ANNALES

de la
SOCIÉTÉ SUISSE DE ZOOLOGIE
et du
MUSÉUM D'HISTOIRE NATURELLE
de la Ville de Genève

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Il est constitué en outre du président de la Société suisse de Zoologie, du directeur du Muséum de Genève et de représentants des instituts de zoologie des universités suisses.

Les manuscrits sont soumis à des experts d'institutions suisses ou étrangères selon le sujet étudié.

La préférence sera donnée aux travaux concernant les domaines suivants: taxonomie, systématique, faunistique, phylogénie, évolution, morphologie et anatomie comparée.

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REVUE SUISSE DE ZOOLOGIE 114 (1): 3-12; mars 2007

Additions à la faune des scorpions de l'Etat du Amapá, Brésil (Chelicerata, Scorpiones)

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Addition to the scorpion fauna of the Amapá State in Brazil (Chelicerata, Scorpiones). - This paper presents the results of our study of a small collection of neotropical scorpions now deposited in the Geneva Museum. The collection is composed of specimens of 6 species in 5 genera and 2 families. One new species, *Auyantepuia amapaensis* sp. n. (Chactidae), is described from the region of the Monte Tipac in Brazil.

Keywords: *Auyantepuia* - new species - Brazil - Amapá State.

INTRODUCTION

La faune des scorpions de la région néotropicale, et en particulier celle du Brésil, peut être considérée comme une des plus étudiées au monde. Dès le début du XIX^{e} siècle, les scorpions du Brésil ont été l'objet de nombreuses contributions, aboutissant à une première synthèse réalisée par Mello-Leitão (1945).

Dans une perspective plus moderne, plusieurs travaux d'ensemble concernant la systématique et la biogéographie des scorpions brésiliens ont été réalisés au cours des trois dernières décennies, parmi lesquels nous pouvons citer Lourenço (1982a, b, 1986, 1994 et 1996). Une synthèse plus récente, réalisée en 2002 par le même auteur, montre qu'au sein de la région néotropicale, le Brésil présente une des faunes scorpioniques les plus diversifiées, ce que confirme de manière fréquente la découverte de nouveaux taxa, et de nouvelles stations pour des espèces déjà connues.

Dans l'ensemble du Brésil, certaines régions demeurent peu explorées. C'est le cas de la région septentrionale, souvent désignée sous le nom de 'Guyane brésilienne', qui comprend l'Etat de l'Amapá et ses environs.

Le présent travail est le résultat de l'étude d'une petite collection de scorpions collectés dans l'Etat de l'Amapá, et déposée au Muséum d'histoire naturelle de Genève. La plupart des espèces identifiées sont déjà connues de la Guyane française voisine (Lourenço, 1983), et certaines sont citées pour la première fois du Brésil. En outre, une nouvelle espèce appartenant au genre *Auyantepuia* Gonzales-Sponga est décrite. La présentation du matériel étudié est faite ci-après dans l'ordre alphabétique des familles, genres et espèces.

Manuscript accepted 21.11.2006

MÉTHODES

Les illustrations et les mensurations ont été réalisées à l'aide d'une loupe Wild M5, équipée d'une Camara Lucida et d'un micromètre oculaire. La nomenclature trichobothrial adoptée est celle de Vachon (1974). Les mensurations sont réalisées selon Stahnke (1970) et données en mm. La terminologie morphologique suit celle proposée par Vachon (1952) et Hjelle (1990).

TAXA CONSIDÉRÉS DANS LE TRAVAIL

FAMILLE DES **BUTHIDAE** C.L. KOCH, 1837

Genre ***Tityus*** C.L. Koch, 1836
Tityus cambridgei Pocock, 1897

MATÉRIEL: Brésil, Etat de l'Amapá, Serra do Navio (J. Lacroix leg.), X/1973, 6 mâles, 4 femelles.

FAMILLE DES **CHACTIDAE** POCOCK, 1893

Genre ***Broteochactas*** Pocock, 1893
Broteochactas delicatus (Karsch, 1879)

MATÉRIEL: Brésil, Etat de l'Amapá, Serra do Navio (J. Lacroix leg.), X/1973, 1 mâle, 2 femelles.

Genre ***Brotheas*** C.L. Koch, 1837
Brotheas gervaisii Pocock, 1893

MATÉRIEL: Brésil, Etat de l'Amapá, Serra do Navio (J. Lacroix leg.), IX/1973, 7 mâles, 4 femelles.

Brotheas granulatus Simon, 1877

MATÉRIEL: Brésil, Etat de l'Amapá, Serra do Navio (J. Lacroix leg.), X/1973, 18 mâles, 6 femelles.

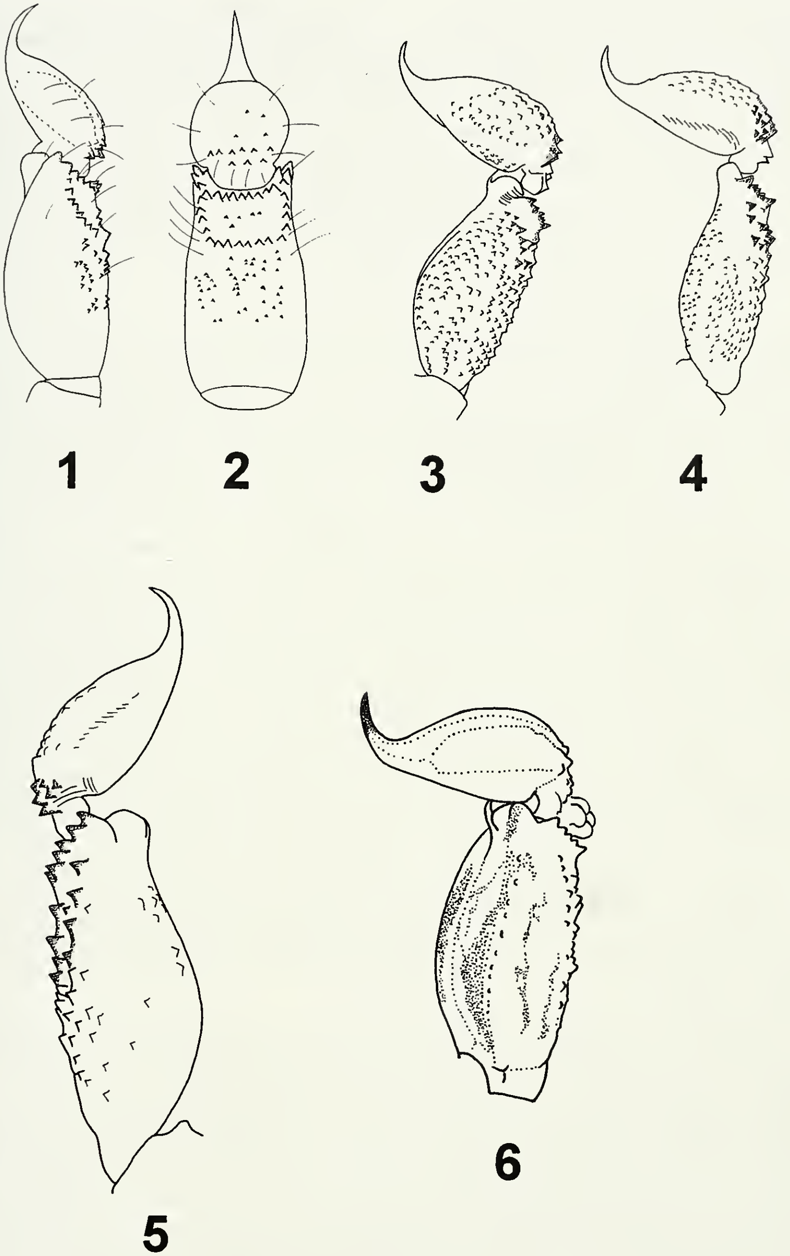
Genre ***Hadrurochactas*** Pocock, 1893
Hadrurochactas schaumii (Karsch, 1880)

MATÉRIEL: Brésil, Etat de l'Amapá, N. Serra do Navio (J. Lacroix leg.), XI/1973, 20 mâles, 3 femelles.

REMARQUE: Espèce nouvelle pour le Brésil.

Genre ***Auyantepuia*** Gonzalez-Sponga, 1978

HISTORIQUE SUR LA SYSTÉMATIQUE DU GENRE *AUYANTEPUIA*: Comme cela a été expliqué dans un travail récent (Lourenço & Souza Araújo, 2004), le genre *Auyantepuia* a été créé par Gonzalez-Sponga (1978) pour accueillir une seule espèce, *Broteochactas scorzai* Dagert, 1957, endémique de la région de l'Auyantepui, formation montagneuse de la région Guayana, au Venezuela. Le genre est resté monotypique jusqu'à la publication par Lourenço (1983), qui y ajoute trois espèces nouvelles de la Guyane française. Peu de temps après, Francke & Boos (1986), dans une publication sur les scorpions Chactidae de Trinidad et Tobago, réévaluent les caractères diagnostiques du genre *Auyantepuia* et le considèrent comme synonyme du genre *Broteochactas* Pocock. Mais dans leur analyse, ces deux auteurs ne tiennent compte



FIGS 1-6

Anneau V du metasoma et telson, vue ventrale (2) et latérale (1, 3-6). (1-2) *Auyantepuia mottai* (holotype femelle). On observe nettement l'arc postérieur formé par des granules spiniformes. (3) *A. fravalae* (holotype mâle). (4) *A. gaillardi* (holotype mâle). (5) *A. sissomi* (holotype femelle). (6) *A. amapaensis* sp. n. (holotype mâle).

que de la seule espèce type du genre, *A. scorzai*. Presque en même temps, Lourenço (1986) dans une étude biogéographique sur les scorpions de la région Guyano-Amazonienne, penche plutôt pour une subdivision par groupes d'espèces au sein du vaste genre *Broteochactas*. Il définit ainsi, en leur attribuant des noms de genre, les groupes 'Auyantepuia', auquel est rattachée l'espèce *Broteochactas parvulus* Pocock, 1897 'Taurepania', 'Vachoniochactas' et 'Hadrurochactas'. Quelques années plus tard, deux nouvelles espèces sont décrites et rattachées au groupe 'Auyantepuia': *Broteochactas kelleri* Lourenço, 1997 et *Broteochactas skuki* Lourenço & Pinto da Rocha, 2000.

Sissom (1990), dans sa classification des Chactidae, ignore les groupes d'espèces proposés par Lourenço (1986). Il fait uniquement mention d'un groupe 'Vachoniochactas' à l'intérieur du genre *Broteochactas*, groupe qui sera réhabilité en tant que genre (Lourenço, 1994). Monod & Lourenço (2001), analysant de manière précise l'ensemble des espèces de *Broteochactas* associées au groupe d'espèces 'Hadrurochactas', mettent en évidence les particularités tant morphologiques que biogéographiques de ce groupe, mais hésitent à le rétablir en tant que genre valable, ce qui sera fait par Soleglad & Fet (2003). Bien entendu nous sommes d'accord avec cette décision. Dans ce travail de Soleglad & Fet (2003) d'autres décisions moins cohérentes à nos yeux sont également prises, comme la description d'un nouveau genre *Neochactas*, dans lequel sont englobées, entre autres, plusieurs espèces du groupe 'Auyantepuia'. Suite à la revalidation du genre *Auyantepuia* par Lourenço & Souza Araújo (2004), Soleglad & Fet (2005) récidivent en considérant à nouveau *Auyantepuia* comme synonyme du genre *Broteochactas*. Cependant, comme il semble que les travaux de Soleglad & Fet (2003, 2005) présentent des nombreuses inadéquations, tout récemment signalées par Prendini & Wheeler (2005), nous adoptons ici la position de ces derniers auteurs. Avec la description d'une nouvelle espèce, un modèle de distribution géographique disjoint et relictuel est confirmé pour le genre *Auyantepuia*, avec néanmoins une forte concentration d'espèces dans la région à l'est de la 'Guayana'. Le modèle de distribution géographique observé pour les espèces du genre *Auyantepuia* est très certainement une conséquence des vicissitudes paléoclimatiques survenues dès la fin du Cénozoïque et surtout au cours du Pléistocène (voir Lourenço, 1986).

Diagnose révisée et simplifiée pour le genre *Auyantepuia*: Scorpions de petite taille, avec une longueur totale allant de 24 à 28 mm. Coloration générale châtain rougeâtre, avec les pattes et les chélicères parfois d'une coloration plus claire, jaunâtre. Tégument presque toujours lisse, chagriné. Pinces des pédipalpes avec les doigts très courts par rapport à la longueur de la main (cette morphologie des pinces aboutit à une position des trichobothries ***db*** et ***esb*** souvent au même niveau, voire plus basale que celle de **Et_5**.) Trichobothriotaxie, néobothriotaxique majorante. Face ventrale de l'anneau V du metasoma avec des gros granules spiniformes qui forment un arc dans la région postérieure, ce caractère étant diagnostique pour le genre (Figs 1 et 2). Peignes réduits en taille, avec 5 à 8 dents.

COMPOSITION DU GENRE *AUYANTEPUIA*:
Auyantepuia amapaensis sp. n. (Brésil)
Auyantepuia scorzai (Dagert, 1957) (Venezuela)
Auyantepuia fravalae Lourenço, 1983 (Guyane française)
Auyantepuia gaillardi Lourenço, 1983 (Guyane française)
Auyantepuia sissomi Lourenço, 1983 (Guyane française)
Auyantepuia parvulus (Pocock, 1893) (Brésil)
Auyantepuia kelleri (Lourenço, 1997) (Guyane française)
Auyantepuia skuki (Lourenço & Pinto da Rocha, 2000) (Brésil)
Auyantepuia mottai Lourenço & Araujo, 2004 (Brésil)

DESCRIPTION DE LA NOUVELLE ESPÈCE

Auyantepuia amapaensis sp. n. Figs 6-19

MATÉRIEL: Brésil, Etat de l'Amapá, région du 'Monte Tipac', 240 m alt., IV/1973 (F. Cardoso leg.). Holotype mâle.

