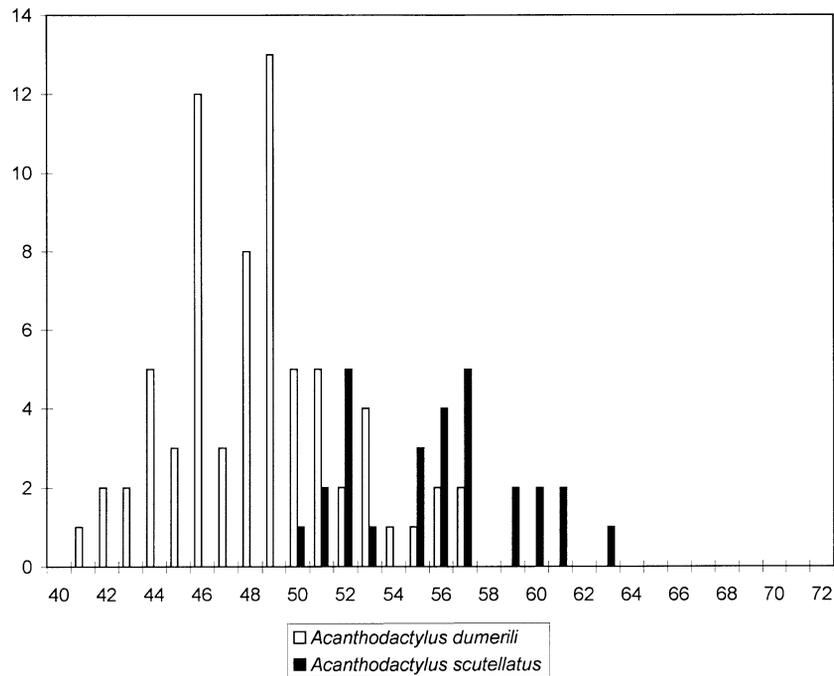
Figure 15. Snout-vent length of females in our samples of continental Sahara *Acanthodactylus dumerili* and *A. scutellatus audouini.*
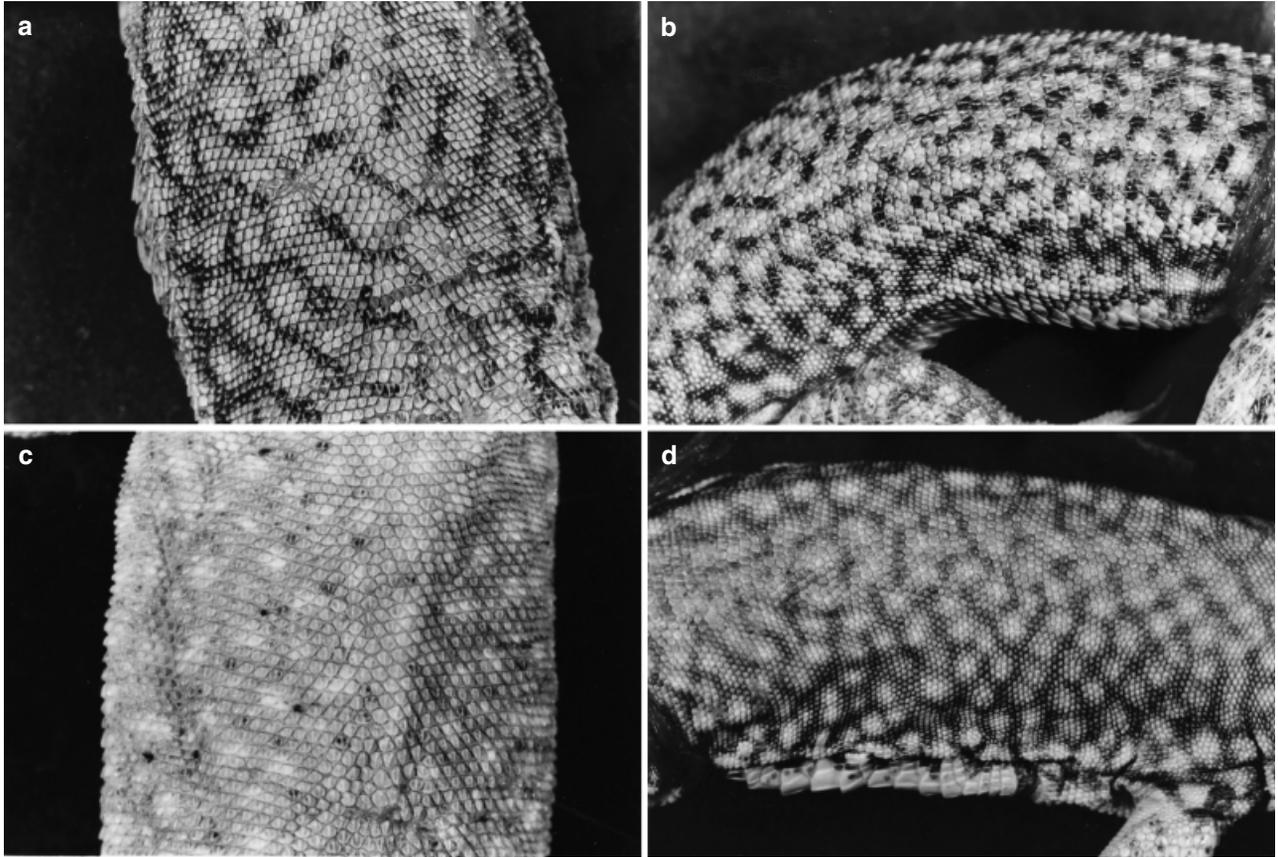
Figure 16. (a) *Acanthodactylus scutellatus audouini*, male, paralectotype of *Acanthodactylus scutellatus* var. *audouini*, BMNH 97.10.28.316, Wadi Halfa (Egypt), close-up of dorsal scales. (b) *A. senegalensis*, male, EPHE Mch1, coast north of Dakar (Senegal), close-up of dorsal scales. (c) *A. dumerili*, male, MNHN 1997.3764, Blaouakh (Mauritania), close-up of dorsal scales. (d) *A. longipes*, male, EPHE AF4, Akreïdil, 50 km NE of Nouakchott (Mauritania), close-up of dorsal scales.

Acanthodactylus scutellatus audouini can be distinguished from the closely similar *A. dumerili* by its larger maximum size and by a different pileus coloration. In *A. dumerili*, as in the remaining species within the *scutellatus* group, the pileus is either uniformly pale or marked with darker vermiculations or small dots, but not with distinct and well-individualized large black spots as in *A. s. audouini*. In addition, a higher proportion of adults *A. s. audouini* have a dorsal coloration consisting of a dark pattern on a uniform background (two colours only on the dorsum, COUL code 4, in 27% of the specimens; Table 3). When other species within the scutellatus group have only two colours on the dorsum, it is usually light spots on a darker ground colour (code 2, Table 3). According to Nouïra (1996; p. 246), *A. s. audouini* and *A. dumerili* also differ in the fragmentation of the cephalic plates, *A. s. audouini* having the first supraocular (SO1) usually separated from the second supraocular (SO2) by a row of proximal granules and a strongly fragmented fourth supraocular (SO4). We checked the validity of

these proposed differences on 116 *A. s. audouini* (most of them from Tunisia) and 298 *A. dumerili*. In *A. s. audouini*, 48% of the individuals have SO1 and SO2 partly or totally separated (including 18% with completely separated SO1 and SO4; Table 4), whereas in *A. dumerili* only 7% of the specimens have SO1 and SO2 partly separated (none having SO1 and SO4 completely separated; Table 4). In *A. s. audouini*, 30% of the specimens have an entire SO4, 33% have a partially fragmented SO4 and 37% have a completely fragmented SO4. In *A. dumerili*, 49% of the specimens have an entire SO4, 38% a partially fragmented one, and only 14% a completely fragmented SO4 (Table 4). The differences described by Nouïra (1996) are thus real but of limited use when trying to identify single specimens.

Geographical variation. Three subspecies have been recognized. The subspecies *hardyi* is recognized as a valid taxon in most of the recent works on the genus (e.g. Bons & Girot, 1964; Salvador, 1982; Arnold, 1986;

Nouïra, 1996). Harris & Arnold (2000) even propose to give specific status to this taxon, although without justification. In addition, Bons & Girot (1964) recognized the subspecies *audouini*, based on an analysis of large series of specimens. We follow their opinion here, based on a preliminary examination of a number of specimens from Egypt and Israel.

Subspecies. Acanthodactylus scutellatus scutellatus in Israel, Sinai and Egypt.

Acanthodactylus scutellatus audouini Boulenger, 1918
Acanthodactylus scutellatus var. A*udouini* Boulenger (1918): 154. Name-bearing type: Boulenger did not refer to any precise specimen in his original description, but stated that he used specimens in the British Museum, especially specimens collected by F. Lataste. These specimens came from 'Egypte, Nubie, Tripoli, sud de la Tunisie'. The following specimens are probably all syntypes (see Salvador, 1982): BMNH 97.10.28.315-319 (Wadi Halfa, Sudan), BMNH 1913.12.30.6-10 (Homs, Tripoli), BMNH 91.5.4.85-91 (Duirat, southern Tunisia), BMNH 1920.1.20.3006 (Wed El Kreil, Tunisia). Considering the uncertainties over the limits of the range of *audouini*, we feel it is important to select a lectotype from an area where *audouini* (as generally understood) is certainly present. We select the specimen BMNH 1920. 1.20.3006 as lectotype. Type locality: Wed El Kreil, Tunisia.

Distributed in the west of the species range, east to north-eastern Sudan (Bons & Girot, 1964).

A. s. hardyi Haas, 1957
Acanthodactylus scutellatus hardyi Haas, 1957: 72. Name-bearing type: holotype by original designation: Hebrew University of Jerusalem 2682. Type locality: 'Hirmas Station, Saudi Arabia'.

Distributed in Northern Saudi Arabia, Kuwait, and Iraq (Salvador, 1982).

We retain for the time being the subspecies *audouini* for the Saharan specimens, characterized by a lower number of more strongly keeled dorsal scales (73 on average in *scutellatus* (Bons & Girot, 1964) against 53 on average, and not more than 68 in *audouini* [own data]) and a smaller size (Boulenger, 1921; Bons & Girot, 1964). A revision of the material included in *Acanthodactylus scutellatus* is needed before any firm conclusion can be drawn. The limits of the range of *A*. s. *scutellatus* and *A*. s. *audouini* follow Bons & Girot (1964).

There is a slight morphological variation among populations of *Acanthodactylus scutellatus audouini* in the Sahara. In Tunisia, most of the individuals have a grey throat and a reddish tail, whereas this coloration is exhibited, more or less markedly, by only a small number of individuals from southern Sahara.

Remarks. Victor Audouin published the description of *Lacerta scutellata* in 1827 and not in 1809 (Salvador, 1982; according to his birth date, V. Audouin was only 12 years old in 1809 [R. Bour, pers. com.]) or 1829 (Arnold, 1983; Brygoo, 1988).

ACANTHODACTYLUS SENEGALENSIS CHABANAUD, 1918

Acanthodactylus senegalensis Chabanaud, 1918: 162. Name-bearing type: MNHN 1918.43, holotype by monotypy. Type locality: 'Sangaleam, près de Rufisque'.

Chresonyms. Acanthodactylus scutellatus var. *dumerili* Milne Edwards, 1829: Boulenger, 1921: 105. *Acanthodactylus dumerili* Milne Edwards, 1829: Bons & Girot, 1964: 331. *Acanthodactylus dumerili dumerili* Milne Edwards, 1829: Salvador, 1982: 128 (part). *Acanthodactylus scutellatus* (Audouin, 1827): Arnold, 1983: 322 (part).

Distribution (Fig. 17). Senegal, Mali and Mauritania (Bons & Girot, 1964; Cissé & Karns, 1978; Salvador, 1982; this study). In Senegal, this species is only present north of approximately 14°N (Cissé & Karns, 1978: 191). The three specimens from Goundam and M'Bouna (Mali) (MNHN 1932.8-9,11) indicate that its range extends inland at least as far as 1300 km from the coast (Goundam). Salvador (1982) mentions two other specimens of '*Acanthodactylus dumerili dumerili*' from Mali, further inland than Goundam. We have not examined these two specimens, but if they also are *A. senegalensis*, as it is likely, it would indicate that the species have a more extensive distribution in the south-western Sahara than our map shows.

Diagnosis. Small size (snout-vent length of adults between 49 and 60 mm, mean: 51.6; Table 2). The subocular in contact with three or (rarely) four supralabials in 100% of the individuals (Table 3) distinguishes *Acanthodactylus senegalensis* from *A. aureus* and *A. taghitensis*. *Acanthodactylus senegalensis* has the lowest scale counts within the group. Low number of large dorsal scales (range: 34–53, mean: 41.3), about twice as large as the flank scales, flat and strongly carinate (code 6 in 89% of the individuals, the remaining ones having code 4 or 5; Table 3, see Fig. 16). Fewer than two rows of supraciliary granules in 59% of our sample, two rows or more in 41% of the specimens (Table 3). Generally 10, 11 or 12 longitudinal rows of ventral scales (in 89% of the specimens, range: 10–14, mean: 12; Table 2). Low number of femoral pores (generally fewer than 18 on each side,
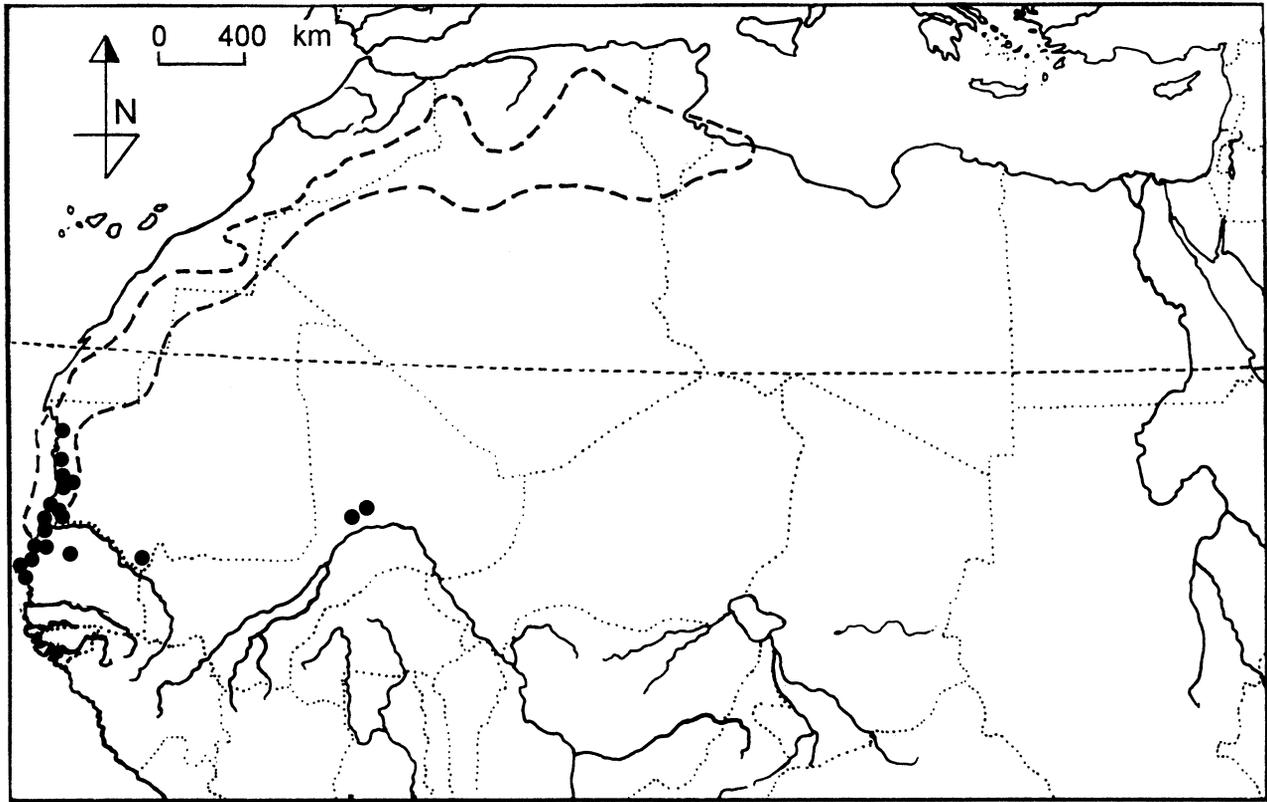
Figure 17. Geographical distribution of *Acanthodactylus senegalensis*. Dotted lines indicate the approximate limits of the distribution of *A. dumerili*. Data from Böhme (1978), Salvador (1982), this study.

range: 11–20.5, mean: 15.6). Always three colours on the dorsum. In males, black dots over a dappled pattern of whitish spots on a beige or russet ground colour, flanks darker than the dorsum. Females have a lineated pattern with a dark vertebral line. Black spots of the males sometimes aligned over the dorsum, resulting in a pattern similar the females pattern. Pileus sandy-coloured with darker, weakly delimited spots. When present, this typical pattern (dark flanks of males, dark vertebral line of females) distinguishes *A. senegalensis* from *A. scutellatus*, *A. dumerili* and *A. longipes* (see Fig. 12a). A further difference from these three species is the obvious size difference between the scales of the flanks and the scales of the dorsum. Number of dorsal scales diagnostic in comparison with *A. longipes* (34–53 dorsal rows in *A. senegalensis* [$n = 187$] against 55–77 dorsal rows in *A. longipes* [$n = 65$]). Dorsal number also useful in comparison with *A. scutellatus*: 47 or fewer rows of dorsals in 95% of *A. senegalensis* specimens, 48 or more in 92% of *A. scutellatus* specimens. Further separated from *A. scutellatus* and *A. longipes* by the lower number of ventrals (13 or more in 96% of the *A. scutellatus* and in 100% of the *A. longipes*, compare also minima and

maxima for *A. senegalensis* and *A. longipes* in Table 2). Dorsal scales also more strongly carinate than in either *A. scutellatus* or *A. longipes*: no specimens of these species reach code 6 for CARE (compare with *A. senegalensis* above). For comparisons with *A. dumerili*, especially in the area of sympatry, see that species.

Geographical variation. None documented.

ACANTHODACTYLUS DUMERILI (MILNE EDWARDS, 1829)

Lacerta dumerili Milne Edwards, 1829: 85, pl. vii, fig. 9 (magnified abdominal scales only). Name-bearing type: in his original description of the species, Milne Edwards refers to one preserved specimen only, still present in the Paris museum collections, but he states in the description '12 or 14 ventrals', which suggests that he examined several specimens. As we are unsure whether the other type specimen(s) belong(s) to the same species as this specimen, we select the specimen in the Paris museum referred to by Milne Edwards (MNHN 2759) as lectotype of *Lacerta dumerili*. Type locality: 'Sénégal' (certainly not present-day

Senegal, but probably another north-western Africa country within the range of *A. dumerili* as understood here).

Junior synonyms

Scapteira inornata Gray, 1838: 281. Name-bearing type: Boulenger (1921) mentions only one specimen as type of *Scapteira inornata* among the British Museum specimens. This specimen (BMNH 1946.9.3.76) has been considered as an holotype by Salvador (1982), despite the fact that Gray (1838) states about his new form: 'praeanal scales 10 or 12', indicating that he examined more than one specimen. As we are unsure whether the other type specimen(s) belong(s) to the same species as this specimen, we designate as lectotype the specimen BMNH 1946.9.3.76. Type locality: 'Tripoli', Libya.

Acanthodactylus scutellatus var. *exiguus* Lataste, 1885: 493. Name-bearing type: syntypes not catalogued but probably (see Salvador, 1982: 130): BMNH 1920.1.20.1349c and BMNH 1920.1.20.1349c2 (Bled Ahmar), BMNH 1920.1.20.1349 (Hadjira), BMNH 1920.1.20.1349d (Tilremt), BMNH 1920.1.20.1349e and MNHN 5838B (Laghouat), BMNH 1920.1.20.1349i (Mraïer), BMNH 1920.1.20.1349g (Biskra), BMNH 1920.1.20.3006 (Oued el Kreil). The specimen BMNH 1920.1.20.1349c2 (Bled Ahmar) is in fact an *A. longipes* (pers. obs.). As several species are included in the original type series, we select as lectotype the specimen BMNH 1920.1.20.1349 (an adult male from Hadjira, Algeria). Type locality: originally 'en Algérie, à Biskra, Mraïer, Tougourt, Bled Ahmar, Hadjira, N'Gouça, Tilremt, Laghouat, Aïn-el-Hel et Bou-Sâada; en Tunisie, à l'oued el Kreil (entre le plateau de Haouaïa et Ghumraçen), Kébili (dans le Nefzaoua), Tozeur, et Nefta (dans le Djérid)', here restricted to Hadjira, Algeria, by lectotype designation.