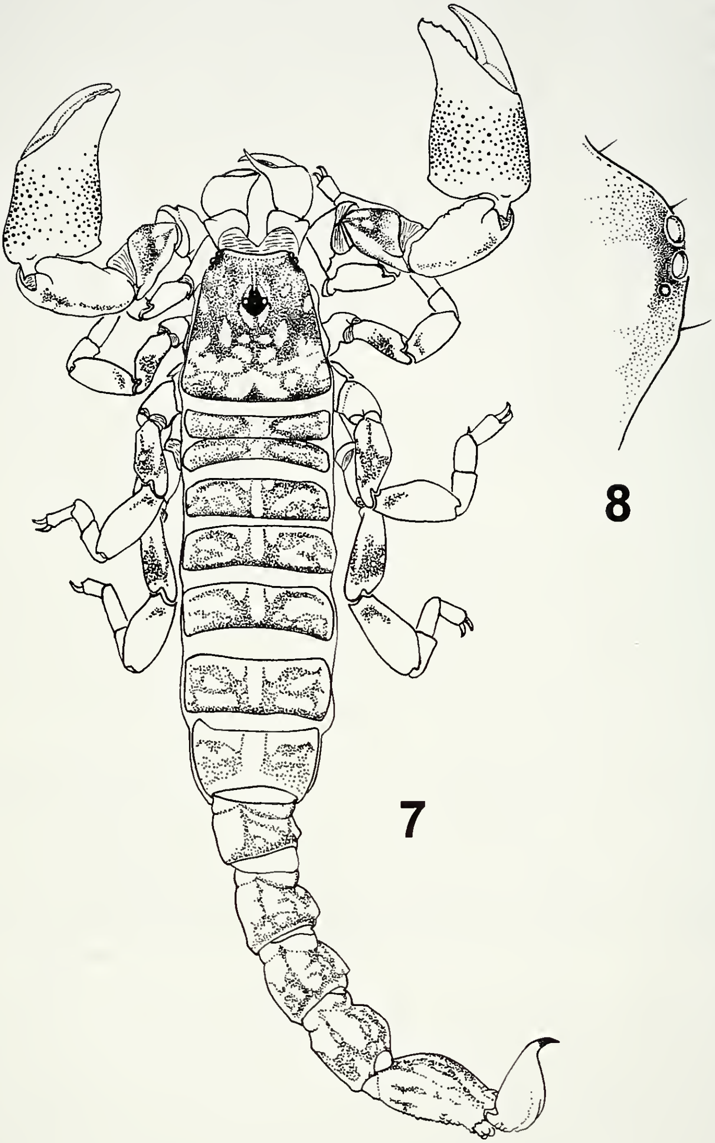
ETYMOLOGIE: Le nom spécifique fait référence à l'Etat de l'Amapá où la nouvelle espèce a été collectée.

DIAGNOSE: Scorpions de petite taille, avec une longueur totale d'environ 18 mm. Coloration générale de jaunâtre à jaune-rougeâtre, avec les pattes et les chélicères plus claires; carapace et tergites avec des taches brunâtres bien marquées; tégument presque lisse, chagriné; carènes latéro-ventrales esquissées sur les anneaux I et II du metasoma; face ventrale de l'anneau V avec des granules spiniformes qui forment un arc dans la région postérieure. Peignes de grande taille, avec 7-6 dents.

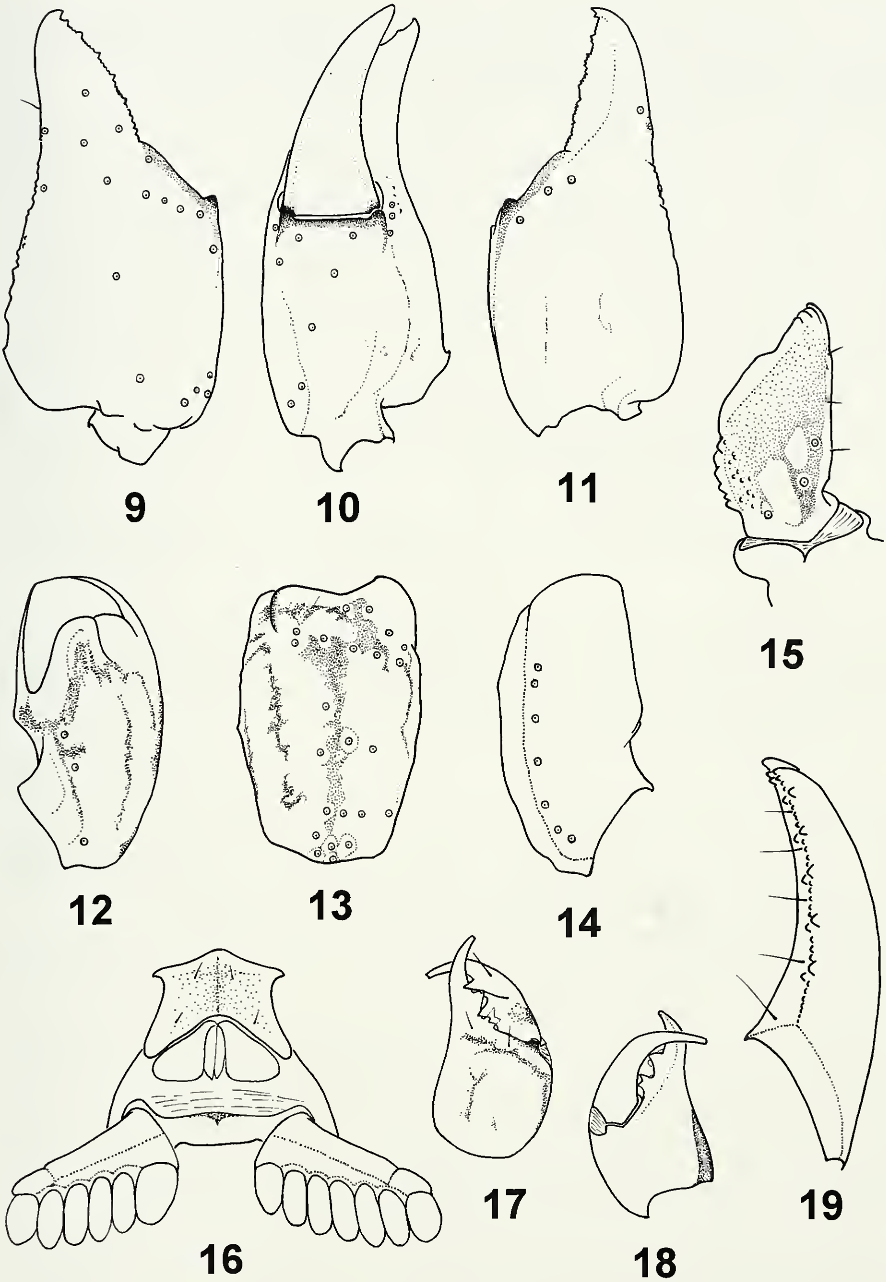
Auyantepuia amapaensis sp. n. est une espèce voisine de *A. sissomi*, dont elle se distingue par: (i) une coloration générale jaune clair avec des taches brunâtres bien marquées sur la carapace et les tergites, (ii) une granulation plus faible sur la pince des pédipalpes, (iii) une taille globale nettement plus petite (voir Tableau I).

DESCRIPTION (basée sur le mâle holotype): Coloration générale de jaunâtre à jaune-rougeâtre. Prosoma: Plaque prosomienne jaune foncé avec des zones très assombries situées en avant et sur les régions latérales de la plaque; les zones des sillons et la région postérieure un peu plus claires; tubercule oculaire noirâtre. Mesosoma: Tergites jaunâtres avec des plages confluentes brun foncé. Metasoma: Tous les anneaux d'une coloration de jaunâtre à jaune-rougeâtre, avec des taches brunâtres présentes sur les faces latérales et dorsale; face ventrale jaunâtre, sans taches. Vésicule jaunâtre avec l'aiguillon rougeâtre. Sternites jaunâtres; peignes et opercule génital, jaune clair; sternum, hanches et processus maxillaires de la même couleur que les sternites. Pattes jaune clair avec des taches brunâtres, un peu diffuses. Pédipalpes jaune-rougeâtre avec des taches brunâtres sur le fémur et très partiellement sur le tibia. Chélicères jaunâtre avec des taches brunâtres très diffuses à la base des doigts; doigts jaunâtres avec des dents légèrement rougeâtres.

MORPHOLOGIE: *Prosoma*. Plaque prosomienne légèrement concave frontalement (Fig. 7). Tubercule oculaire en position antérieure par rapport au centre de la plaque prosomienne. Ecartement des yeux médians un peu supérieur à un diamètre



FIGS 7-8
Auyantepuia amapaensis sp. n., holotype mâle. (7) Habitus. (8) Yeux latéraux en détail.



FIGS 9-19

Auyantepuia amapaensis sp. n., holotype mâle. Trichobothriotaxie. (9-11) Pince du pédipalpe, vues externe-dorsale, ventrale et interne. (12-14) Tibia du pédipalpe, vues dorsale, externe et ventrale. (15) Fémur du pédipalpe, vue dorsale. (16) Sternum, opercule génital et peignes, vue ventrale. (17-18) Chélicère, vues dorsale et ventrale. (19) Tranchant du doigt mobile.

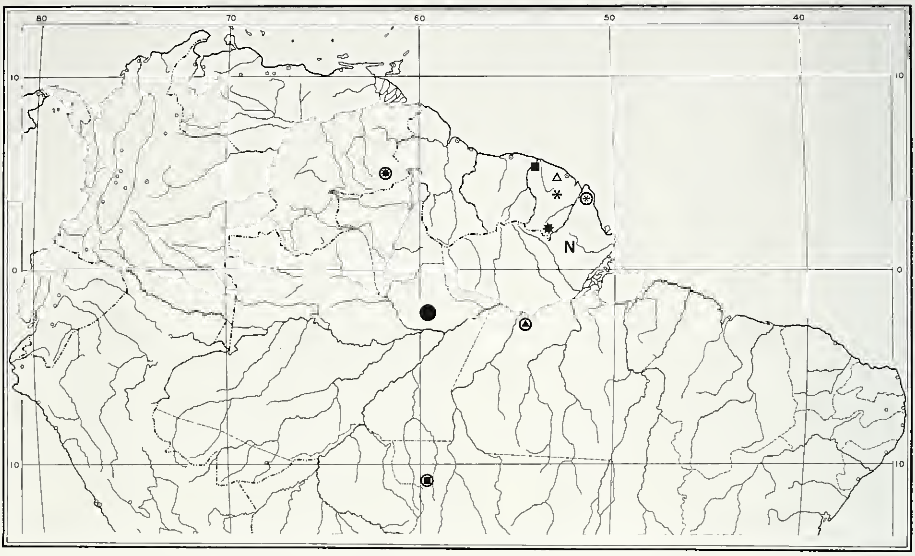


FIG. 20
Carte d'Amérique du Sud Tropicale, avec la distribution des espèces du genre *Auyantepuia* dans les régions Guayana et Amazonienne. *Auyantepuia scorzai* (cercle avec étoile noire). *A. fravalae* (fleur noire). *A. gaillardi* (carré noir). *A. sissomi* (étoile noire). *A. parvulus* (cercle avec triangle noir). *A. kelleri* (triangle). *A. skuki* (cercle avec carré noir). *A. mottai* (cercle noir). *A. amapaensis* sp. n. (cercle avec fleur noire). N = Serra do Navio.

oculaire. Deux paires d'yeux latéraux; présence d'une troisième paire d'yeux vestigiaux, situés derrière la deuxième paire (Fig. 8). Plaque prosomienne avec quelques micro granules sur les régions latérales (Fig. 8); autres zones lisses, chagrinées. *Mesosoma*. Tergites avec quelques rares granules très épars dans leur région postérieure. *Metasoma*. Carènes dorsales et latéro-dorsales esquissées sur les anneaux I à IV; carènes latéro-ventrales esquissées sur les anneaux I et II; les autres carènes absentes. Face ventrale de l'anneau V avec une granulation spiniforme et des granules qui forment un arc dans la région postérieure. Vésicule aplatie avec des gros granules spiniformes sur la région antérieure de la face ventrale; aiguillon bien plus court que la vésicule (Fig. 6). Sternites à stigmates arrondis; tégument lisse. Peignes de grosse taille avec 7-6 dents, sans fulcres (Fig. 16). *Pédipalpes*. Fémur à carènes dorsale externe, dorsale interne et ventrale interne moyennement marquées, presque complètes; tibia à carène dorsale interne esquissée; pince pratiquement lisse, sans carènes; fémur avec une faible granulation sur la face interne; face dorsale de la pince avec quelques granules; les autres faces lisses. Tranchant du doigt mobile avec une série linéaire de granules divisée en 6 séries par des granules plus gros (Fig. 19). *Pattes*. Télotarses avec des nombreuse soies irrégulièrement distribuées. Chélicères avec la dentition caractéristique des Chactidae (Vachon, 1963); présence d'une faible serrula sur la face ventrale du doigt mobile (Figs 17-18). Trichobothriotaxie du type C; néobothriotaxie majorante (Vachon, 1974) (Figs 9 à 15).

TABLEAU I: Mensurations (en mm) de l'holotype mâle d'*Auyantepuia amapaensis* sp. n. et de l'holotype femelle d'*A. sissomi* (d'après Lourenço, 1983).

	Auyantepuia amapaensis sp. n.	*Auyantepuia sissomi**
Longueur totale	17,9	26,2
Prosoma		
- Longueur	2,8	3,6
- Largeur antérieure	1,9	2,4
- Largeur postérieure	2,8	3,6
Anneau caudal I		
- Longueur	1,3	1,5
- Largeur	1,8	2,4
Anneau caudal V		
- Longueur	2,2	3,0
- Largeur	1,4	1,7
- Hauteur	1,1	1,4
Vésicule		
- Largeur	1,0	2,1
- Hauteur	0,7	1,4
Pédipalpe		
- Fémur longueur	1,7	2,1
- Fémur largeur	0,9	1,1
- Tibia longueur	2,1	2,7
- Tibia largeur	1,0	1,3
- Pince longueur	3,5	5,4
- Pince largeur	1,3	2,0
- Pince hauteur	1,7	2,3
Doigt mobile		
- Longueur	2,0	2,6

* Valeurs données à titre comparatif.

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Aphanius almiriensis, a new species of toothcarp from Greece (Teleostei: Cyprinodontidae)

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***Aphanius almiriensis*, a new species of toothcarp from Greece (Teleostei: Cyprinodontidae).** - *Aphanius almiriensis*, new species, is described from a brackish water spring and from a lagoon (and its inflowing freshwater spring) in the Peloponnese (Greece). It is distinguished by the yellowish caudal fin of the male that has a wide faint grey margin and by the colour pattern of the female (7-11 dark, roundish blotches on the side, more or less connected by an irregular dark midlateral stripe). *Aphanius almiriensis* is critically endangered; it is possibly extinct at the type locality and the second locality is much impacted. The identity, type material and type locality of *A. fasciatus* are discussed, and a neotype is designated. Several species are possibly confused under the name *A. fasciatus*.

Keywords: fish - Cyprinodontidae - *Aphanius* - Peloponnese - extinction.