Chresonyms. Acanthodactylus scutellatus var. *inornatus* (Gray, 1838): Boulenger, 1921: 104. *Acanthodactylus inornatus inornatus* (Gray, 1838): Bons & Girot, 1964: 330. *Acanthodactylus dumerili dumerili* (Milne Edwards, 1829): Salvador, 1982: 128 (part). *Acanthodactylus dumerili exiguus* Lataste, 1885: Salvador, 1982: 130. *Acanthodactylus scutellatus* (Audouin, 1827): Arnold, 1983: 322 (part). Harris & Arnold, 2000: 352 (part).

Distribution (Fig. 18). Mauritania, especially its littoral part, Western Sahara (excluding a coastal fringe of about 100 km wide), Saharan Morocco, northern half of Algeria, Tunisia and north-western Libya (Salvador, 1982; Nouïra, 1996; this study).

Diagnosis. Small species (maximum of 61.5 mm snout-vent length, often less). The subocular in contact with three or (rarely) four supralabials in virtually 100% of the individuals (Table 3) distinguishes *Acanthodactylus dumerili* from *A. aureus* and *A. taghitensis*. Dorsal scales small and relatively numerous (range: 39–69, mean: 48.9; Table 2), roughly the same size on the dorsum and on the flanks, carinate (code 4 or 5 in 87% of the specimens, Table 3, Fig. 16c). Fewer than two rows of supraciliary granules in 75% of the specimens, two rows in 24.5% (Table 3). Usually 12, 13 or 14 longitudinal rows of ventrals (in 90% of the specimens, range 11–17, mean: 13.3, Table 2). Variable number of femoral pores (range. 15–26, mean: 19.3; Table 2). Male dorsal coloration usually with three colours (black, beige and white), but dark colour regularly lacking in Mauritania, leaving only white patches on a beige ground colour (see Figs 12b.c). Females often pale with small, dark, sometimes indistinct, spots on the back (see Figs 12b.d): a confusion with *Acanthodactylus longipes* is possible in such cases. Pileus either uniformly pale or marked with darker vermiculations or small dots. For separation from *A. scutellatus* and *A. longipes*, see these species. In Mauritania (see below), *A. dumerili* is more similar to *A. senegalensis* than in other parts of its range. Mauritanian specimens of *A. dumerili* have frequently 12 rows of ventrals (Fig. 7), a lower number of dorsal scales (Fig. 8), which can be strongly carinated (CARE code 6 in 11% of the specimens), and a lower number of femoral pores. Mauritanian *Acanthodactylus dumerili* can be distinguished from sympatric *A. senegalensis* by the scales on the dorsum which are not much larger than the flank scales, by the dorsal scales which are less strongly carinate (89% of Mauritanian *A. dumerili* specimens have CARE code 3, 4 or 5 against 10% of *A. senegalensis* specimens; Table 3) and a different colour pattern. Males of *A. dumerili* do not have flanks clearly darker than the dorsum, and females *A. dumerili* are not clearly lineated. Dark elements never disappear from the pattern of *A. senegalensis* as they do in 32% of the Mauritanian *A.dumerili*. The same characters separate *A. senegalensis* from allopatric specimens of *A. dumerili*. In addition, *A. dumerili* specimens outside Mauritania and Western Sahara have always 13 or more rows of ventrals (89% of *A. senegalensis* specimens have 12 or fewer rows of ventrals).

Geographical variation. Specimens from continental Sahara differ from the Mauritanian animals by their higher number of dorsal scales (on average, 51.74 longitudinal rows at mid-body in the Saharan specimens, 57% of the animals have more than 49 dorsal rows; in Mauritania, the mean number of dorsal scale rows is 46.94 and 81% of the specimens have
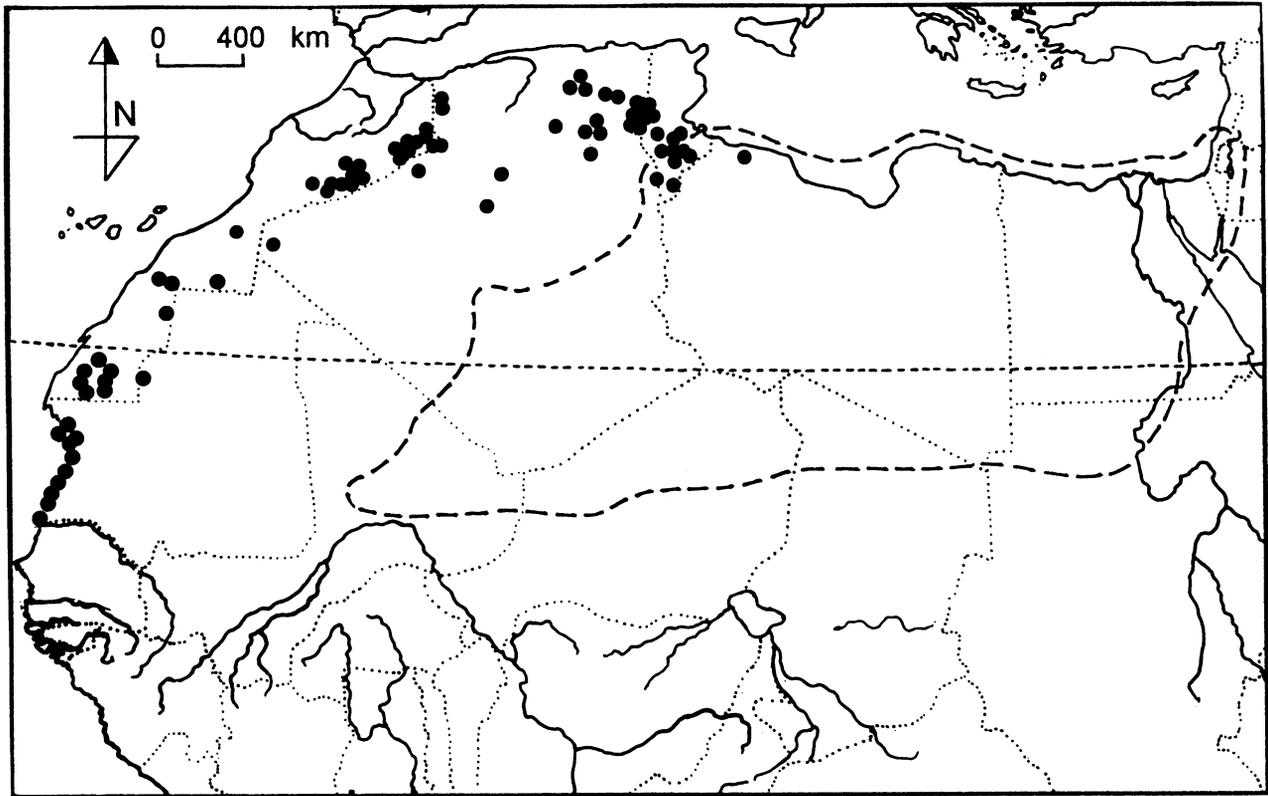
Figure 18. Geographical distribution of *Acanthodactylus dumerili*. Dotted lines indicate the approximate limits of the distribution of *Acanthodactylus scutellatus* in the Sahara. Data from Salvador (1982), Bons & Geniez (1996), Nouïra (1996), this study.

fewer than 50 dorsal rows; cf. Table 2), their higher number of ventrals (14 or more longitudinal rows in 82% of the Saharan specimens; fewer than 14 longitudinal rows in 70% of the Mauritanian specimens; Table 2, Fig. 7). Saharan subadults and adults animals almost always show numerous black dots on the dorsum (three colours dorsal pattern), whereas in 32% of the Mauritanian adult specimens the dark elements disappear (two colours dorsal pattern, whitish mottling on a pale ground colour). Moreover, in the continental Saharan animals, each dorsal black spot usually covers several scales, whereas in *Acanthodactylus dumerili* from Mauritania, these spots are often reduced to a single black scale.

In Western Sahara, in contrast to what is found in Mauritania, *A. dumerili* is absent from the oceanic littoral fringe where it is replaced by *A. aureus*. In these continental localities of Western Sahara, the colour pattern is similar to the one found in Morocco, Algeria and Tunisia, but these specimens have fewer black spots on the back and a reduced number of longitudinal rows of ventral plates (12 in our 10 specimens) and femoral pores (from 16 to 20 for the Western Sahara specimens against a mean of 19 [15–23] for the spec-

imens of coastal Mauritania and 20 [16–26] for the specimens of continental Sahara).

Among our Saharan sample, specimens from eastern Algeria, Tunisia and Libya differ from those of Morocco and western Algeria by a reduced number of dorsal scale rows (39–58, mean = 47.96 for the 'eastern' specimens against 48–69, mean = 58.18 for the 'central' specimens; Fig. 8) and the presence of 13 longitudinal rows of ventral plates in 27% of the 'eastern' specimens (see also Fig. 7). Slight differences also exist in the dorsal coloration: some eastern specimens loose the light patches which give the characteristic mottled pattern to the *scutellatus* group, leaving only indistinct dark spots on a beige ground colour. As discussed above (see 'Results'), the geographical variation is complex, with some characters (e.g. ventrals number) opposing the 'western' animals to the specimens from the rest of the range, whereas other characters (e.g. dorsals number) separate the 'central' specimens from both 'eastern' and 'western' animals, and many specimens cannot be assigned to their respective population. Thus, for the time being, we refrain from proposing subspecific status for any of these populations.

ACANTHODACTYLUS LONGIPES BOULENGER, 1918

Acanthodactylus scutellatus var. *longipes* Boulenger, 1918: 154. Name-bearing type: Boulenger does not refer in his original description to any specimen but he clearly used several individuals housed in the British Museum and coming from the Algerian Sahara. He latter talks about five specimens (Boulenger, 1921), which are apparently all syntypes. These specimens are (see also Salvador, 1982): BMNH 1946.8.30-32 (Wargla), BMNH 1946.9.3.75 (between the Wed Nça and El Alia), BMNH 1946.9.3.74 (El Wed, East of Tuggurt). As the original type series might have included more specimens, including members of other species, we select as lectotype the specimen BMNH 1946.8.4.31 (an adult male from Wargla, Algeria). Type locality: restricted by lectotype designation to Wargla [= Ouargla], Algeria.