INTRODUCTION

Tooth carps of the genus *Aphanius* are small fishes that inhabit fresh to hypersaline waters around the Mediterranean and Red Seas and the coasts of the Indian Ocean eastwards to Pakistan and southwards to Somalia. Several endemic species are also known from inland waters in arid areas, many of them in Turkey on the Anatolian plateau (Vilwock, 1984; Wildekamp *et al.*, 1999; Hrbek & Wildekamp, 2003). The small size of these fishes, their low dispersal ability, the isolation of their populations, the small size of the habitats and the even smaller size of the areas of occupancy, lead to the evolution of very localised endemics. A few species, usually coastal ones, have a distribution range that appears very wide, e.g., *A. fasciatus* (Valenciennes) that is recorded around most of the Mediterranean and its islands. In fact, the distribution of the latter is better described as a long succession of more or less isolated populations (Bianco & Taraborelli, 1988; Wildekamp, 1993; Bianco *et al.*, 1996). While a number of studies were performed on the life history, ecology and genetics of local *Aphanius* populations (often within a national framework) (e.g., Kiener & Schachter, 1974; Boumaiza, 1980; Tigano, 1982; Ferrito *et al.*, 2003), a large scale comparison of

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populations throughout the range of the species is still missing. Such a comparison is likely to reveal that several species have been confused under the name *A. fasciatus*. We describe here a new species of *Aphanius* from Greek waters, firstly discovered in 1997 in a brackish spring. We also clear the nomenclature and the identity of the 'real' *A. fasciatus*.

There have been arguments in recent years on the name to be used for the current genus *Aphanius*, with Lazara's (1995) attempt to pose *Lebias* as the valid name. To change the name of a genus, whose species are listed as endangered in numerous national and international legal instruments, was unfortunate, especially since a critical re-analysis of the case demonstrated this decision to be based on misinterpreted data (Kottelat & Wheeler, 2001). To close the case, Kottelat & Wheeler (2001) requested a ruling from the International Commission of Zoological Nomenclature [ICZN]. The ruling (ICZN, 2003) definitively conserves *Aphanius* and places *Lebias* on the list of names not available for the zoological nomenclature.

METHODS

Ideally, we tried to adopt the Phylogenetic Species Concept (Cracraft, 1989; Kottelat, 1997, 1999) as an operational tool for the evolutionary species concept (Wiley & Mayden, 2000; Mayden, 2002), which is closest to our perception of what a species is. The reality is that outside the academic world it is seldomly possible to investigate the phylogeny of a given group with enough detail to demonstrate the monophyly of all the included taxa. In the context of biodiversity inventories and conservation, alpha-level taxonomy is facing priorities strikingly different from those of academic research. The goals are different, and the approach has to be adjusted. Therefore, we often have to resort to the 'Pragmatic Species Concept' (Kottelat, 1995; see also Kottelat & Ng, 1994).

Methods for counts and measurements follow Kottelat (2001). Standard length (SL) is measured from the tip of the snout to the end of the hypural complex. Length of caudal peduncle is measured from behind the base of the last anal-fin ray to the end of the hypural complex, at the mid-height of the caudal-fin base. Scales on lateral series are counted from the anteriormost scale (the first one to touch the shoulder girdle) to the posteriormost one (at the end of the hypural complex). Scales on the caudal fin itself are indicated by "+". Transverse scales are counted as the number of longitudinal scale rows. The scale row on the dorsal and ventral mid-lines is noted as "1/2". All measurements are made point to point.

Abbreviations used: CMK, collection of first author; FSJF, collection of Jörg Freyhof, Berlin; HCMR, Hellenic Centre for Marine Research (formerly National Centre for Marine Research), Athens; MHNG, Muséum d'histoire naturelle, Genève; MNHN, Muséum National d'Histoire Naturelle, Paris.

COMPARISON MATERIAL

Aphanius fasciatus: Italy: Sardinia: MNHN 2005-1975, neotype, 39.5 mm SL; CMK 18600, 85, 32.9-47.8 mm SL; Italy: Sardinia: Cagliari, stagno di Cagliari, Primo Bacino (saltworks); A. Cau, 22 March 2005. – MNHN A.3968, male, 29.1 mm SL; MNHN 187, 3 syntypes of *Poecilia calaritana*, 33.9-35.7 mm SL; MNHN 92, 1, 37.5 mm SL; CMK 18599, 17, 29.2-

35.4 mm SL; CMK 18786, 3, 36.3-41.6 mm SL; FSJF 209, 6, 10.9-26.7 mm SL; Cagliari. – FSJF 183, 3, 18.1, 24.3 & 27.9 mm SL; Arbarax.

Italy: MNHN 197, 1 female, 43.7 mm SL, possible syntype of *Lebias flava*; Napoli. – MNHN 1888-112-115, 4, 31.8-33.0 mm SL; MNHN 1899-249, 5, 40.7-46.0 mm SL; Venezia.

France: Corsica: MNHN 1985-204, 1 (female), 44.2 mm SL. – MHNG uncat., 8, 26.1-42.0 mm SL; MHNG uncat., 2, 35.1-43.3 mm SL; MHNG 1321.34-38, 5, 26.8-29.2 mm SL; Bonifacio.

Greece: CMK 17015, 17; CMK 16976, 6; Messolonghi. – HCMR 1471, 14; CMK 18452, 2; Kato Basiliki. – HCMR 1121, 14; CMK 18541, 2; Prokopos. – HCMR 1188, 7; Kaiafa lake. – HCMR 1318, 170; Thermissia lagoon. – HCMR 1319, 48; Sachtouri lagoon. – HCMR 1321, 74; Metochi lagoon. – HCMR 1390, 16; Aitoliko. – HCMR 1418, 29; Gialova lagoon.

Turkey: MNHN 1927-79-80, females, 31.9-54.1 mm SL; MNHN 1927-78, 20 males, 23.5-48.9 mm SL; MNHN A.3796, 10, 25.9-42.0 mm SL; Izmir. – MNHN 1928-210-211, 23; Konya.

Israel: MNHN A.2809, 13, 15.4-24.9 mm SL; Ramle.

Egypt: MNHN A.5254, 6, 25.6-41.1 mm SL; no locality. – MNHN 4991, 1 male, 35.0 mm SL; Suez.

Tunisia: MNHN 1904-48, 8, 28.9-40.0 mm SL; no locality. – MNHN 1883-1031, 8, 26.7-36.4 mm SL.; Blidet Ahmar.

Algeria: MNHN 4392, 8 syntypes of *Cyprinodon doliatus*, males, 22.8-34.7 mm SL; MNHN 3218, 5 syntypes of *C. cyanogaster*, females, 24.9-32.6 mm SL; Biskra. – MNHN A.2367, 1 female, 36.7 mm SL; Touggourt. – MNHN 1999-542, 2 females, 19.0-31.6 mm SL; Annaba.

Aphanius sp.: MNHN 1923-29, 1 male, 28.4 mm SL; MNHN 1922-72, 1 female, 37.6 mm SL; Tunisia: Gabes.

RESULT

Aphanius almiriensis, new species Fig. 1

HOLOTYPE: MHNG 2654.087, 35.1 mm SL; Greece: Peloponnese: Korinthia Distr.: brackish water spring Kokosi at southern end of Almiri beach, at Kato Almiri, about 4 km south of Loutra Elenis; 37°50'32"N 23°00'58"E; R. Barbieri & A. Economou, 13 May 1997.

PARATYPES: HCMR 1064, 14, 24.5-38.8 mm SL; CMK 17296, 3, 25.9-29.8 mm SL; same data as holotype. – HCMR 1473, 5, 13.4-22.1 mm SL; same locality as holotype; R. Barbieri & M. Tsatsas, 26 Oct 2003.

ADDITIONAL MATERIAL (NON TYPES): HCMR 1478, 12, 14.9-29.4 mm SL; Greece: Peloponnese: channel close to sea at east side of Meligou Lagoon; 37°23'07"N 22°45'02"E; R. Barbieri & M. Stoumboudi, 29 July 2004. – HCMR 1314, 190, 20.9-37.7 mm SL; MHNG 2654.088, 3, 23.4-30.2 mm SL; CMK 18370, 11, 19.1-33.1 mm SL; same locality; R. Barbieri & A. Economou, 13 Oct 1998. – HCMR 1477, 36, 9.4-26.0 mm SL; Greece: Peloponnese: freshwater spring at edge of Meligou Lagoon; R. Barbieri & M. Stoumboudi, 29 July 2004.

DIAGNOSIS: *Aphanius almiriensis* is distinguished from all other species of *Aphanius* in Europe by the yellow caudal of the male, with a wide faint grey margin (vs. hyaline, greyish, greyish blue, or bright yellow with or without a black subdistal bar) and by the colour pattern of the female (7-11 dark, roundish blotches on the side, more or less connected by an irregular dark midlateral stripe). Additional characters useful to distinguish the species (but not unique to it) are: male with 6-10 dark, broad, regularly set bars on the body; neuromasts in interorbital area in deep open grooves; 25-28+2 scales in lateral series on body; and 15-16 pectoral rays.

DESCRIPTION: Main morphometric data of the holotype and 13 paratypes are given in Table 1. General appearance is shown in Fig. 1. Head with relatively massive appearance. Dorsal profile of head and body convex, with a slight nuchal concavity in largest males. Mouth subterminal, oriented upwards, lower jaw almost vertical.

TABLE 1. Morphometric data of holotype and 13 paratypes of *Aphanius almiriensis* from type locality and of neotype of *A. fasciatus*. Holotype data included in range of female values.

	A. almiriensis			*A. fasciatus*
	female holotype	males (n= 7) range	females (n=7) range	male neotype
Standard length [mm]	35.1	24.5 - 28.5	25.2 - 38.8	39.5
Total length [mm]	43.2	30.5 - 35.8	31.1 - 46.6	48.2
In percents of standard length				
Head length	31.9	30.1 - 32.1	29.9 - 31.9	29.4
Predorsal length	64.1	60.4 - 62.0	61.0 - 64.7	61.0
Prepelvic length	52.0	50.2 - 53.1	52.0 - 54.9	52.9
Preanal length	70.8	64.3 - 65.9	67.6 - 70.8	62.8
Body width	23.5	20.4 - 22.1	22.1 - 23.5	17.5
Head depth	19.1	18.6 - 19.8	19.1 - 19.2	21.0
Body depth	28.3	24.9 - 27.8	25.6 - 28.6	28.9
Depth caudal peduncle	16.5	16.0 - 17.6	15.2 - 16.5	17.0
Length caudal peduncle	22.8	23.4 - 25.3	22.2 - 24.1	23.8
Depth of 1st simple dorsal ray	14.7	15.0 - 16.5	13.1 - 15.5	13.9
Length of middle caudal rays	21.9	24.2 - 26.2	20.2 - 23.9	23.5
In percents of head length				
Head depth	59.8	58.6 - 63.8	59.8 - 63.8	71.6
Eye diameter	27.7	30.9 - 33.6	27.6 - 31.1	25.9
Snout length	32.6	28.4 - 30.5	29.7 - 32.6	34.5
Interorbital width	49.6	47.3 - 52.6	47.7 - 51.0	39.7

Posterior extremity of maxilla under tip of snout. Eye diameter about equal to snout length. Depth of caudal peduncle 1.35-1.55 times in its length.

Dorsal-fin origin in front of anal-fin origin and behind midlength of body. Dorsal fin with 9-11 (modally 10) rays; anal with 10-11 (modally 10) rays, pectoral with 15-16 rays. 25-28+2 scales in lateral series, 1/2 8-9 1/2 in transverse row between dorsal origin and ventral midline in front of pelvic-fin base; 1/2 6-7 1/2 on caudal peduncle. Small ctenii along posterior edge of scales on caudal peduncle in largest males. Cephalic neuromasts in interorbital area in deep open grooves (Fig. 2).

Males slightly more robust than females, up to 28.5 mm SL in available material. Dorsal rounded, anal and caudal truncate. Females larger than males, up to 38.8 mm SL, body less laterally compressed. All unpaired fins rounded. Anus and genital openings separated.

COLOUR PATTERN: Based on the type series: Males with 6-8 dark bars on body, wider above than below, more or less reaching ventral midline and more or less fused along dorsum in front of dorsal-fin origin. Caudal and anal fins yellow, caudal fin with a greyish distal band. Dorsal fin yellowish, with an obvious black margin along anterior and upper margins, and a few dark dots near its base. Females with 7-11 dark, roundish blotches on side, more or less connected by an irregular dark midlateral stripe; no remains of other colour marks.

No observation on life colour of material from Almiri, but unpaired fins of males probably brighter yellow in life than in Fig. 1. In material from Meligou, all adult males with yellow caudal and anal fins.

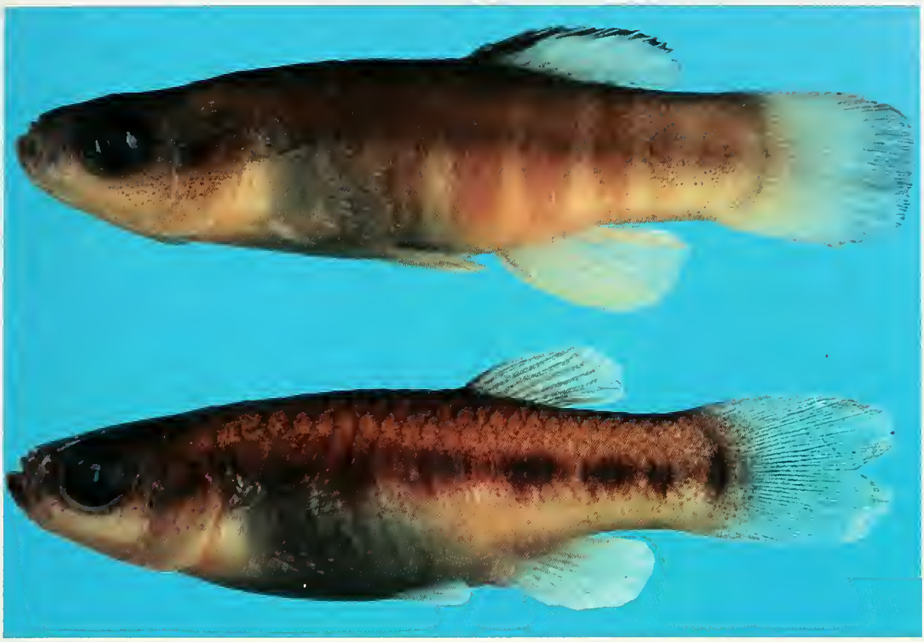

FIG. 1

Aphanius almiriensis; Greece: Kato Almiri; CMK 17296, paratype, male, 29.8 mm SL (above); holotype, MHNG 2654.087, 35.1 mm SL (below).