Junior synonym. *Acanthodactylus longipes panousei* Bons & Girot, 1964: 327. Name-bearing types: two syntypes MNHN 1963.1013-1014 (called 'holotypes' in Bons & Girot, 1964). Type locality: 'Bord de l'Erg Chebbi au niveau de Merzouga'.

Chresonyms. *Acanthodactylus longipes* Boulenger, 1918: Bons & Girot, 1964: 324; Salvador, 1982: 132; Arnold, 1983: 324.

Distribution (Fig. 19). Most of the Sahara from coastal Mauritania (this study; A. Foucart, pers. com.), southern Morocco (Tafilalet, Iriki) (Geniez & Soto, 1994), northern Mali, northern Niger, northern Chad, Algerian Sahara, Tunisia, Libya (Salvador, 1982; this study), to Egypt (Baha El Din, 1994).

Diagnosis. Medium-sized species (reaching 61 mm snout-vent length, mean: 52.4). The subocular in contact with three or (rarely) four supralabials in 100% of the individuals (Table 3) distinguishes *Acanthodactylus longipes* from *A. aureus* and *A. taghitensis*. Dorsal scales small, very numerous (range: 55–77, mean: 66.4; Table 2), elongate, smooth except in the vertebral area where they can be weakly to moderately keeled (code 3 or less in 97% of the individuals, no individual reaching code 5; Table 3, see Fig. 16d). Two rows or more of supraciliary granules in 86% of the individuals (Table 3, see Fig. 20b). Large number of longitudinal rows of ventral plates (15 or more in 95% of the individuals, range: 13–19, mean: 16.1; Table 2) arranged in oblique rows. Large number of femoral pores (range 17–28, mean = 21.5; Table 2). Coloration distinctive: flanks have a mottled pattern which usually tends to disappear towards the vertebral area (Fig. 20a). Females can have small, regularly disposed spots. Red spots can occur on the dorsum. Pileus weakly vermiculated with red. The combination of dorsal pattern and scale structure gives to the skin of *A. longipes* a fragile and translucent aspect. This spe-cies is further characterized by an elongate and pointed snout compared to *A. scutellatus audouini*, *A. dumerili* and *A. senegalensis*. See *A. senegalensis* for additional differences from that species. Several scalation characters separate *A. longipes* from the broadly sympatric *A. dumerili* and *A. s. audouini*. A strongly fragmented fourth supraocular is found in 73% of the *A. longipes* individuals but in 14% of the *A. dumerili* and 37% of the *A. s. audouini*. Granules are often inserted between the parietal plates in *A. longipes*, which is exceptional in *A. s. audouini* and *A. dumerili*. The number of longitudinal rows of ventrals is often nearly diagnostic: most *A. longipes* (81% of the specimens) have 16 ventrals rows or more, which is extremely rare in *A. s. audouini* (1% of the specimens) or *A. dumerili* (less than 1% of the specimens). *Acanthodactylus longipes* is the only species to possess dorsal scales small, elongate and smooth except in the vertebral area. The dorsal scales in the vertebral area are only weekly keeled, a further distinction from most *A. s. audouini* and *A. dumerili*: 84% of the *A. longipes* individuals have CARE code 2 or (rarely) 1, whereas less than 2% of the *A. dumerili* specimens have CARE code 2 or 1. The typical dorsal pattern is also characteristic. It should be noted, however, that some *A. longipes* females present a uniformly pinkish coloration with small dark spots, making them similar to *A. dumerili* or *A. s. audouini*, although their pattern is less contrasting than in these species. In conclusion, although no single character is fully diagnostic between *A. longipes* and the sympatric species, a combination of several scalation and coloration features will enable to identify the vast majority of specimens. In ambiguous cases, the elongate and pointed shape of the snout and the structure of the dorsal scales are often useful, although occasional individuals remain impossible to identify safely. It should be stressed than other characters proposed by earlier authors (number of supralabials in contact with the subocular, length of hindlegs) proved to be useless.

Geographical variation. The subspecies *panousei*, described from south-eastern Morocco, does not seem to be valid (Salvador, 1982; own results). In some populations from the eastern part of the species distribution, specimens tend to have more strongly carinate dorsal scales.

ACANTHODACTYLUS AUREUS GÜNTHER, 1903

Acanthodactylus scutellatus aureus Günther, 1903: 298. Name-bearing type: Günther's original description was based on 'a considerable number of this species'. More than 30 specimens were examined from Rio de Oro (former Western Sahara) and several from Southern Algeria. The syntypes listed by Salvador
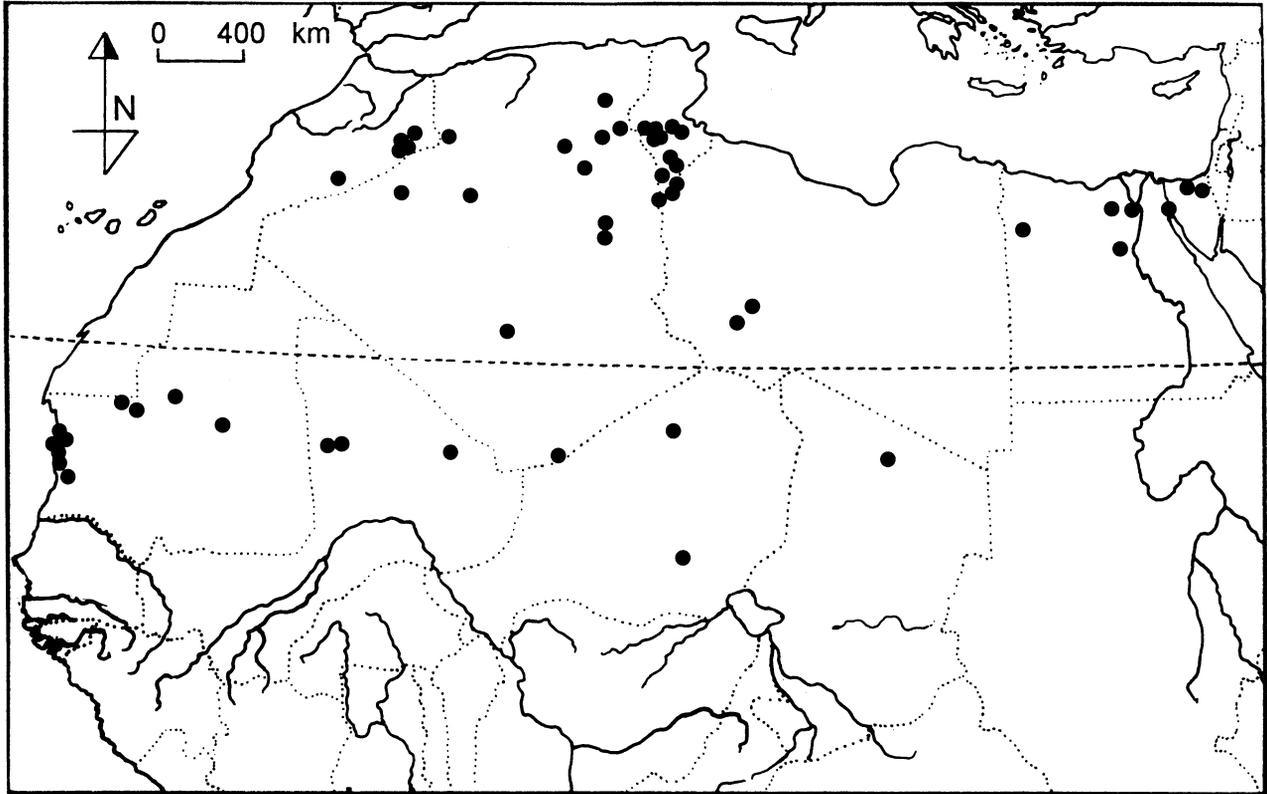
Figure 19. Geographical distribution of *Acanthodactylus longipes*. Data from Salvador (1982), Baha El Din (1994), Bons & Geniez (1996), Nouïra (1996), this study.

(1982) are thus clearly a part of the types only: BMNH 1946.8.5.2-26, USNM 33109-33111, MNHN 1918.11-12. The syntypes from Southern Algeria are most likely specimens of *A. taghitensis,* but we could not find them. It is thus important to select a lectotype which belongs to *A. aureus* as understood now. We select as lectotype the specimen MNHN 1918-11, an adult male from 'Villa Cisneros' [= Dakhla], Western Sahara. Type locality: originally Rio de Oro and Southern Algeria, restricted to 'Villa Cisneros' [= Dakhla], Western Sahara, by lectotype designation.

Chresonyms. *Acanthodactylus inornatus aureus* Günther, 1903: Bons & Girot, 1964: 330. *Acanthodactylus aureus* Günther, 1903: Salvador, 1982: 122; Arnold, 1983: 328 (part).

Distribution (Fig. 21). Saharan oceanic fringe from Agadir (Morocco) to the Cap Blanc Peninsula (Western Sahara/Mauritania). The species is further encountered at two points in Mauritania (Salvador, 1982) and three stations of the Senegal coast (Böhme, 1978; Salvador, 1982). It reaches as far as 200 km inland in Western Sahara (pers. obs.). The animals from Fderik (Mauritania) are referable to *Acanthodactylus taghit-*

ensis. The Atar locality (specimen BMNH 1982.294) is wrongly positioned (far inland) in Salvador (1982) and Arnold (1983). It is in fact situated near Nouadhibou, i.e. near the coast. *A. aureus* is the most common lacertid on the whole oceanic side of Western Sahara.

Diagnosis. A species of variable size according to populations (reaching a maximum snout-vent length of 65 mm, mean: 53.65). Only two supralabials in contact with the subocular in 99% of the specimens, as a result of the fusion of the third and fourth (rarely the fourth and fifth) supralabials (Table 3). Dorsal scales relatively large, not very numerous (range: 38–59, mean: 46.7; Table 2), slightly larger on the dorsum than flanks, pyramidal, and obtusely carinate (CARE code 3 or 4 in 99% of the individuals; Table 3). Fewer than two rows of supraciliary granules in 97% of the individuals (Table 3). Generally 14 or (less often) 13 longitudinal rows of ventrals (in 77% of the specimens, range: 12–17; mean: 13.9; Table 2). Femoral pores rather numerous (range: 19–26, mean: 21.2; Table 2). Dorsal coloration distinctive, comprising dark rectangular blotches longitudinally aligned over light longitudinal lines. In old males, however, the dark blotches

Figure 20. (a) *Acanthodactylus longipes*, male, MNHN 1997.4771, Azzefâl (Mauritania). (b) *Acanthodactylus longipes*, male, lectotype, BMNH 1946.8.4.31, Wargla (Algeria), close-up of head. (c) *Acanthodactylus aureus*, male, PHG 35, Sidi Ouassaï, near Massa (Morocco), picture by P. Geniez. (d) *Acanthodactylus taghitensis*, female, PHG 28, 5 km SSW of Taghit (Algeria), picture by M. Geniez.
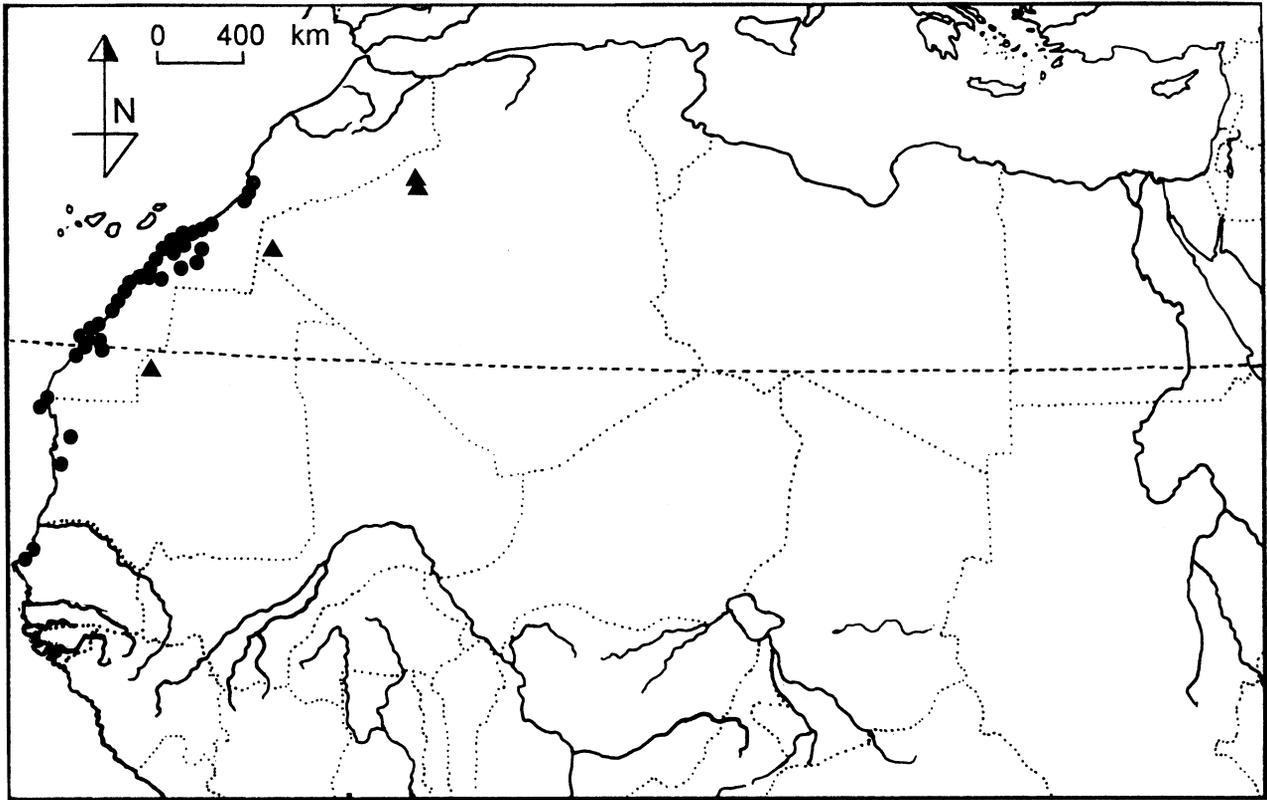
Figure 21. Geographical distribution of *Acanthodactylus aureus* (circles) and *Acanthodactylus taghitensis* (triangles). Data from Böhme (1978), Salvador (1982), Geniez & Foucart (1995), Bons & Geniez (1996), Hasi *et al.* (1998), Donaire *et al.* (2000), this study.

and the light lines can produce a mottled or even reticulate pattern. A golden yellow tone appears on the dorsum of males during reproduction. Further characterized by a concave forehead following a short but strongly acuminate snout. Supralabials sometimes uniformly greyish or purplish-blue. Easily separated from *A. scutellatus*, *A. senegalensis*, *A. dumerili* and *A. longipes* by the peculiar conformation of the supralabial scales bordering the subocular. The exceptional individuals lacking this feature can be recognized by the typical habitus of the species, resulting from its distinctive colour pattern and peculiar head profile. For distinction from *A. taghitensis*, see that species.

Geographical variation. None documented.

ACANTHODACTYLUS TAGHITENSIS GENIEZ & FOUCART, 1995

Acanthodactylus taghitensis Geniez & Foucart, 1995: 7. Name-bearing type: MNHN 1995.1201, holotype by original designation. Type locality: '36 km au sud-sud-ouest de Taghit (30°41′N, 2°07′W), région de Beni

Abbès, Algérie' (= 36 km SSW of Taghit, Beni Abbès area, Algeria).

Chresonyms. *Acanthodactylus aureus* Günther, 1903: Arnold, 1983: 328 (part).

Distribution (Fig. 21). Southern Algeria, near Taghit (Beni Abbes area), and Mauritania, at Fderik (see examined material). Recently discovered at El Gor (27°28′N, 7°56′W), near Tindouf, Algeria (Donaire *et al.*, 2000). This new locality suggests that the species might have a more or less continuous distribution along the border area between Algeria and Morocco and between Western Sahara and Mauritania.

Diagnosis. This species is only known from three adult females and three adult males (including the specimens reported by Donaire *et al.*, 2000). Probably closely related to *Acanthodactylus aureus*, with an allopatric distribution. Like *A. aureus*, but can be distinguished from this species by the abrupt transition between the small flank and large dorsal scales, the former being twice as large as those of the flanks, by its wider, bulkier head, and its strongly raised nostrils. Colour pattern similar to that seen in *A. aureus*. No information on the back colour in adult males.

Geographical variation. None documented.

ECOLOGICAL REQUIREMENTS OF THE SPECIES OF THE *ACANTHODACTYLUS SCUTELLATUS* GROUP IN MAURITANIA

All the species of the *scutellatus* group live exclusively in sandy areas, but they usually prefer different sand types, even if several species can occur together within the same ecotone areas.

In Mauritania, *Acanthodactylus aureus* seems to be restricted to the Cap Blanc Peninsula, where in the absence of any competitor (it is the only *Acanthodactylus* present in that area), it occupies all types of sandy habitats, from the large littoral dunes to the smallest sand banks on hardened soils.

Acanthodactylus longipes seems to reach the littoral zone by following the large continental dunes of bare sand which constitute the western prolongation of the ergs from the Azeffâl and Akchâr regions (Mauritania). In Morocco, it is similarly restricted to the only available large Saharan eolian dunes, the erg Chebbi and the ergs of Mhamid – Iriki, whereas *A. dumerili* lives on the periphery of those ergs (cf. Geniez & Soto, 1994). In Agnéitir, Mauritania, *A. longipes* was observed in depressions with scattered vegetation between the dunes. This is also in agreement to observations in Morocco, where *A. longipes* reaches high densities in depressions between dunes providing that they are isolated from surrounding habitats. When such depressions are not isolated, they are colonized by *A. dumerili*, which excludes *A. longipes* more or less completely. The occurrence of *A. longipes* at Iouik cape, the northernmost locality in Mauritania, far away from any inland dunes complex, cannot yet be explained.

In Mauritania, *Acanthodactylus senegalensis* seems to reach its highest densities on the red continental sand dunes of eolian origin covered with the plant (*Euphorbia balsamifera*), whereas *A. dumerili* is mainly found on the white littoral sand dunes of marine origin. South of the North-Nouakchott station, the amount of rainfall increases and *Euphorbia* are more frequent. From there, *A. senegalensis* is the most abundant member of the *scutellatus* group and *A. boskianus* is constantly, rather than sporadically, present. North of this site, *A. senegalensis* persists mainly as a relic on the red continental sand dunes isolated from the large dune beds of the ergs Azzefâl, Agneïtîr and Akchâr (Ineich, 1997). Where these formations are in contact, both species can be encountered in close parapatry. The ecology of *A. senegalensis* (under the name *A. dumerili*) has been studied in the Dakar area in Senegal by Cissé & Karns (1978).

Acanthodactylus dumerili is the only taxon which inhabits the white littoral sand dunes and the shell sands with *Zygophyllum gaetulum* in Mauritania (in Senegal, *A. senegalensis* inhabits this habitat also [M. Cheylan, pers. com.], a fact that may be explained by the absence of *A. dumerili* in Senegal). In Mauritania, the station of Tamzakt (see Fig. 1) constitutes an area of great interest for the understanding of the distribution patterns in the species of the *scutellatus* group in Mauritania. The white littoral sand dunes next to the beach are separated from the red continental dunes by the Aftout-es-Saheli, a salted, sterile area regularly flooded by the sea and which can constitute a barrier for lizards. *Acanthodactylus senegalensis* is only found east of this area, in red continental sands, whereas *A. dumerili* is restricted to the white littoral dunes. Immediately east of those littoral dunes, the edge of the Aftout-es-Saheli is constituted by a hardened soil where numerous euphorbs grow. The only *Acanthodactylus* present is *A. boskianus*, abundant and accompanied by *Latastia longicaudata* and *Agama boueti*, which are totally absent on the white littoral sand dunes. A similar situation occurs south of the Tamzakt station.