VARIATION: Material from Meligou lagoon generally agrees with the above description, except for a single very large female (37.7 mm SL) that has the flank colour pattern consisting in slightly elongated bars. Most males have a few broad bars, but there are a few individuals with a few more and narrower bars (7-10). We do not adopt the hypothesis that these individuals may be hybrids between *A. almiriensis* and *A. fasciatus*, because the latter (although it is widely distributed along the eastern coast of the Peloponnese) was never observed at Meligou lagoon despite intense search for it.

DISTRIBUTION: Greece, only two populations are known to date, in the spring near Almiri (Saronikos Gulf) and in the Meligou lagoon (Argolikos Gulf). In 1997-2004, we searched about fifteen springs and brackish water systems along the coast of the Peloponnese and Southwestern Greece and found *Aphanius* in eleven (Fig. 3). Only *A. fasciatus* was observed and/or collected in all but the two aforementioned localities, including the Thermisia and Metochi lagoons that are located between the Almiri spring (Fig. 4) and the Meligou lagoon.

HABITAT: Almiri spring is a permanent brackish water spring (23‰) adjacent to the sea, which it joins after a few meters. The spring itself is now contained by a concrete wall and the enclosure is filled with typical halophytic aquatic vegetation.

Meligou lagoon is a permanent brackish marsh (11-25‰). Until the second half of the 20th century it occupied an area of about 2.6 km^2. Later on, reclamation works

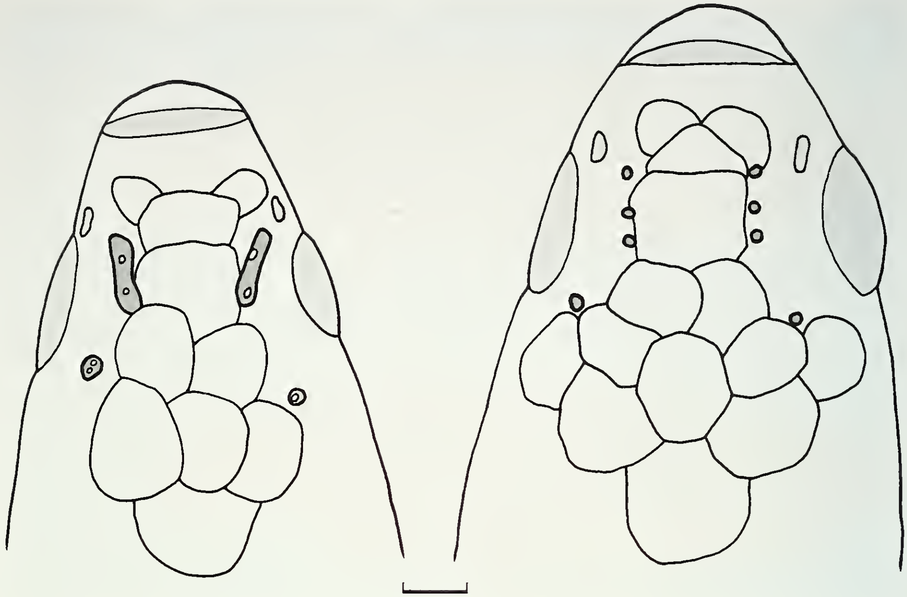

FIG. 2

Dorsal view of head (schematised) of: *Aphanius almiriensis*, CMK 17269, 29.6 mm SL (left); *A. fasciatus*, CMK 17015, 35.8 mm SL (right). Dark grey: canal and pores in interorbital area. Scale bar 1 mm.

reduced its surface area to 1.5 km^2. There is a spring along the west side of the lagoon, with permanent freshwater discharge.

BIOLOGY: *Aphanius almiriensis* is benthopelagic, observed in shallow areas with slow current, among vegetation, as well as in the water column. It is a very fast swimmer and forms schools. It is a short-lived species and a fractional spawner that breeds in late spring - early summer, spawning 1-3 eggs a time. However, larvae were collected in Meligou in September 1998 (HCMR 1314), showing that the reproductive period may be prolonged until late summer.

CONSERVATION STATUS: *Aphanius almiriensis* was discovered in 1997 in the Almiri spring, which at the time released brackish water of constant salinity. During various visits at this location, between 1997 and 2000, the observed salinity was 23‰. However, in 2002 the spring was releasing pure seawater and the only fish observed there were mugilids. At the same time, the spring was occupied by unidentified sea grasses and sea anemones. The species was then believed to be extinct, but a visit in October 2003 yielded 5 juveniles 13.4-22.1 mm SL (HCMR 1473). In July 2004, no *A. almiriensis* were observed in Almiri despite intensive search.

After realizing the distinctness of the Almiri population, older collections were re-examined for possible additional localities with *A. almiriensis* and a sample obtained in Meligou lagoon in October 1998 was discovered. In that sampling

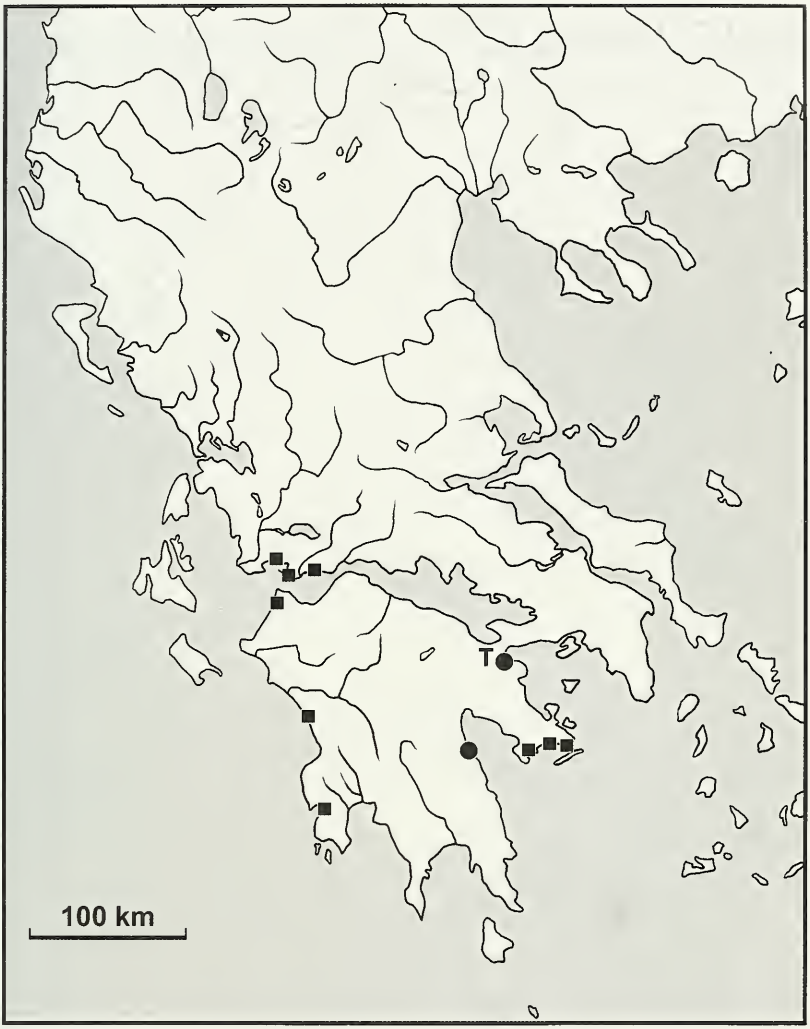

FIG. 3

Distribution of *Aphanius almiriensis* (circles) and *A. fasciatus* (squares) in the water systems investigated along the coast of Peloponnese and southwestern Greece. **T,** type locality.

occasion, *A. almiriensis* was estimated as abundant in the main freshwater spring supplying the lagoon at its NW side. However, recently, this spring was dammed with rocks, to create a "natural swimming pool". During a visit in July 2004, no fish were present in the modified spring area. However, *A. almiriensis* was collected from different areas of the lagoon.

According to the above, the species is considered to be critically endangered (CR A2ace+3ce; B1ab(i,ii,iii,iv,v)+B2ab(i,ii,iii,iv,v)c(iv) according to IUCN criteria.

FIG. 4

Brackish water spring at Kato Almiri (Greece), type locality of *Aphanius almiriensis*.

DISCUSSION

COMPARISON WITH *A. FASCIATUS*: *Aphanius fasciatus* has a wide distribution, occurring along the northern coast of the Mediterranean from the Rhône delta (France) and Corsica eastwards, and along the southern coast from Algeria eastwards. It is missing in France west of Camargue, along the Spanish coast and in western Algeria (Wildekamp, 1993: 48; Römer, 1991). The species is reported to be variable in shape, colour pattern and coloration (e.g., Wildekamp, 1993), but our observations (unpublished) show that part of this variability in fact should be re-interpreted as interspecific differences.

The aim of the present paper is the description of *A. almiriensis*, which urgently needs a formal name. Conservation measures for a critically endangered species are impossible to be implemented if this does not have a formal name. A species without a name simply does not exist for policy makers, even though scientists recognise it. Our aim is not to revise *A. fasciatus* sensu lato, which we reserve for a later opportunity. In this context, we compare *A. almiriensis* with the populations of *A. fasciatus* present in coastal waters adjacent to the range of *A. almiriensis*, and with the population at the type locality of *A. fasciatus* (with the available data, these populations of *A. fasciatus* are conspecific). Our logic in doing so is that, as discussed below, we doubt the conspecificy of several of the populations usually referred to *A. fasciatus*. At the present stage what matters is to show that *A. almiriensis* is distinct from the species in adjacent waters, distinct from topotypical *A. fasciatus*, and distinct from the nominal species placed in the synonymy of *A. fasciatus*. To resolve these problems, a comparison of *A. almiriensis* with remote populations (species) (e.g., from France, Algeria, Egypt) is irrelevant, whatever the academic interest might be.

For the present discussion, data on *A. fasciatus* are based on material obtained in Greece (Messolonghi, Kato Basiliki, Prokopos) and Sardinia (Cagliari; type locality), unless otherwise stated.

Three valid species of *Aphanius* have so far been recorded in European waters and *A. almiriensis* is easily distinguished from them. In *A. iberus* (Valenciennes) from Spain, the caudal fin of the male is hyaline to bluish-grey, with 2-5 dark grey bars; the female has numerous dark brown spots on the side and the back. In *A. baeticus* Doadrio, Carmona & Fernández-Delgado, also from Spain, the caudal fin of the male is dark grey, with one distinct submarginal bar and 4-5 vertical rows of hyaline dots sometimes organised in regular bars; the female has a few large black spots on the side, usually organised in two rows, one on the middle of the flank, one at the level of the pectoral-fin base. In *A. fasciatus*, the male has 8-15 dark bars on the body; the female has 11-17 narrow, elongated dark bars occupying about half of the body depth on the side of the body, over a faint greyish midlateral stripe (Fig. 5b).

The males of *A. almiriensis* and *A. fasciatus* share the yellow caudal fin, but in *A. almiriensis* the caudal fin has a greyish distal edge, while in *A. fasciatus* the caudal fin is plain yellow (bright yellow in life) with or without a black subdistal bar (Figs 5a, 6). The colour pattern of the female *A. almiriensis* is not observed in other peri-Mediterranean *Aphanius*. The female colour pattern of many populations referred to *A. fasciatus* remains undescribed or only succinctly described, and reported as very variable. Our examination of material from all around the Mediterranean shows that while there is some intra-population variability (as for any other character), this intra-population variability is limited, and that the inter-population variability is not random but corresponds to a zoogeographic pattern and defines a number of (diagnosable) clusters of populations. The above-mentioned *A. fasciatus* female colour pattern is that of the

Fig. 5

Aphanius fasciatus, CMK 18451; Greece: Prokopos lagoon; male, 35.7 mm SL (above); female, 40.6 mm SL (below).

populations of the Tyrrhenian, Adriatic, Ionian and western Aegean basins. The eastern Mediterranean populations also differ from *A. almiriensis*; the female colour pattern consists, among others, in a row of very short, narrow, black, vertical bars.

Aphanius almiriensis also differs from *A. fasciatus* by its general appearence (compare Figs 1 and 5), with *A. almiriensis* having the dorsal head profile less convex than *A. fasciatus*, the ventral head profile more angular, the dorsal and anal fins of the male not reaching the caudal-fin base (vs. reaching), a quadrangular caudal fin (vs. somewhat trapezoidal), all characters difficult to quantify. Further, *A. almiriensis* has a stouter caudal peduncle (depth 1.4-1.6 times in its length, vs. 1.4-1.9), a wider interorbital (14.6-16.9% SL, vs. 11.6-14.4; 47-53% HL, vs. 40-47) and a larger eye (diameter 27-34% HL, vs. 24-32). The largest examined specimen of *A. almiriensis* is 38.8 mm SL, while the largest recorded size of *A. fasciatus* in Greek waters is 75.5 mm TL (estimated 60 mm SL) (Leonardos & Sinis, 1999). This is an unusually large size, and most adult specimens are in the size range 35-50 mm SL. The above comparison is based on specimens of similar sizes (*A. almiriensis* 24.5-38.8 mm SL, *A. fasciatus* 25.2-42.3 mm SL) and excludes the hypothesis that the characters distinguishing *A. almiriensis* from *A. fasciatus* are juvenile characters or size-dependant.

We also observe differences between the two species in the number and organisation of the neuromasts in the interorbital areas. In *A. almiriensis*, there are 2 neuromasts on each side, located in deep grooves (Fig. 2a). In *A. fasciatus* from Greece and the Adriatic and Tyrrhenian basins (including Sardinia and the neotype), there are three neuromasts in closed canals pierced with 3 pores (Fig. 2b). A single specimen of

A. almiriensis (the largest female, 38.8 mm SL) has the grooves partly closed, with two pores. In *A. fasciatus*, only few of the smallest males (less than about 30 mm SL) have the three neuromasts in wide, shallow grooves (vs. conspicuous, deep grooves in *A. almiriensis*). In juveniles of the eastern Mediterranean populations, there are three neuromasts in shallow grooves, which start closing anteriorly at about 30 mm SL; in most large specimens the posterior half of the groove remains open. All conditions are present in the material from Tunisia and Algeria.

Examination of type material, topotypes or original descriptions of all nominal species usually listed in the synonymy of *A. fasciatus* (see, e.g., Kottelat, 1997) shows that *A. almiriensis* is distinct from all of them. Their identities are discussed below.

ON THE IDENTITY AND TYPE LOCALITY OF *A. FASCIATUS*: Although it is not within the scope of the present paper to revise *A. fasciatus* sensu lato, it is necessary to briefly discuss the diversity within this 'species', as most *Aphanius* populations from the eastern Mediterranean drainages have been at some point referred to *A. fasciatus*. Also it needs to be ascertained that *A. almiriensis* is distinct from all the nominal species listed as synonyms of *A. fasciatus* (see Kottelat, 1997).