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APPENDIX I

List of examined specimens. Museum acronyms follow Leviton *et al*. (1985) except Estación Biologíca de Doñana of Sevilla, Spain (EBD); collection of Charles-P. BLANC, Montpellier, France (CPB); Laboratoire de Biogéographie et Ecologie des Vertébrés de l'EPHE, Université Montpellier II, France (EPHE), and pictures collection of Philippe Geniez (PHG). Data concerning the examined material are presented in the following way: locality; deposit location and collection number; examined sample size (in brackets). Geographical co-ordinates are given in degrees, minutes, and hundredths of minutes. Note that some specimens are not included in the multivariate analyses (specimens with missing data, non adult specimens, specimens seen in pictures only).

Acanthodactylus scutellatus audouini (n = 131)
Niger: In Bkikas, Tamesna; EPHE AF12 (1). Ajir, 110 km north-east of Arlit, Tamesna; EPHE AF13, AF15 (2). Imourarem, 65 km south-south-west of Arlit, Tamesna; EPHE AF14 (1). North of the Zeline well; MNHN 1936.76 (1).

Algeria: Aoulef; EPHE 0261, 0361, 0461, 0561 (4). Ouallen; EPHE 4161-4162, 6462, 7562, HB2 (5). Tesejefite (Ouallen area); EPHE 7362 (1). Foum d'Ahagerine (Ouallen area); EPHE 7262 (1). Wadi of Ahagerine (Ouallen area); EPHE 7162 (1). Southern Tassili valley bottom (Ouallen area); EPHE 6562 (1). Djanet; EPHE/CNHM 80007 (1).

Tunisia: Tripolitan Limès, 60 km west of Gabès; EPHE BGP.14.58, 15.58, 16.58 (3). Wadi El Kreïl (syntype of *Acanthodactylus scutellatus* var. *audouini*); BMNH 1920.1.20.3006 (1). Douirat; BMNH 91.5.4.85-91A (8). Aloues Saïour, crossing between the track and the Edgelé pipe-line; CPB 2820L (1). 14–15 km west of Bordj Bourguiba; CPB 2815L (1). Dar Zaoui, Chaalonya; CPB 1235L-1238L (4). 15 km north of Remada; CPB 2457L, 2459L, 2462L, 2464L, 2466L, 2468L-2469L, 2471L-2473L, 2475L-2478L (14). 13 km north of Remada; CPB 2798L, 2801L (2). Wadi Oum Souikh, near Bir Oum Souikh (18 km east of Remada); CPB 2862L (1). 4 km beyond Beni Kheddache towards Ghomrassen; CPB 1358L-1360L, 1473L, 1476L-1479L, 1481L, 1486L-1487L (11). 4 km beyond Tatahouine towards Kirchen; CPB 1394L, 1397L (2). 4 km beyond Tatahouine towards Kridhaou; CPB 1402L (1).

23 km beyond Tatahouine towards Remada; CPB 1122L, 1124L, 1125L, 1127L-1130L, 1132L, 1136L, 1139L, 1168L, 1170L, 1171L, 1173L, 1174L, 1176L-1179L, 1181L, 1183L, 1194L-1196L, 1199L, 1205L-1207L, 1209L, 1280L (30). 45 km beyond Tatahouine towards Remada, departure of the track to Bir Amir; CPB 2454L, 2482L-2483L (3). 47 km beyond Tatahouine towards Remada, 1,5 km south of the departure of the track to Bir Amir; CPB 2479L-2481L (3). 65 km beyond Tatahouine towards Remada; CPB 2451L-2453L (3). Henchir Es-Siane, Chaalonyia; CPB 1226L (1). El Borma; CPB 735L, 737L (2). Bordj Bourguiba; CPB 2817L-2819L (3). Track to Bir Amir, 5 km west of the road Tatahouine-Remada; CPB 820L, 826L (2). Toguelmit (south of Ben Gardane); CPB 651L (1). Ras El Abiod (16 km south of Bordj Bourguiba); CPB 2826L (1). Bir Soltane; CPB 641L (1). Wadi Dekouk; CPB 2485L (1). Plain of the Djebel Semmama; CPB 2696L (1). Tunisia, unknown precise locality; CPB 3786 (1).

Libya: Bou Ngem = Abu Njaym (Tripolitania); EPHE/CNHM 82965 (1). Khoms, Tripoli (syntypes of *Acanthodactylus scutellatus* var. *audouini*); BMNH 1913.12.30.6-9 (4).

Sudan: Wadi Halfa (syntypes of *Acanthodactylus scutellatus* var. *audouini*); BMNH 97.10.28.315-319 (5).

Acanthodactylus senegalensis (n = 187)
Senegal: Sangaleam, near Rufisque; MNHN 1918.43 (holotype of *Acanthodactylus senegalensis*). Mboro sur Mer; ZFMK 17433-17453, 17455-17467 (35). Nianing; ZFMK 17508-17520 (13). Pikine, near Dakar; ZFMK 17499-17507 (9). Niakoul Rap; ZFMK 20148-20152 (5). Cambérène; ZFMK 20153-20157 (5). Malika-Plage; ZFMK 20159-20163 (5). Between Kayr and Bayakh; ZFMK 20158 (1). 20 km south of Richard-Toll; ZFMK 17468-17484 (17). Ndioum; ZFMK 17485-17491 (7). 10 km west of Linguére; ZFMK 17492-17498 (7). Coastal sands north of Dakar; EPHE MCh.1-3 (3). Senegal, unknown precise locality; MNHN 7029, 1991.2947 (2).

Mali: Goundam; MNHN 1932.8, 1932.11 (2). M'Bouna; MNHN 1932.9 (1).

Mauritania: 12 km north of Nouakchott, 18°12′88″ N, 16°02′06″ W; MNHN 1997.4628-4635, 1999.9213 (9). 12 km north of Nouakchott, 18°12′90″ N, 16°01′28″ W; MNHN 1997.4636-4639 (4). Tamzakt, 17°24′41″ N, 16°03′66″ W; MNHN 1997.4649-4682 (34). 4 km north-west of Tamzakt; MNHN 1997.4683-4689 (7). Continental red dunes of Tamzakt, 17°25′58″ N, 16°02′84″ W; MNHN 1997.4690-4692, 4701 (4). Akchar, 120 km north of Nouakchott, 19°07′50″ N, 16°16′50″ W; MNHN 1997.3829 (1). Dar es Salam, 26 km south of Chott

Boul, 16°22′32″ N, 16°28′19″ W; MNHN 1997.4749-4750 (2). Chott Boul, 16°35′46″ N, 16°26′38″ W; MNHN 1997.4720 (1). Tanit, 60 km north of Nouakchott, 18°36′50″ N, 16°06′50″ W; MNHN 1997.3860, 1997.3863 (2). 10 km north of Nouakchott, 18°09′06″ N, 16°01′43″ W; MNHN 1997.4627 (1). 156 km beyond Nouakchott towards Rosso, red continental dunes; MNHN 1997.4751-4752 (2). Tafarit cape, around the village, 20°07′50″ N, 16°15′41″ W; MNHN 1997.4762 (1). Hasseï Gâboûn, 25 km northeast of Nouakchott, 18°16′22″ N, 15°51′01″ W; EPHE AF11, 16-19 (5).

Acanthodactylus dumerili (n = 578)
'Sénégal' (probably not Senegal as understood today): unknown precise locality; MNHN 2759, holotype of *Lacerta dumerili* (1).

Morocco: Flat open country of Tagounite (south of Zagora); EPHE Tagounite A-B (2). Zaouia Sidi Salah, near Tagounite (south of Zagora); EPHE Tagounite 1-5 (5). 2 km beyond Zagora towards Tagounite; EPHE Zagora 1 (1). Dunes of Bounou, between Tagounite and Mhamid; EPHE Bounou 1-2 (2). Taouz; Y. Vial; EPHE Sau10 (1). Erg Chebbi; EPHE Sau14.1-14.2 (2). 23 km beyond Errachidia towards Erfoud; EPHE st12m.1, st12m.2, st12f (3). 10 km beyond the Errachidia-Erfoud road towards Boudenib; EPHE st6m.1-5 (5). 36 km beyond Aïn Chair towards Bou Arfa, colour pictures PHG Ph1-2 (2). 12 km beyond Mecissi towards Rissani; colour pictures PHG Ph3 (1). 2 km beyond Mecissi towards Alnif; colour pictures PHG Ph4 (1). Erfoud-Merzouga track, 3.5 km before wadi Talremt; colour pictures PHG Ph5 (1). Erg of El Maâdid (north of Erfoud); colour pictures PHG Ph6-7, Ph11 (3). 12.5 km beyond Erfoud towards Errachidia; colour pictures PHG Ph10 (1). North-western fringe of the erg Chebbi; colour pictures PHG Ph12-14, Ph25 (4). Northern fringe of the erg Chebbi; colour pictures PHG Ph27 (1). R'Gabi dam, 2 km north of Oulad Driss (wadi Drâa valley); colour pictures PHG Ph15 (1). Erg Ebidliya, north of the dayet Chegaga (south-west of Mhamid); colour pictures PHG Ph22-23 (2). Morocco, unknown precise localities; EPHE 48, 52, 53m, 53f, 54, 55m, 55f, 56-59, 61, 63, 65-67, 72, A48, A63, A65, B61, B63, B65, C61, R114, BGP.164. 1882, 182. 1880, 191. 1881, Ac2778, Ac3778 (30).

Algeria: Wadi Saoura, Beni Abbes area; EPHE Saoura 1-3, 5 (4). Beni Abbes; EPHE BA1, 10-12 (4). Hodna; MNHN 8539 (1). Laghouat; MNHN 8538B (syntype de *Acanthodactylus dumerili* var. *exiguus*); BMNH 1920.1.20.1349e1-e3 (4). Bled Ahmar (syntype of *A. d.* var. *exiguus*); BMNH 1920.1.20.1349c (1). Between Tilremt and Toughourt (syntype of *A. d. exiguus*); BMNH 1920.1.20.1349d (1). Biskra; BMNH 1920.1.20.1349g1-g2 (2). Hadjira; BMNH

1920.1.20.1349 (1). 20 km beyond Bou Saada towards Biskra; CPB 1285L (1). Half way between Ouargla and Ghardaïa; CPB 1253L, 1255L (2). 10 km east of Bou Aroua (near the Tunisian frontier); CPB 1251L (1).