There has been a number of publications describing or discussing variability within *A. fasciatus*. We will not discuss them in detail, for most suffer from being only of limited, local interest, neglecting other populations or with problematic methodologies. Frequent problems are the use of morphometrics and meristics without defining the methods used, and misunderstanding of taxonomic procedures.

Aphanius fasciatus was originally described (as *Lebias fasciata*) by Valenciennes (in Humboldt & Valenciennes, 1821: 160, pl. 51 fig. 4). Valenciennes indicated neither the origin nor the number of his specimens. Kottelat (1997: 161) commented that Valenciennes (in Cuvier & Valenciennes, 1846: 156) later stated that these specimens were from Cagliari (Sardinia). In fact, the case is more complex. Valenciennes' 1846 account is somewhat ambiguous and it appears that the species was most likely based on a single specimen (thus holotype) of unknown origin and that in 1846 Valenciennes re-described *A. fasciatus* on the basis of additional (non-type) material from Cagliari obtained by Bonelli and Marmora. After describing the Cagliari specimens, Valenciennes stated (in Cuvier & Valenciennes, 1846: 158) that he compared them with the specimen (singular) "preserved for a long time in ... the museum". In 2005 we searched for the holotype in MNHN but it is no longer extant.

Valenciennes further commented that this specimen has broken dorsal and anal fins and that the artist should have made them higher, implying that this very specimen is the model of the plate. Valenciennes' 1821 description indicates 10-12 whitish bars while the figure shows only 8, but in 1846 he commented that the colour pattern too is not correctly depicted and that the artist had "exaggerated the bars, especially the anterior ones, believing that they were less contrasted because of the effect of alcohol".

Valenciennes (in Cuvier & Valenciennes, 1846: 159) commented "[in 1821] I gave only the description and figure of these two species [*L. fasciata* and *L. rhomboidalis*], whose origin I ignored. By doing this, I only wanted to complete what Mr. Cuvier [1816] had left to be done in the first edition of his *Règne animal*, where the only two species of the genus then known are designated as new". In a footnote to the very brief diagnosis of his Lebias [a vernacular name], Cuvier (1816: 199) had merely mentioned that he knew two species of this genus, both new, but he neither named them nor provided any data. The meaning of Valenciennes' last sentence may seem ambiguous, but the context and his comments pp. 146-150 make it clear that he described the two unnamed species mentioned by Cuvier [implying he named them on the basis of the material on which Cuvier based his statement].

Identification of *Lebias fasciata* as the species presently called *Aphanius fasciatus* goes back to Valenciennes (in Cuvier & Valenciennes, 1846: 158) who simply stated that he compared the holotype with specimens from Cagliari and that he was "convinced of their being the same". (It is puzzling that on p. 146 Valenciennes mentioned "one of them [...] is my *Lebias fasciata*, which the late Mr. Delalande very recently brought back from the vicinity of Rio de Janeiro". The meaning of this sentence should not be misunderstood as 'the specimen being brought by Delalande from Brazil', but that Delalande had since brought specimen(s), which Valenciennes considered conspecific with his *L. fasciata*. Delalande [1787-1823] collected in Brazil in 1817 [Cuvier, 1828: 254; Bauchot *et al.*, 1990: 72], which was too late for him to have collected the holotype that was already examined by Cuvier before 1816. It is difficult to understand how Valenciennes could identify his *L. fasciata* being identical on the one hand with a Brazilian species and on the other hand with a Sardinian fish; this may relate with the small size of these fishes, the optical equipment, the state of preservation, etc.)

As the holotype was already in the MNHN in 1816, its origin might be speculated to be in areas from which the museum had received fish collections before that date. Noteworthy within the distribution range of *A. fasciatus* s.l. are the collections obtained by Geoffroy Saint-Hilaire in Egypt in 1798-1799 and by Delalande in Toulon (France) in 1813.

In conclusion, the type locality of *A. fasciatus* remains unknown and, as the holotype is now missing, it will remain impossible to establish from the original description either its identity or its type locality. This problem can be solved only by a neotype designation. We designate here MNHN 2005-1975, 39.5 mm SL (Fig. 6), as neotype. This specimen was collected in the salt-works of Cagliari in 2005, at the same locality as the material of Bonelli and Marmora, on which Valenciennes based his 1846 description. As this locality has long been erroneously considered as type locality of *A. fasciatus* (see above), the present neotype designation best creates stability in definitively linking the name to this locality. Morphometric data of neotype are listed in Table 1. Meristic data: 10 dorsal-fin rays; 9 anal-fin rays; 12 pectoral-fin rays; 26+2 scales in midlateral series; $1/2$ 10 $1/2$ scales in transverse row between dorsal origin and ventral midline in front of pelvic-fin base; $1/2$ 7 $1/2$ scales in transverse row on caudal peduncle.

WESTERN MEDITERRANEAN *A. FASCIATUS* S.L.: The material presently available to us and the published information are still insufficient to satisfactorily answer questions like the number of species hiding under the name *A. fasciatus*, their distribution and their diagnostic characters. Nevertheless, it is possible to comment on some populations and on the nominal species traditionally placed in the synonymy of *A. fascia-*

FIG. 6

Aphanius fasciatus, Italy: Sardinia: Cagliari; MNHN 2005-1975, neotype, male, 39.5 mm SL (above); CMK 18600, female, 42.6 mm SL (below).

tus. Up to now, attention has focussed on the western Mediterranean populations (Corsica, Sardinia, Sicily, Tyrrhenian slope of Italy, Malta, Tunisia). The different studies have been based only on a few populations and a few characters and therefore there are no characters with data homogeneously available for all populations. The colour pattern, however, is described or figured for a number of populations large enough to allow a comparison.

Valenciennes' figure (in Humboldt & Valenciennes, 1821: pl. 60) of *A. fasciatus* depicts a male, as shown by the conspicuous dark bars. An interesting character shown on the figure is the absence of the black margin of the dorsal fin. Even if the distal part of the fin was missing (as stated by Valenciennes, in Cuvier & Valenciennes, 1846), the membranes between the anterior rays should have been coloured dark or black. A perusal through the pictures of *A. fasciatus* in the literature shows all males to display this marking, except for material from Corsica in Kiener & Schachter (1974: 323), from Sardinia in Wagner (1828: 1055, pl. 12) and a population from Tunisia in van der Zee & Vonk (1991).

Kiener & Schachter (1974) figured specimens from 3 populations in Corsica (Diana and Biguglia in northeastern Corsica; Porto-Vecchio in southeastern Corsica) and compared them with material from Comacchio (northern Italy, Adriatic coast). They mention having seen males from Corsica up to 65 mm TL (that is, large adults) and state that the most salient features of the northeastern individuals when compared to the Comacchio ones are the shorter dorsal fin, a less vivid coloration and the absence of the black stripe in the anterior part of the dorsal fin. The drawings in Kiener &

Schachter show deep-bodied fishes with a general appearance and markings similar to those of Valenciennes' figure (their photograph -Fig. 6- shows a more slender individual). Kiener & Schachter (1974: 324) comment that a few of the Porto-Vecchio individuals show the characters of the Comacchio population, albeit attenuated. They also mention having seen material from Sardinia, but do not mention coloration; they only mention a shorter dorsal fin than the Comacchio specimens. Kiener & Schachter's material is not known to have been preserved; it is not in MNHN collections.

We could not find other published figures of Corsican populations, but S. Valdesalici provided us with photographs of fishes from Furiani (northeasten Corsica) without the black margin in the dorsal fin and from Porto-Vecchio (southeastern Corsica) with obvious black margin. Males from Bonifacio (southern Corsica; MHNG uncat.) have the obvious black margin. The account of *A. fasciatus* in Keith & Allardi (2001: 278) shows a fish with a faint dark distal margin (but no dark anterior margin). However, we cannot give any value to this drawing as it is obviously based on the one in Maitland (1976), itself based on unknown sources and not very realistic.

Valenciennes (in Cuvier & Valenciennes, 1846: 156) re-described *A. fasciatus* based on fresh material from Cagliari, Sardinia. The colour pattern he described for the males agrees with what was reported by Kiener & Schachter (1974) from Comacchio and by van der Zee & Vonk (1990) as 'short' form from Tunisia.

Valenciennes (in Cuvier & Valenciennes, 1846: 151) also described a *Cyprinodon calaritanus* from the same swamp in Cagliari as the neotype of *A. fasciatus*, which is the female of his 1846 *A. fasciatus* (confirmed by examination of 3 syntypes MNHN 187). He recorded the presence of narrow bars on the body and one or two, sometimes three, black spots at caudal-fin base, which is also agreeing with the Comacchio females figured by Kiener & Schachter and others. (*Lebias calaritana* is a name available from a very brief diagnosis by Cuvier [1829: 280], from which one deducts that the name is based on material from Sardinia sent by Bonnelli and that most likely is the material used by Valenciennes in 1846.)

Wagner (1828) figured individuals from Cagliari, Sardinia (his figures show his *Lebias sarda* and *L. lineopunctata*, unambiguously male and female, respectively, of the same species). The type material of both nominal species is lost (Kottelat, 1997). The male has a relatively deep body and a short dorsal fin. There is no indication of a black anterior margin in the dorsal fin. The female has very narrow bars on the body, the posteriormost ones replaced by a number of small spots over the whole depth of the caudal peduncle. This pattern is also distinct in the Corsican females figured by Kiener & Schachter (1974) and in some populations (not all) from Tunisia figured by Boumaiza (1980: 87) (the figured Tunisian males have a large dorsal fin with a black margin).

The variability among the different accounts of material from Cagliari is intriguing, but can only be interpreted after more populations can be examined. Comparing Valenciennes' and Wagner's descriptions and figures and our material from Cagliari remains inconclusive. It might be that Wagner's figure is faulty or based on a not well preserved specimen; or it might mean that two 'forms' or species are (or were) present in Sardinia; or, that Wagner might have based his descriptions on material with erroneous locality data.

Lebias nigropunctata Schinz (1840: 334) is also described from Sardinia, but the text is uninformative and does not allow to objectively identify the species; there is no known surviving type material (Kottelat, 1997). The identity of these three nominal species based on non-extant Sardinian material can only be cleared by the designation of neotypes. We designate MNHN 2005-1975 (the neotype of *A. fasciatus*) as the common neotype of *Lebias sarda* Wagner, 1828, *L. lineopunctata* Wagner, 1828, and *L. nigropunctata* Schinz, 1840. This makes them objective synonyms of *A. fasciatus*.

We have seen photographs of *A. fasciatus* from Sardinian localities provided by S. Valdesalici. Adult males from Stagno di Pilo, near Porto Torres (northwestern Sardinia) have no black margin on the dorsal fin, while the black margin is present in specimens from northeastern Sardinia (no precise locality data).

Some data on the genetic diversity within the western Mediterranean populations is available, however in a format presently not compatible with a taxonomic analysis. Nevertheless, they somehow provide information paralleling the observations on the colour pattern. An electrophoretic analysis based on 11 populations from Corsica, Sardinia, Sicily, the Tyrrhenian and Adriatic coasts of Italy, and Tunisia shows that the 3 Sicilian and Tunisian populations constitute one unit, the 2 Adriatic ones a second unit, and the Tyrrhenian, Sardinian and Corsican ones a third unit (Maltagliati, 1999). Within that last unit, the mainland and Corsican populations are closer to each other than to the Sardinian ones. Another allozyme study of 20 Corsican and Sardinian populations shows that the Corsican populations have closest similarity with some populations from the northeastern tip of Sardinia (Maltagliati, unpublished, pers. comm.). Tigano *et al.* (2004) noted differences in the number and location of NOR loci on chromosomes of Adriatic and Sicilian populations.

Tigano *et al.* (1999) report differences in the morphology of pharyngeal bones between Sicilian and Adriatic populations. Ferrito *et al.* (2003) compared some morphological traits and allozymes of two Sicilian, one Sardinian and one Adriatic populations. Although the number of populations is limited, the three units reported by Maltagliati (1999) also show up in these studies.

Wildekamp (1993: 50) figures a specimen from Malta with more and narrower bars than the Adriatic ones, probably similar to the Tunisian ones. (Gulia [1861: 11] made a laconic description of two new species from Malta, *Micromugil timidus* and *M. macrogaster*, apparently the male and the female; there is no known type material.) Material from Sicily is figured by Wildekamp *et al.* (1999: 35) and its fins by Tigano (1982: 175). Material from Tunisia is figured by Boumaiza (1980) and van der Zee & Vonk (1991; see below). In all, the pre-dorsal bars tend to be vertically split in at least their lower extremity, and there is a tendency to have very thin bars intercalated between larger ones. This is not the case in material, figures and photographs we have seen from the Adriatic, Greece and Turkey (pers. obs.; Wildekamp, 1993 and unpublished photographs); in these populations, the bars tend to be fewer, wider and more regular.

Cyprinodon cyanogaster and *C. doliatus* were both described by Guichenot (1859: 379) from Biskara in northeastern Algeria. They are respectively female and male, and apparently conspecific (8 syntypes of *C. doliatus* MNHN 4392 and 5 syntypes of *C. cyanogaster* MNHN 3218 examined). Presently, we are unable to distinguish them morphologically from the Sardinian populations of *A. fasciatus* and we consider them as conspecific. The Algerian and most of the Tunisian material that we examined, as well as that figured by Boumaiza (1980) and van der Zee & Vonk (1990; 'short form'), also are conspecific. As observed in *A. fasciatus*, the syntypes of *C. doliatus* (males) have the black margin in the dorsal fin and the black subdistal bar on the caudal fin and the syntypes of *C. cyanogaster* (females) have the small spots on the caudal peduncle.

Van der Zee & Vonk (1990) have photographs of live specimens of an *Aphanius* from Tunisia with a deep body, short dorsal fin, pallid coloration and without dark margin in the dorsal fin. It differs from *A. fasciatus*, as now fixed by the neotype, in having more dark bars (about 20 vs. 8-15). Most interesting is that van der Zee & Vonk report the presence of two 'forms' of *A. fasciatus* in sympatry in Lake Kelbia drainage, the one mentioned above, which they call normal form (their figure 2), and a more stocky one, which they call 'short' form with a vivid coloration, fewer bars and a very conspicuous dark margin in dorsal fin. The two 'forms' reportedly also differ in their way of swimming (Wildekamp, 1993: 50). This is strongly suggesting that two species are involved: the 'short' form with an appearance identical to that of the Sicilian populations, and the 'normal' form possibly endemic. We had the possibility to examine only two specimens that possibly belong to this 'normal' form (Gabes, Tunisia; MNHN 1922-72, 1923-29).

Concluding, the data and material presently available to us justify investigating the possible existence of at least two species within *A. fasciatus* s.l. in the Western Mediterranean: 1) *A. fasciatus* from the Tyrrhenian basin, Sicilia, Malta, Tunisia and Algeria; and 2) an unnamed species from Tunisia. The status of some Corsican and Sardinian populations (without the black margin on the dorsal fin) also requires investigation. There are no available names for the Tunisian species or the last mentioned Sardinian-Corsican populations.

EASTERN MEDITERRANEAN *A. FASCIATUS* S.L.: Data on the Eastern Mediterranean populations are less numerous and less detailed. The earliest record of *Aphanius* from the Adriatic is apparently by Nardo (1827: 488) who recorded *A. fasciatus* and described a new species (*A. nanus*). Nardo did not give precise locality data, but his introductory paragraph makes it clear that his work was based mainly on his observations along the shores of Istria and additional observations in Dalmatia and Romandiola (Ravenna Province, Italy). Although brief, his account of *A. fasciatus* refers to 8-9 bluish bars on body and dorsal fin black anteriorly. His *A. nanus* is diagnosed by having 12-13 irregular black bars and black spots and refers to the female.

Lebias flava Costa (1838: fasc. 19: 35, pl. 17 fig. 1) was described from lake Varano, on the Adriatic shore of southern Italy. Valenciennes (in Cuvier & Valenciennes, 1846: 159) saw no difference between Costa's plate and his material from Sardinia.

Wildekamp (1993: 48) figures a male from Dalmatia with a colour pattern similar to that of the Comacchio (near Ravenna, Italy) material figured by Kiener & Schachter (1974). The material of *A. fasciatus* (of unknown origin) figured by Gandolfi *et al.* (1991: 617) shows the same colour pattern.

Cyprinodon desioi described by Gianferrari (1932: 214, fig. 1) from north-eastern Libya has been considered as a synonym of *A. fasciatus* (e.g. by Wildekamp, 1993: 49). Neither the description nor the figure mention dark markings in the dorsal fin. The figure does not show any pattern on the caudal fin, but the description mentions that there are one, two or no brown bars. With the presently available material and data, we are unable to distinguish any of these population and nominal species from *A. fasciatus* as recognised above.

Cyprinodon hammonis Valenciennes (in Cuvier & Valenciennes, 1846: 169) (type locality: Egypt [Siwa oasis, along the Libyan border] and Syria) is listed as a synonym of *A. fasciatus* by Wildekamp (1993: 48), who comments that the Syria specimens are *A. dispar*. Valenciennes' description of colour pattern (dorsal, caudal and pectoral fins blackish, without bars or spots) does not seem to be based on *A. fasciatus*.

Hrbek & Meyer (2003) examined the phylogeny of *Aphanius* using mtDNA. Their study included 7 populations that they identified as *A. fasciatus*; 6 of them pooled closely together (Prokopis [Prokopos], Greece; Ravenna and Palermo, Italy; Tarsus, Turkey; Corsica; Malta) and one slightly more distant (Lake Bafa, Turkey), but the data cannot be used to reach taxonomic conclusions.

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Pupal morphology in the subfamily Paussinae (Coleoptera: Carabidae)

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Pupal morphology in the subfamily Paussinae (Coleoptera: Carabidae). - Pupae of the Ozaenini lineage (*Pachyteles vignai* Deuve, 2000, *P. digiulioi* Deuve, 2000 and *Physea setosa* Chaudoir, 1868) and the Paussini lineage (*Platyrhopalopsis melleii* (Westwood, 1833) and *Paussus kannegieteri* Wasmann, 1896), are described and shown in figures, and compared with other adephagan taxa. In contrast to the customary assumption that pupal characters are uninformative with regard to systematics, this analysis shows the importance of pupal characters for phylogenetic reconstruction at different levels. Differences between basal and derived Paussinae occur in the arrangement of setae and in the folding of gonothecae, while some characters, like the microsculpture, the inversion of the last abdominal segments and perhaps the reduction of the 7th abdominal spiracle, support Paussinae monophyly. The extent of pubescence is a morphocline among Adephaga, with reduction in several unrelated taxa. Finally, the possibility of recognising distinct abdominal segments and antennal articles at the pupal stage, in taxa where they appear fused at the adult stage, may provide an ontogenetic basis for elucidating phylogenetic relationships.

Keywords: Coleoptera - Carabidae - Paussinae - pupae - morphology - phylogeny.

INTRODUCTION

Coleoptera have exarate pupae with free body appendages. The body is slightly bent, with the head sharply turned downwards. The legs (podothecae) lay in a backward position appressed to the ventral side of the body, the pterothecae (covers of the wings) are turned downwards and partially cover the hind legs. As stated by Jeannel (1941, 1949), and Sturani (1962), both pairs of metapterothecae are generally fully developed in Adephaga, even in the pupae of non-alate species. The antennothecae are turned backwards and lay between the mid legs and the mesopterothecae. The only residual larval characters are the sometimes remnant urogomphi and the pigment of the

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stemmata, which is only present in young pupae, disappearing later during the pupal stage.

While knowledge about larval morphology of Carabidae has grown very quickly in the last decades, the pupal morphology has rarely been investigated. Also, most of the research on the morphology of adephagan pupae has dealt with the description of the habitus, and no structure has been characterised in terms of its taxonomic importance.

The scarce interest in pupal biology may be a consequence of the difficulties encountered in obtaining and identifying pupae, as well as the perception that pupal morphology is of minor systematic importance, generally reflecting characters of the adult stage. Although pupae exhibit a number of characters shared with adults and larvae (such as those mentioned above), they also possess some unique characters.

The pupae of Coleoptera are immobile and they do not feed. Therefore the main function of the pupal integument is to protect the body as it undergoes metamorphosis. All carabid pupae have specialised setae on the dorsal surface, which are unique to this life stage (von Lengerken, 1924; Jeannel, 1949). However, the distribution of these setae differs considerably among lineages within the Carabidae (see Fig. 1). Dorsal setae may be found on the head, on one of the three tergites of the thorax, on the abdominal tergites 1 to 8, on the abdominal pleurites 2 to 7, and, if everted, also on the 9th and 10th abdominal segments. During the pupal stage, which lasts about 14 to 28 days in Carabidae (Sturani, 1962), the pupa rests in a prostrate position in the pupal chamber. These setae most likely function to isolate the body from the surface of the pupal chamber. In contrast, the ventral surface and the legs are completely glabrous, presumably because they are not in contact with the ground. Therefore the distribution of the pupal setae generally allows one to infer the resting position of the pupae within the pupal chamber. However, pupae of Amphizoidae, Hygrobiidae and Dytiscidae, are exceptions to this general rule. Although dorsal setae are fully developed in these groups (Bertrand, 1972), the pupae rest in labile equilibrium on their prolonged urogomphi and on the setae on the head and the anterior region of the pronotum, with their dorsal surface directed upwards and not in contact with the ground. As far as we know this resting position is unique to these taxa and represents a derived condition (Ruhnau, 1986).

Very few adephagan pupae have been described. The resulting lack of knowledge impedes detailed phylogenetic analyses based solely on pupal characters. However, some hypotheses about the phylogenetic utility of these characters can be inferred based on our present knowledge of Adephagen phylogeny.

Complete dorsal pubescence is present in *Dyscolus* (Carabidae, Platyninae) and *Dromius* (Carabidae, Lebiini), and in most Hydradephaga, where it occurs on the head, as well as all segments of the thorax and abdomen (Bertrand, 1972). This pattern indicates that the full set of setae covering head, pro-, meso-, metanotum, abdominal tergites 1-8 (and the following tergites if everted), and pleurites 2-8, represents an ancestral (plesiomorphic) condition. Consequently, the lack of pubescence on one of these body parts represents a derived (apomorphic) condition. For example, the pupae of *Clinidium* have dorsal pubesence on all segments except for the head. In other groups of carabids the dorsal pubescence is lacking from additional segments. For

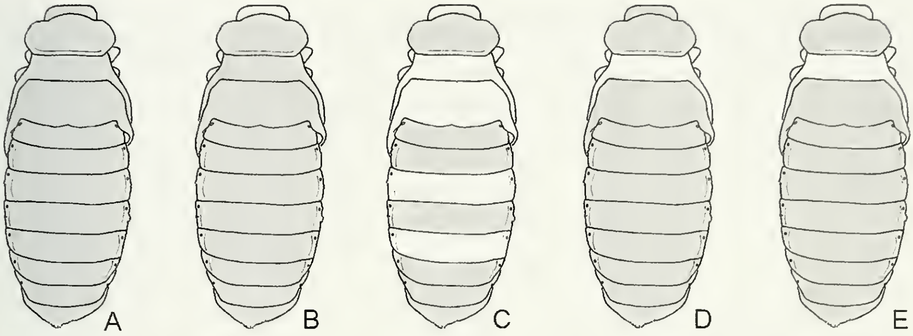


FIG. 1
Cartoons of Adephagan pupae, showing the distribution of dorsal setae in various lineages. The presence of dorsal setae in various segments is indicated by the gray color. Note that the head is drawn in unnatural position for illustrative purposes. (A) Hydradephaga, *Dyscolus* and *Dromius*. (B) *Clinidium*. (C) *Carabus*. (D) Ozaenini. (E) Paussini.

example, the pupae of *Carabus* and *Cychrus* lack setae on the head, mesonotum and metanotum, in addition some species in these groups lack setae on some of the abdominal segments (Sturani, 1962).

Another important pupal character is the number and shape of the spiracles. According to Jeannel (1949), the pupae of Adephaga possess a pair of spiracles on the mesothorax, and 6 or 7 spiracles on the abdominal segments, with the spiracles 6th and 7th closed. The 8th abdominal spiracle is always missing in both pupae and adults. The mesothoracic spiracles are closed in the pupae of Hydraenidae, Amphizoidae, Hygrobiidae and Dytiscidae (Ruhnau, 1986), open in Carabidae (Sturani, 1962), including Paussinae.

Within the subfamily Paussinae, pupae have been described from only 5 species, all belonging to the tribe Paussini: *Paussus kannegieteri* Wasmann, 1896 (Böving, 1907), *P. curtisi* (Westwood, 1864) (Luna de Carvalho, 1951), *P. cridae* (Gestro, 1916) and *P. cucullatus* (Westwood, 1850) (Luna de Carvalho, 1959) and *Platyrhopalopsis melleii* (Westwood, 1833) (Luna de Carvalho, 1977). Most of these descriptions are too superficial for well-founded morphological comparison.

In this paper, we provide the first comparative study of the pupal morphology of Paussinae. In particular, pupae of the tribe Ozaenini are described and illustrated for the first time. Detailed redescriptions and figures of Paussini pupae are also provided for comparative purposes. The pupae of Paussinae are compared with those of other Carabidae and some other adephagan groups, and the morphological characters with potential phylogenetic significance are discussed.

MATERIAL EXAMINED

CARABIDAE, PAUSSINAE, OZAENINI

1) *Pachyteles vignai* Deuve, 2000: 3 pupae (1 ♂ and 2 ♀♀) and 2 pupal exuviae (1 ♂ and 1 ♀). Pupae were obtained from 1st and 2nd instar larvae reared in the laboratory. The larvae were collected along a riverbank, where they had constructed

burrows in the sandy soil. Before pupation, larvae close the entrance of these burrows with ground taken from inside, forming a rounded pupal cell (Di Giulio & Vigna Taglianti, 2001). Material labelled "Ecuador, Cotopaxi. San Francisco de las Pampas, str. S. F. de las Pampas-La Union del Toachi, Km 1.300, 1550 m, 7.XII.1997, I. Tapia leg." and deposited in Di Giulio & Vigna Taglianti's collection (Università La Sapienza, Roma, Italy).

2) *Pachyteles digiulioi* Deuve, 2000, one 3rd instar larva dead during the pupation, labelled: "Ecuador, Cotopaxi. Between Otonga and Las Pampas, about 1700 m, 1.VI.1997, A. Di Giulio & A. Tapia leg." and deposited in Di Giulio & Vigna Taglianti's collection (Università La Sapienza, Roma, Italy).

3) *Physea setosa* Chaudoir, 1868, 2 pupae (1 ♂ and 1 ♀) and 1 male pupal exuvia collected together with larvae and adults in small holes near the "mushroom chambers" within a nest of leafcutter ants *Atta sexdens* (Linnaeus, 1758) (van Emden, 1936). Material labelled "Mendes, 25.9.1933, Ausgrabungsbau, in Erdhöhlen zwischen den Panellas, H. Eidmann" and deposited at the Naturhistorisches Museum, Basel (Switzerland).

CARABIDAE, PAUSSINAE, PAUSSINI

4) *Platyrhopalopsis melleii* (Westwood, 1833), 1 male pupa, labelled "India, Kerala Periyar – Lake, près de l'Hotel Aranya Nivas, 4.XI.1972, 950 m", preserved at the Natural History Museum of Geneva (Switzerland). The pupa is one of seven ones, collected by Besuchet in the ground at the foot of an old trunk, together with 8 larvae and 80 adults; no ants were observed nearby (Luna de Carvalho, 1977), even though *Platyrhopalopsis* species are considered to be myrmecophilous.

5) *Paussus kannegieteri* Wasmann, 1896, 3 male and 2 female pupae labelled "Java, Buitenzorg, Pangerango, 15-21.III.1904, Hjalmar Jensen" and deposited in the Zoological Museum of Copenhagen (Denmark). The pupae were collected together with some larvae and many adults inside an ant nest (Böving, 1907).

CARABIDAE, PLATYNINAE

6) *Dyscolus megacephalus* (Bates, 1891): 2 female pupae labelled "Ecuador, Cayambe, 4300 m, 01.IX.85 P. Moret", deposited in Moret's collection (Toulouse, France).

RHYSODIDAE

7) *Clinidium canaliculatum* (Costa, 1839), 1 female pupa labelled "Italia, Calabria, Pollino, Colle Gaudolino, 10.VII.71, V. Vomero", deposited in Di Giulio & Vigna Taglianti's collection (Università La Sapienza, Roma, Italy).

METHODS

All pupae were studied and drawn by using a stereomicroscope equipped with drawing tube. The description of chaetotaxy refers to only one half of the pupal body, since the positioning of the setae are nearly symmetrical on both sides of the body. One female pupa of *Pachyteles vignai*, was mounted on stub after critical point dehydration and gold sputtering, and examined and photographed (Figs 5-11) using a scanning electron microscope (S.E.M.) Philips XL 30 (Interdepartmental Laboratory of Electron Microscopy, L.I.M.E., University 'Roma Tre', Rome, Italy).

The pupa of *Platyrhopalopsis melleii* was examined and photographed using a Philips E.S.E.M. (Labor für Raster-Elektronenmikroskopie, Universität Basel, Switzerland) without drying and sputtering. All pupae (except that of *P. vignai* mounted on a stub) are preserved in 70% ethanol.