Tunisia: Dunes of Nouïl, Kebili; EPHE Tun1-2 (2). Gouifla bridge, 25 km north of Tozeur; CPB 352L-353L, 357L-358L, 367L-370L, 379L-380L, 384L-385L, 388L-389L, 486L-487L, 491L-492L, 494L, 496L-502L, 504L-505L, 618L-620L, 622L-623L, 625L, 657L, 707L-708L, 710L, 712L-714L, 767L-768L, 782L-784L, 786L-787L, 791L-793L, 796L-797L, 829L, 997L, 999L, 1542L, 2217L, 2219L, 2242L-2244L, 2246L-2250L, 2252L-2258L, 2260L-2262L, 2264L-2266L, 2268L, 2271L, 2273L-2274L, 2277L-2278L, 2281L-2282L, 2284L, 2290L, 2308L-2314L, 2316L (98). Djebel Zanghar; CPB 2829L (1). Hazoua, Algerian frontier; CPB 1538L-1539L, 1583L-1591L (11). 5 km south of Hazoua; CPB 2955L (1.18 km south of Hazoua; CPB 2958L (1). Nefta, near Hazoua; CPB 123L (1). Bir Zouita; CPB 2892L-2893L, 2895L-2897L, 2899L, 2901L-2902L (8). Djebel 5 km north of the Djebel Tabouna; CPB 1742L (1). 4 km beyond Beni Kheddache towards Ghomrassen; CPB 1356L, 1483L, 1485L, 1488L (4). Sidi Lakbache, Djebel Djebil; CPB 2918L (1). Chéraff, Dahar; CPB 1393L, 1395L, 1398–1399L, 1401L, 1433L,1435L, 1438L, 1441L-1443L, 1445L (12). Chott El Rharsan side, El Hamma-Chebika track; CPB 766L (1). Garaet El Khil, erg Djeneien; CPB 2852L-2853L, 2855L-2856L (4). Wadi Djeneien; CPB 2841L (1). 2 km west of Bir Rhezène; CPB 2940L, 3003L (2). Bir El Aïn; CPB 2964L (1). Ksar Rhilane, 'Colonne Leclerc' memorial; CPB 2384L (1). South of Ksar Rhilane, pipe-line road; CPB 648L (1). Aloues Saïour, at the crossing of the track and the Edgelé pipe-line; CPB 2830L-2833L, 2837L, 2883L (6). Northern foothill of the Djebel Tebaga, 52.5 km beyond Gabès towards Chenini; CPB 1917L (1). Eastern slope of the Djebel Tebaga, near Kebila; CPB 1909L-1910L (2). Rhdima (between Zaafrane and Sabria); CPB 1898L, 1900L-1901L, 1903L-1905L (6). 3 km west-south-west of Zaafrane; CPB 1919L-1920L (2). 10 km beyond Sabria towards Rhdima; CPB 1891L-1897L (7). Bir El Halma; CPB 2882L, 2884L-2885L (3). Kattana, south of Gabès; CPB 284L (1). Dahrat El Caïd; CPB 2921L (1). Between Tamerza and Midès; CPB 1396L (1). 34 km west of Bordj Bourguiba; CPB 2809L-2812L (4). 13 km beyond Remada towards Dehibat; CPB 2799L (1). Bou Biakra road, PK.55; CPB 1279L-1282L (4). Zafrana (near Douz); CPB 853L (1). Oued Dzou, 12 km east of the Kébili-Douz road; CPB 2873L (1). 64 km beyond Gapa towards Tozeur; CPB 307L-308L (2). Between Tozeur and Nefta; CPB 309L (1). 10 km south-west of Nefta; CPB 1557L (1). Bir El Rey; CPB 833L-834L (2). Djebel Nekrif (south-east of Remada); CPB 2797L (1). Tiarete, military post 20 km north of the wadi M'Cheguigia; CPB 716L, 718L (2).

Aïn Tiarete, palm-grove south of the wadi Mechiguir; CPB 2858L (1). El Borma; CPB 734L, 739L, 741L, 2843L (4). Wadi Mecheguig; CPB 715L (1). Between the Negga and Tombar oasis; CPB 1907L-1908L (2). Bir El M'izil (56 km south of Kébili); CPB 2906L-2907L (2). El Aïmaa (76 km south of Kébili); CPB 2909L-2911L (3). Sahane El Mahadess (106 km south of Kébili); CPB 2938L-2939L, 3002L (3). Exit of Degache towards Tozeur; CPB 1352L (1). 3 km east of Tamezret, new city; CPB 1889L (1). Ras El Abiod (16 km south of Bordj Bourguiba); CPB 2823L (1). Guelb El Anz (50 km north of Bordj El Khadra); CPB 2865L, 2869L (2). Military camp of Rejem Maatoug; CPB 2886L-2887L (2). Margueb Mohamed; CPB 2889L-2890L (2). Mazouzia Kralet Et-Tabel; CPB 2941L-2944L, 3005L, 3008L-3010L (8). 3 km south-east of Bir Roumia; CPB 2960L-2961L (2.8 km east of Ksar Rhilane; CPB 2980L-2981L (2). Tunisia, unknown precise localities; CPB 3235, 3735, 3783, 3794, 3820, 3827, 3830 (7).

Libya: Tripoli (lectotype of *Scapteira inornata*); BMNH 1946.9.3.76 (1).

Mauritania: 12 km north of Nouakchott, 18°12′88″N, 16°02′06″W; MNHN 1997.3873-3900, 1997.4580-4625, 1997.4645-4648, 1999.9212; MNHN 1997.4642-4644 (82). 12 km north of Nouakchott, 18°12′90″N, 16°01′28″W; MNHN 1997.4626 (1). 800 m south of the Tamzakt camp, 17°24′41″N, 16°03′66″W; MNHN 1997.4698-4700 (2). White coastal dunes, 2 km north of the Tamzakt camp located at 17°25′29″N, 16°08′68″W; MNHN 1997.4693-4697 (5). Continental dunes of Tamzakt, 17°25′58″N, 16°02′84″W; MNHN 1997.4702-4703 (2). Chott Boul, 16°35′46″N, 16°26′38″W; MNHN 1997.4707-4710 (4). Chott Boul, 16°35′15″N, 16°25′79″W; MNHN 1997.4711-4713 (3). 6 km south of the Chott Boul, 16°38′01″N, 16°26′60″W; MNHN 1997.4714-4719 (6). 15 km south of the Chott Boul, 7.5 km north of Lekseyr, 16°28′54″N, 16°27′42″W; MNHN 1997.4704-4706 (3). 3.4 km north of Dar es Salam, white coastal dunes, 16°23′66″N, 16°28′71″W; MNHN 1997.4723-4726 (4). Coastal dunes of Dar es Salam, 16°23′85″N, 16°28′56″W; MNHN 1997.4738-4748 (11). Dar es Salam, 26 km north of the Chott Boul, 16°22′32″N, 16°28′19″W; MNHN 1997.4722, 1997.4792, 1999.9210 (3). 2.5 km from Dar es Salam, coastal dunes, 16°22′59″N, 16°29′15″W; MNHN 1997.4727-4737, 1997.4753 (12). Akchar, 120 km N. Nouakchott, 19°07′50″N, 16°16′50″W; MNHN 1997.3814-3828, 1997.3830-3835 (23). Akchar, 120 km N. Nouakchott, 19°07′52″N, 16°13′78″W; MNHN 1997.3801 (1). Akchar, 19°07′90″N, 16°15′60″W; MNHN 1997.3802 (1). Akchar, 19°06′50″N, 16°12′02″W; MNHN 1997.3803-3805, 1997.3807-3813 (10). Tanit, 60 km north of Nouakchott, 18°34′60″N, 16°05′42″W; MNHN 1997.3840-3847, 1997.3861-

3862, 1997.3864, 1997.3848-3856; MNHN 1997.3838-3839, 1999.9203 (23). Near Tanit, 18°35′99″ N, 16°04′74″ W; MNHN 1999.9200-9201 (2). Near Tanit, 'Maison de la Mendès', 18°36′81″ N, 16°06′73″ W; MNHN 1997.3836-3837 (2). Near Tanit, 3 km north of 'Maison de la Mendès'; MNHN. 1997.3865 (1).10 km north of Nouakchott, 18°09′06″ N, 16°01′43″ W; MNHN 1997.3866-3872, 1997.4640-4641 (9). Banc d'Arguin National Park, Serreni; MNHN 1997.4754-4759, 1999.9202 (7). Azeffâl, 19°49′03″ N, 16°11′70″ W; MNHN 1997.4768-4769 (2). Blaouakh, 18°30′98″ N, 16°04′45″ W; MNHN 1997.3759-3781 (23). Tiouilît village, camp; MNHN 1997.4788, 1997.4790 (2). North of Tiouilît, El Hazra, 18°58′43″ N, 16°12′07″ W; MNHN 1997.4787, 1997.4789 (2). El Mhaïjrât, 19°02′01″ N, 16°12′62″ W; MNHN 1997.4786 (1). El Mhaïjrât, Hassi Loubbou, 19°02′43″ N, 16°09′30″ W; MNHN 1997.4785 (1). Agneïtîr, 145 km north of Nouakchott, 19°24′74″ N, 16°12′86″ W; MNHN 1997.4776-4777 (2). Agneïtîr, 145 km north of Nouakchott, 19°24′78″N, 16°15′07″W; MNHN 1997.4778. Agneïtîr, 145 km north of Nouakchott, in a between dunes depression, 19°24′51″ N, 16°16′35″ W; MNHN 1997.4779 (1). Agneïtîr, Elb Aouarouâr, 30 km from Jreïf, 19°11′13″ N, 16°19′25″ W; MNHN 1997.4775, 1997.4780 (2). Agneïtîr, Manate, 19°26′66″ N, 16°16′95″ W; MNHN 1997.4774 (1). Tafarit Cape, around the village, 20°07′32″N, 16°15′41″W; MNHN 1997.4763-4766 (4). Southern tip of Tidra Island, 19°35′95″N, 16°25′97″W; MNHN 1999.9214-9215 (2). Tagarit Cape, 20°09′75″N, 16°13′25″W; MNHN 1997.4761 (1). Unknown precise locality; EPHE AF1-3 (3). Akchar, base of a dune, 19°05′51″N, 16°15′25″N; MNHN 1999.9206 (one *Acanthodactylus* sp., possible hybrids between *A. dumerili* and *A. senegalensis*). Akchar, top of a dune, 19°04′83″N, 16°13′97″N; MNHN 1999.9204-9205, 1999.9207 (3 *Acanthodactylus* sp., possible hybrids between *A. dumerili* and *A. senegalensis*).

Western Sahara: Sidi Bulla (Laâyoune area); EBD 6219 (1). Wadi Meharitz; EBD 2453-2454 (2. Entayat; EBD 2439 (1). 98 km beyond Awserd towards Dakhla; colour pictures PHG Ph16-17 (2). 25 km north-west of Awserd; colour pictures PHG Ph18-21 (4).

Acanthodactylus longipes (n = 84)
Mauritania: 6 km south of the Chott Boul, 16°38′01″N, 16°26′60″W; MNHN 1997.4721 (1). Banc d'Arguin National Park, St-Jean area, inland; MNHN 1997.4760 (1). Azeffâl, 19°49′N, 16°08′W; MNHN 1997.4770-4771 (2). Azeffâl, 19°42′76″ N, 16°09′39″ W; MNHN 1997.4773, 4799 (2). Azeffâl, 19°42′06″ N, 16°09′52″ W; MNHN 1997.4772 (1). North of Tiouilît, El Hazra, 18°58′43″ N, 16°12′07″ W; MNHN 1997.4791 (1). 1.5 km east of Iouik, 19°52′25″ N,

16°18′40″ W; MNHN 1997.4767 (1). Agneïtîr, 145 km north of Nouakchott, 19°24′74″ N, 16°12′86″ W; MNHN 1997.4782-4784 (3). Agneïtîr, 145 km north of Nouakchott, 19°24′14″ N, 16°10′69″ W; MNHN 1997.4781 (1). Akchar, *c*. 120 km north of Nouakchott, 19°06′50″ N, 16°12′02″ W; MNHN 1997.3806 (1). Akreïdîl, 50 km north-east of Nouakchott, 18°25′55″ N, 15°35′58″ W; EPHE AF4-10 (7).

Niger: Erg of Admer, near the Algerian border; MNHN 1936.72 (1). 15 km west of Termet; MNHN 1960.186 (1).

Morocco: 25 km beyond the Erfoud-Errachidia road towards Boudenib; EPHE St7/1, St7/2 (2). 35 km west of Boudenib, sandy wadi; EPHE RCP249.st12m, 12f (2. North-western fringe of the Erg Chebbi; colour pictures PHG Ph8-9, 24 (3). North-western fringe of the erg of Iriki; colour pictures PHG Ph26 (1). Morocco, unknown precise locality; EPHE X1-6 (6).

Algeria: Beni Abbes; EPHE 375-376, BA2-9, 13-17 (15). Ouallen; EPHE HB1 (1). Ouargla (syntypes of *A. longipes*); BMNH 1946.8.4.30-32 (3). Bled Ahmar (syntype of *Acanthodactylus exiguus*); BMNH 1920.1.20.1349c2 (1). El-Oued, west of Touggourt; BMNH 1946.9.3.74; EPHE 1883, Léz249-251 (4). Wadi Nça, El Alia (Ghardaïa area); BMNH 1946.9.3.75 (1).

Tunisia: Gouifla bridge, 25 km north of Tozeur; CPB 626L (1). Erg Djeneien, near Bordj Bourguiba; CPB 2806L-2807L (2). 7 km north of Bordj El Khadra; CPB 2850L (1). Guelb El Anz (50 km north of Bordj El Khadra); CPB 2863L-2864L, 2867L-2868L (4). Mazouzia Kralet Et-Tabel; CPB 2945L, 3007L, 3014L (3). Erg of El Borma; CPB 2383L (1). Wadi Mechiguir, 10 km south of Tiarete; CPB 2847L (1). Dahrat El Gaïd; CPB 2920L, 2922L (2). 2 km before Sahane El Mahadess, 104 km south of Kébili; CPB 2924L, 2926L-2927L (3). Tunisia, unknown precise localities; CPB 3737, 3758, 3808, 3815 (4).

Acanthodactylus aureus (n = 85)
Senegal: Mboro sur Mer; ZFMK 17430-17432, 17454 (4).

Mauritania: Cap-Blanc peninsula, 20°46′75″ N, 17°02′85″ W; MNHN 1997.4796-4798 (3). Cap-Blanc peninsula, 21°07′46″ N, 16°58′15″ W; MNHN 1997.4793-4795 (3). Port-Etienne (= Nouadhibou); EPHE 371.74, MNHN 1923.160 (2). Atar, near Nouadhibou; BMNH 1982.294 (1).

Western Sahara: 26 km beyond Smara towards Laâyoune; EPHE PG1 (1). Amgrou, 25 km south of Tarfaya; EPHE Amgrou/1-6 (6). Wadi Lemsid, south of Tarfaya; EPHE Lemsid/1-2 (2). El Argoub; MNHN 1938.188 (1). Laâyoune; EBD 2022 (1). Ad-Dakhla; EBD 7220 (1). La Palangana Grande; EBD Pal1-7 (7).

Morocco: Agadir; MNHN 1980.1515-1517, 1980.1519-1525 (10). Souss estuary; EPHE Souss/1

(1). Kasba Et-Tahat, near the Souss estuary; EPHE St.39 (1). Sidi Rbat, Massa estuary; EPHE Massa/1 (1). Wadi Aouedri (north-east of the Khnifiss lagoon); EPHE St.T24/1-2 (2). Ed-Dzeroua, kreb above the Khnifiss lagoon; EPHE 13.4. 1961 (1). 27 km east/north-east of Tarfaya; EPHE 67.A.39/1-4 (4). Sidi Moussa d'Aglou; EPHE St.32/1-3, SMA/1-8 (11). Aoreora beach; EPHE BGP.28.55, 29.55; EPHE St.34 (3). Khnifiss lagoon; EPHE Khnifiss/1-3 (3). Graret El Khaïma, 10 km west of the Khnifiss lagoon; EPHE St.T22 (1). Hassi Zehar; EPHE St.T33/1-2 (2).

Morocco, unknown precise localities; EPHE 264.52/1-4, 40-42, 46, 264.56/1-5, 264.60 (13).

Acanthodactylus taghitensis (n = 4)
Mauritania: Fderik (= Fort-Gouraud); BMNH 1982.292-293 (2).

Algeria: 36 km south/south-west of Taghit, 30°41′N, 2°07′ W; MNHN 1995.1201 (holotype of *Acanthodactylus taghitensis*) (1). 5 km south/south-west of Taghit; colour picture by M. Geniez: PHG Ph28 (1).

APPENDIX II

KEY TO THE SPECIES OF *ACANTHODACTYLUS* OF THE SCUTELLATUS GROUP IN WESTERN NORTH AFRICA
(COLOUR CHARACTERS ARE ONLY VALID FOR ADULT SPECIMENS)

1a. Two supralabials in contact with the subocular; the supralabial in contact with the anterior part of the subocular originates form the fusion of two supralabials and is twice as long as the next supralabial....................................2
1b. At least three supralabials in contact with the subocular; the supralabial in contact with the anterior part of the subocular has roughly the same length as the next supralabial 3
2a. Dorsal scales not much larger on the back than the flanks. Rather pointed snout, nostril only slightly raised. Males in breeding period typically have golden tinges on the back. Distribution: South-western Morocco, Western Sahara, Mauritania and Senegal; does not reach further inland than 200 km from the coast..........*Acanthodactylus aureus*
2b. Dorsal scales on the back flat and twice as large as those on the flanks, with a sharp limit between the large scales of the back and the small scales on the flanks. Broader snout than the previous species and strongly raised nostrils. Distribution: inland in Mauritania and Algeria .... *Acanthodactylus taghitensis*
3a. Usually more than 14 longitudinal rows of ventral scales (on the longest row); numerous dorsal scales (from 55 to 80, 66 on average), small, smooth except on the vertebral area where they can be weakly keeled; usually two complete rows of supraciliary granules on each side; often some granules inserted between the cephalic plates in the occipital area; fourth supraocular strongly fragmented; long and pointed snout; in live animals, pileus often with reddish spotting; a warm, sandy to orange-tinged dorsal coloration, slightly translucent, often with reddish vermiculations (even in young specimens, but disappearing in preserved specimens); typically, spotted pattern on the flanks fading toward the vertebral area, which can be uniform. Distribution: all over the Sahara, from the Atlantic coasts to Israel. ....*Acanthodactylus longipes*
3b. Usually fewer than 15 longitudinal rows of ventrals; usually fewer than 65 dorsal scales (from 34 to 69, the highest mean being 53), uniformly and obviously keeled; no red spots on the pileus or on the body; often a grey colour on the back; mottled pattern, when present, regularly spread over the back, including the vertebral area. ....4 (Identification of these three species can be very difficult on single specimens. See systematic account above).
4a. Flat and strongly keeled dorsals, nearly twice as large on the back as on the flanks; usually fewer than 45 transversal rows of dorsals (34–53); usually 12 longitudinal rows of ventrals (10–14); usually fewer than 17 femoral pores (11–21); longitudinally striped dorsal pattern on females, less so on males. Distribution: mainly coasts of Senegal and Mauritania, locally east to Mali .... *Acanthodactylus senegalensis*
4b. Dorsal scales granulate, moderately keeled, roughly of the same size on the flanks than the back; usually more than 45 rows of dorsals (40–69); usually 13 or 14 rows of ventrals (11–17, frequently 12 in Mauritania and Western Sahara); usually more than 16 femoral pores (15–26); dorsal coloration never longitudinally striped but spots can be disposed in longitudinal lines on females. 5
5a. Large size, often more than 60 mm from snout to vent; usually (85% of the specimens) at least one granule inserted between the first two supraoculars; back strongly reticulated, sometimes spotted, with black, light spotting usually absent; pileus strongly spotted with black spots, rather large and regularly spaced; throat often grey; underside of the tail sometimes tinged red. Distribution: eastern half of the Sahara, north-west to Tunisia, south-west to northern Mali.. *Acanthodactylus scutellatus audouini*
5b. Smaller size (SVL often under 60 mm); no granules inserted between the first and second supraoculars in 60% of the specimens; black colour on the back forming a dotted rather than reticulated pattern, light spotting always present except on some specimens also lacking dark spots; pileus uniform or with fine dark vermiculations; throat, belly and underside of the tail nearly always white. Distribution: western half of the Sahara, from coastal Mauritania to north-western Libya... *Acanthodactylus dumerili*