The characters of *Carabus* and *Cychrus* were obtained from Sturani (1962), those of *Dromius* from Casale *et al.* (1996), and those of Hydradephaga from Bertrand (1972).

RESULTS

Pachyteles vignai Deuve, 2000 Figs 2-11, 22-23

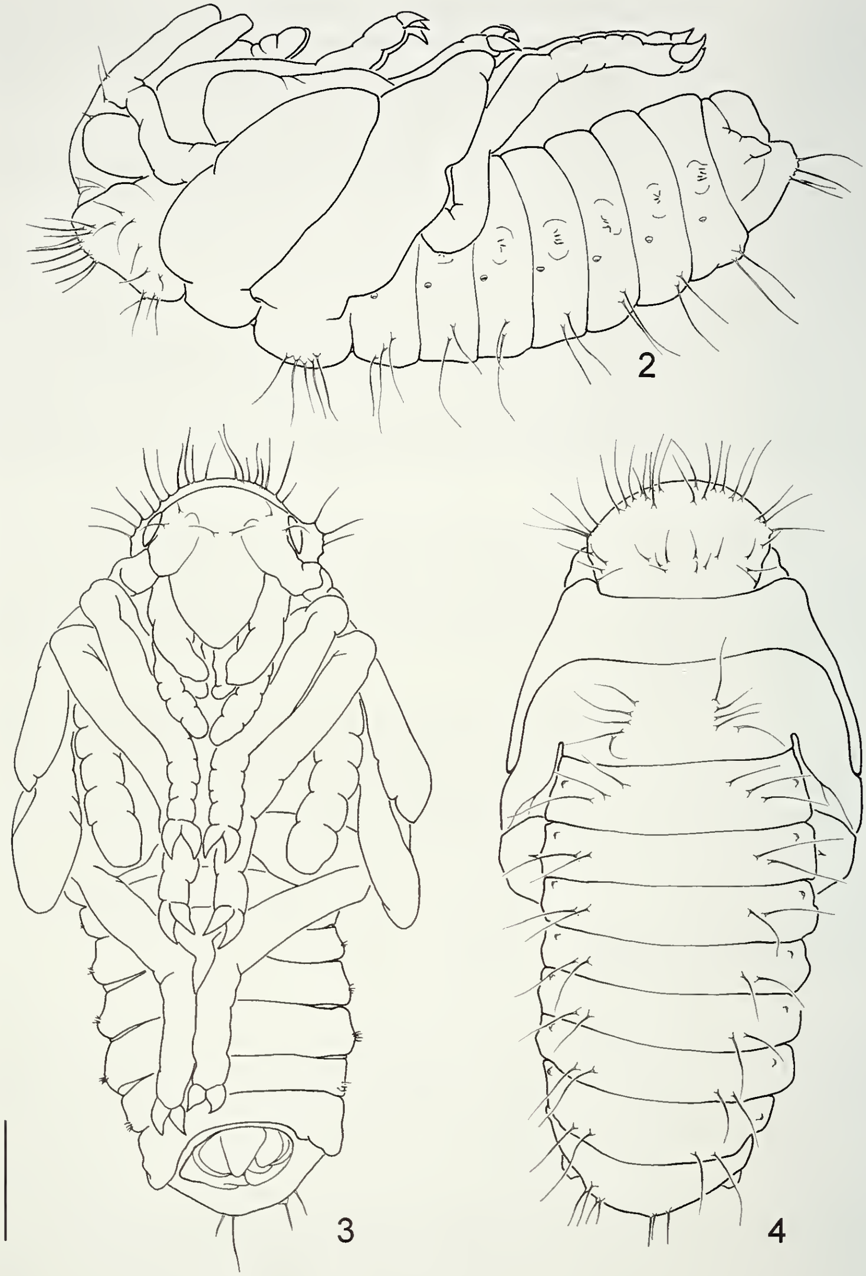
Pupa exarate, whitish, translucent; eyes and apex of mandibles brownish in more mature specimens; abdomen cylindrical (Figs 2-5). Total length about 6 mm.

Microsculpture. Consisting of small subtriangular thorns regularly dispersed all over the body. Gonothecae of female corrugated (Fig. 10). Setae on notum and pleurae longitudinally corrugated (sensilla chaetica), inserted on small conical tubercles (Fig. 11).

Head. Bent downward; general characters as in the adult (Figs 2, 3, 5); two setae between the antennal base and the eye (Figs 2, 3) and one medial seta on the vertex (Fig. 3); antennothecae folded between mid legs and mesopterothecae. In newly formed pupae, the pigment of larval stemmata (one on each side) is still visible at the position of the compound eyes.

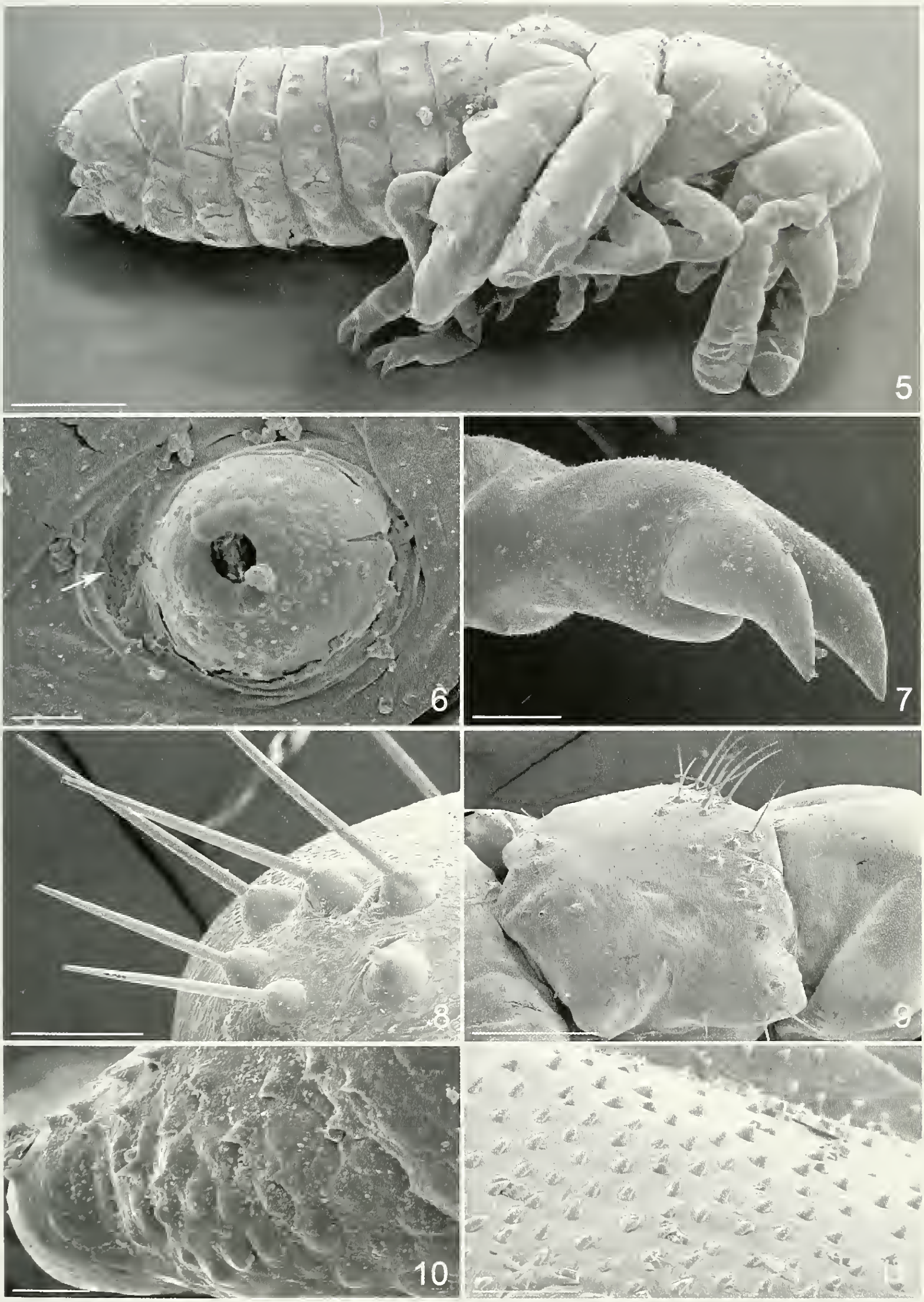
Thorax. Pronotum transverse (Fig. 4), with 17-19 setae on each side of the medial groove, positioned as follows: one group of 7-8 long setae anterior, 6-7 setae along the lateral margin and one group of 4 setae, shorter than the others, in the middle of the posterior part of the discal area. Medial groove not apparent. Mesonotum strongly transverse, without setae. Mesothoracic spiracle annular. Metanotum with 5 long setae on each side, longitudinally lined on the discal area; metaptheroteca longer than mesopterotheca (Fig. 2), ending at the level of the abdominal segment IV. Podothecae smooth, with tarsi touching one another along the midline; metatarsi reaching sternite VIII (Fig. 3).

Abdomen. Segments I-VIII visible in dorsal view (Fig. 4); segments IX-X inverted into the body, urogomphi absent. Tergite I with 3 long dorsal setae on each side, transversally lined; tergites II-VII with only one pair of dorsal setae on each side; tergite VIII with 7-8 setae on the posterior margin of the abdomen; pleurae of segments II-VII with 3-6 very small setae each; pleural areas of segment VIII produced in two conical protuberances, without setae (Figs 2, 22, 23). Spiracles dorsolateral (Figs 2, 4, 5), annular (Fig. 6), with a small posterior area rich of pores and with possible glandular function (Fig. 6, arrow); spiracles of first segment slightly wider and more cylindrical than the following (see Fig. 6). Sternite I divided by the metacoxae in two lateral sclerites; sternites II-VII entire, 6 separate sternites distinguishable, sternites I-III not fused. Male gonotheca (Fig. 22) asymmetrical, well visible, composed of a medial swollen and multilobed area, aedeagus not clearly turned toward the left side, as in the majority of carabid pupae (Jeannel, 1941; Sturani, 1962); female gonothecae (covering the two gonapophyses) conical and symmetrical (Figs 5, 10, 23), pointed at the tip, touching one another along the midline.



FIGS 2-4

Pachyteles vignai, male pupa: (2) habitus from left lateral, (3) ventral and (4) dorsal view. Scale bar = 1 mm.



Figs 5-11. *Pachyteles vignai*, female pupa: (5) habitus, right lateral view; (6) right abdominal spiracle II with posterior glandular area (arrow); (7) claw of right metathoracic leg; (8) group of setae on abdominal tergum VIII; (9) pronotum, right lateral view; (10) microsculpture at apex of right gonoteca; (11) microsculpture on head. Scale bars: Fig. 5 = 1 mm; Figs 6, 11 = 20 μm; Figs 7, 8 = 100 μm; Fig. 9 = 500 μm; Fig. 10 = 10 μm.

A male pupa of *Pachyteles digiulioi*, deceased during pupation and partially still enveloped by the 3rd instar larval exuvia, shows morphological characters, including the chaetotaxy, very similar to those of *Pachyteles vignai*.

Physea setosa Chaudoir, 1868 Figs 12-14, 24-25

The general pupal morphology and chaetotaxy of *Physea setosa* (Figs 12-14) and *Pachyteles vignai* are similar. Differences in the habitus, mostly of the prothorax, abdomen, legs and gonothecae (Figs 24, 25), reflect those of the adults. *Physea setosa* is one of the few myrmecophilous species of Ozaenini with adaptations for living with ants during both the adult stage (e.g. flattening of legs and body) and larval stage (e.g. physogastry of the body, cf. van Emden, 1936, Di Giulio *et al.*, 2003). In the following, we concentrate on the differences between the two taxa. Most setae of the specimens examined are broken, but their position is marked by small conical tubercles. Total length about 14 mm.

Head. One seta on the vertex near the antennal base; frons with 2 small swollen areas.

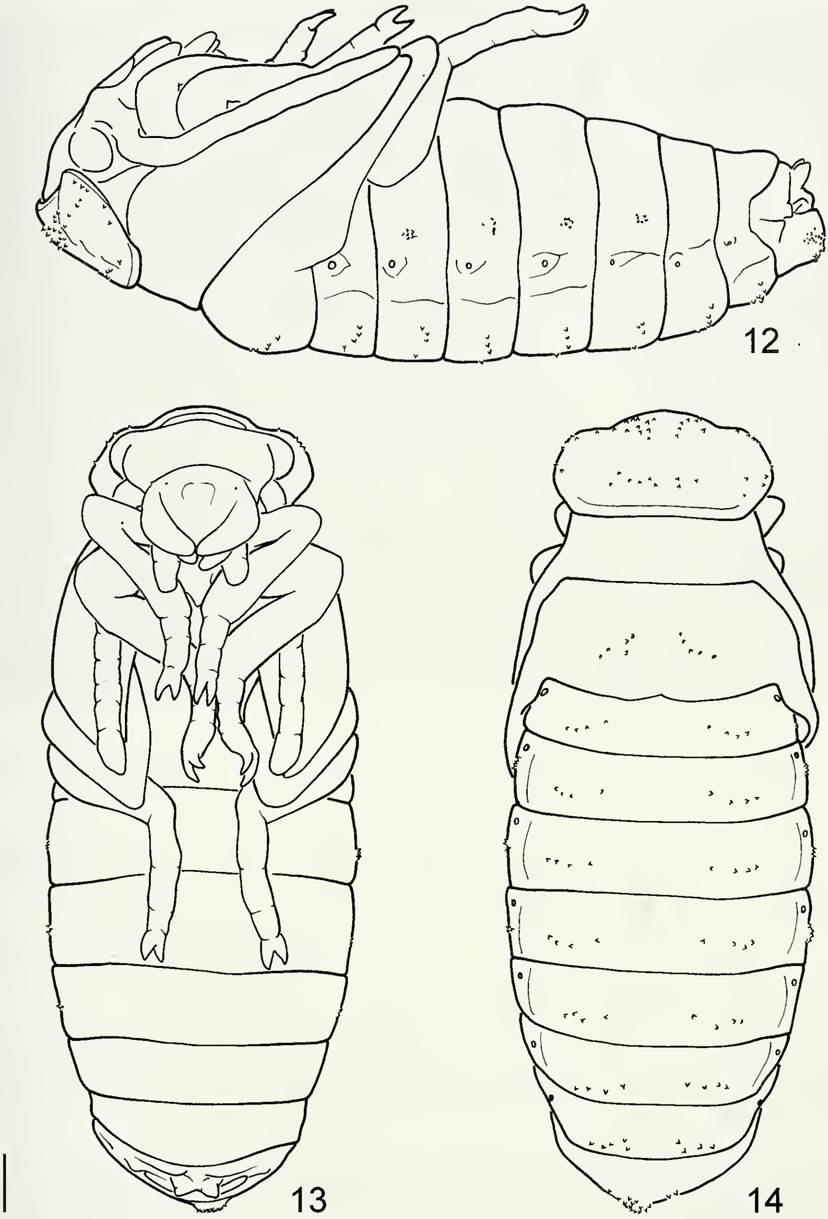
Thorax. Pronotum strongly transverse, flattened, with 20-25 setae on each side of the medial groove, disposed as in the following: one group of 8-10 anterior setae, 7-10 setae irregularly dispersed from the anterior corner to the lateral side and one group of 4-6 setae, medially on the posterior part. Mesonotum transverse and slender, without setae. Metanotum with 5 setae on each side, transversally lined on discal area; stigma of mesothorax well developed; metaptheroteca smaller than in *Pachyteles vignai* in respect to body size, ending at the level of abdominal segment III. Podothecae smooth, with pro- and mesotarsi touching one another along the midline; metatarsi reaching the sternite IV.

Abdomen. Tergite I with 3 long dorsal setae on each side, transversally lined; tergites II-VII with only one pair of dorsal setae on each side; tergite VIII with 7-8 setae on the posterior margin of the abdomen; pleurae of segments I-VII each with 2-6 very small setae; pleural areas of segment VIII produced in two small conical protuberances, without setae; sternites like in *Pachyteles vignai*. Male gonotheca (Fig. 24) asymmetrical, well visible, composed of a medial, swollen and multilobed area very similar to that of *Pachyteles vignai*; female gonothecae (Fig. 25) conical and symmetrical, pointed, smaller than those of *Pachyteles vignai*.

Platyrhopalopsis melleii (Westwood, 1833) Figs 15-18

Highly specialised adult characters (e.g. flattened legs, lens-shaped antennal club, subrectangular and flattened abdomen, small prothorax) are also visible in the pupa (Figs 15-17). The main differences from the pupae of Ozaenini include a richer chaetotaxy of notum and pleurae, and a different position of the gonothecae, partially hidden in the large sternite VII. The number of the visible tergites and sternites is the same as in the Ozaenini.

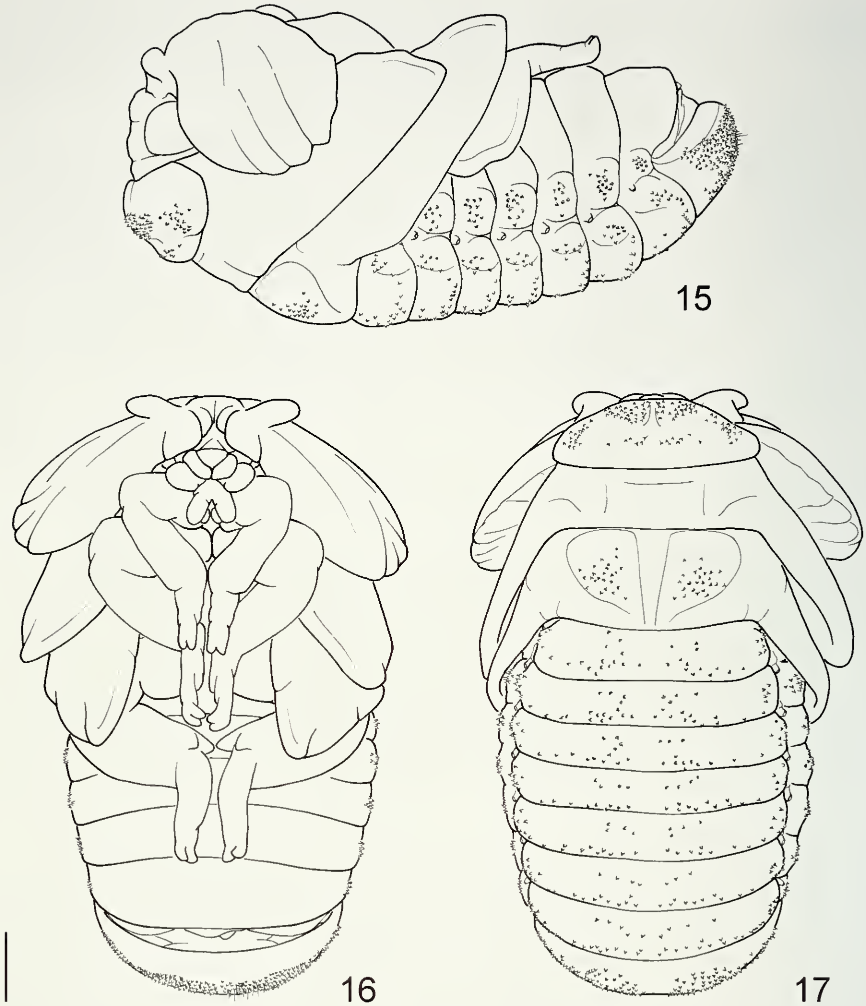
Almost all setae are broken but marked by small conical tubercles. Total length about 9 mm.



FIGS 12-14

Physea setosa, female pupa: (12) habitus from left lateral, (13) ventral and (14) dorsal view. Scale bar = 2 mm.

Microsculpture. Similar to that of *Pachyteles vignai*, with small triangular thorns (length about 3 μm, distance between thorns about 15 μm).



FIGS 15-17

Platyrhopalopsis melleii, male pupa: (15) habitus from left lateral, (16) ventral and (17) dorsal. Scale bar = 2 mm.

Head. Bent downward; no setae present. Antennothecae partially covering the fore-pterothecae (as in *Paussus kannegieteri* Wasmann, 1896, cf. Böving, 1907); 3 subapical denticulations present at the posterior margin of the antennal club of the antennotheca; in contrast to the adult, 6 or 7 antennomeres can be identified by transverse grooves, one small protuberance at the apex (Fig. 18).

Thorax. Pronotum transverse, subtriangular, with more than 50 setae on each side of the medial groove on the discal area, disposed as in the following: 26-30 anterior setae, 17-18 lateral setae and 6-8 posterior setae. Medial groove not apparent. Mesonotum highly transverse, without setae; mesothoracic spiracle annular. Meta-

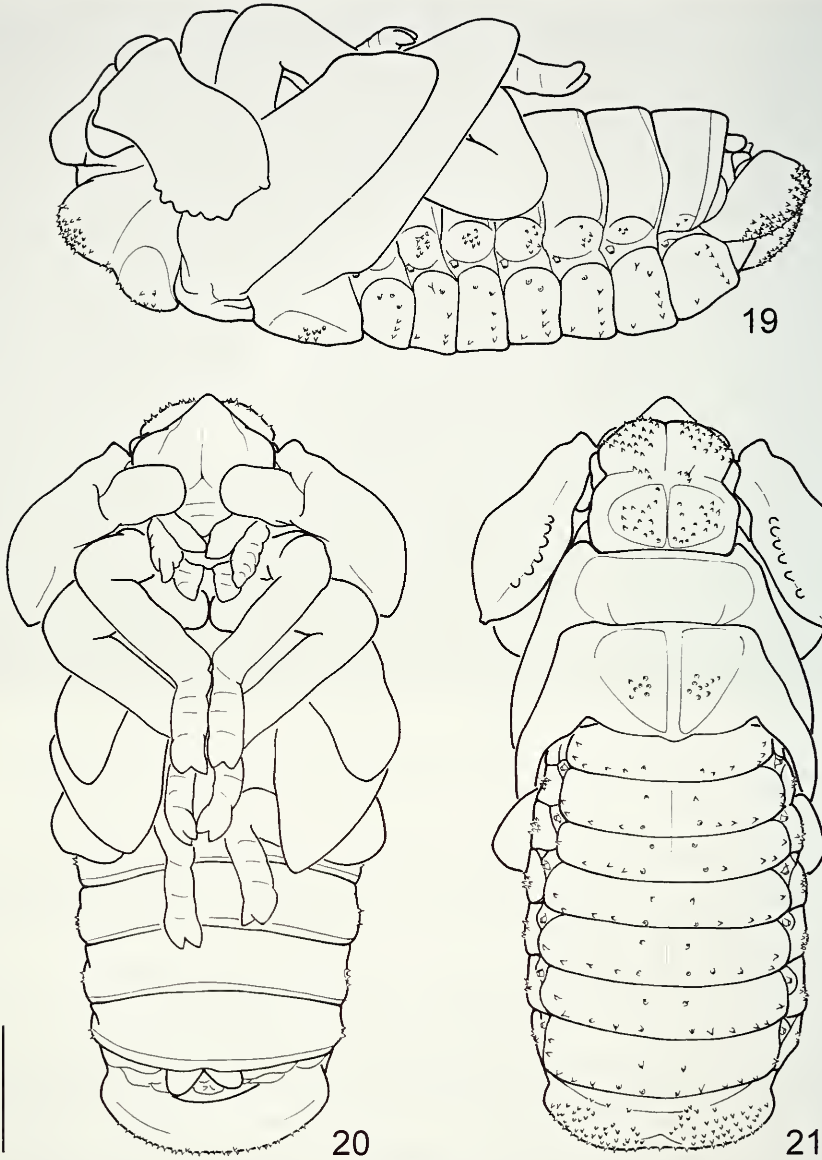
FIG. 18
Platyrhopalopsis melleii: antennotheca of male pupa in dorsolateral view. Scale bar = 500 μm.

notum with two symmetrical, slightly swollen areas on the discal part, with 24 setae each; metaptheroteca longer than mesopterotheca, ending at the level of abdominal segment IV. Podothecae flattened, with tarsi touching one another along the midline; metatarsi reaching sternite VIII.

Abdomen. Segments I-VIII visible from dorsal view; segments IX-X inverted, urogomphi absent. Tergites I-VII with 20-30 setae on each side of the midline, mostly on the discal area and on the posterolateral part; tergite VIII with more than 100 setae on each side of midline; pleurae of segments II-VII each with 10-15 small setae; pleural areas of segment VIII not clearly produced in conical protuberances. Spiracles annular, dorso-laterally positioned in a tergopleural groove. Sternites as in the Ozaenini, the basal three not fused. Male gonotheca asymmetrical, not protruding, composed of a medial swollen and multilobed area, partially hidden under the sternite VII.

Paussus kannegieteri Wasmann, 1896 Figs 19-21, 26-27

Body elongate, subcylindrical, with chaetotaxy similar to that of *Platyrhopalopsis melleii*, but less rich. The setae of the available pupae are almost all broken. Total length about 6 mm.

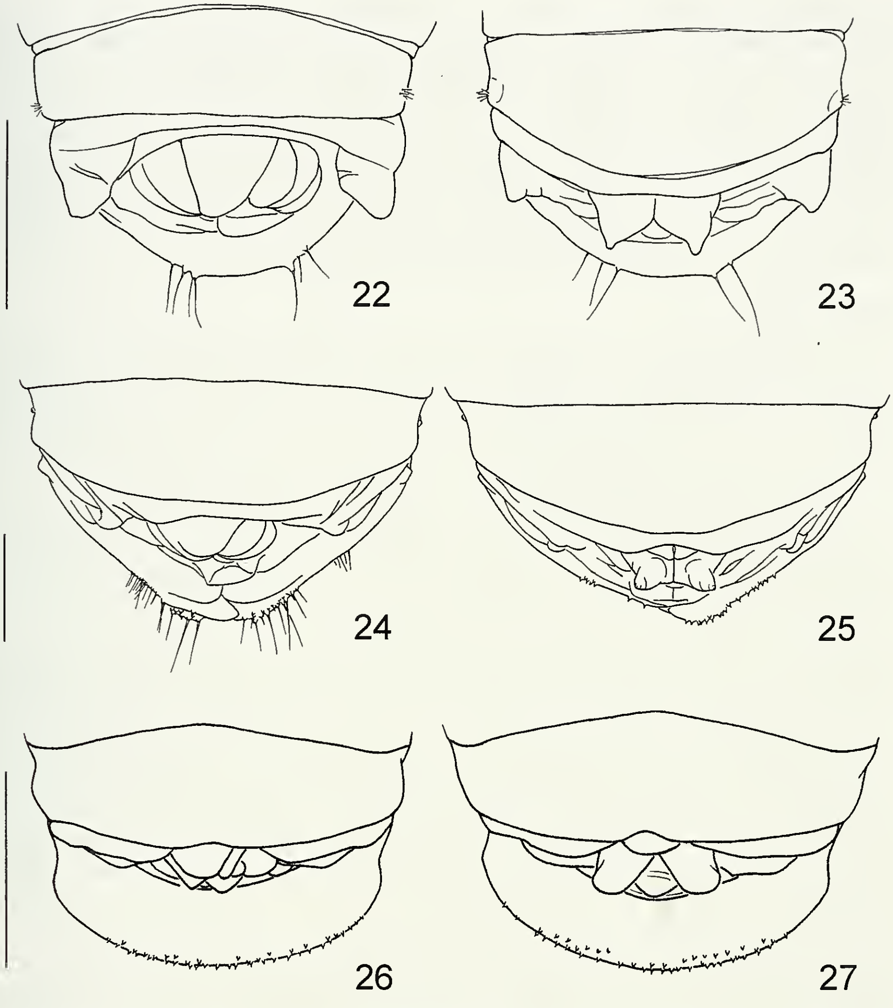


FIGS 19-21

Paussus kannegieteri, female pupa: (19) habitus from left lateral, (20) ventral and (21) dorsal view. Scale bar = 1 mm.

Microsculpture. As in *Platyrhopalopsis melleii*.

Head. Bent downward; no setae present. Antennothecae partially covering the anterior pterothecae; the 6 teeth on the posterior margin of the antennal club clearly visible; transversal sutures on the antennotheca absent; small protuberance present at apex.



Figs 22-27

Last abdominal segments of the pupae of in ventral view: (22) *Pachyteles vignai* male. (23) *P. vignai* female. (24) *Physea setosa* male. (25) *P. setosa* female. (26) *Paussus kannegieteri* male. (27) *Paussus kannegieteri* female.

Thorax. Pronotum subquadrate, divided in four parts by a distinct transverse constriction and a slight longitudinal medial groove; posterior half longer and slightly wider than the anterior; about 50 setae on each side of the medial groove, positioned as follows: about 25 anterior setae, 4-5 medial setae and 14-16 posterior setae. Mesonotum shorter than metanotum, highly transverse, without setae; mesothoracal stigma present. Metanotum with two symmetrical, slightly swollen areas on the discal part, with 7-9 setae each; metaptheroteca longer than mesopterotheca, ending at the level of abdominal segment IV. Podothecae cylindrical, slightly flattened, with tarsi touching one another along the midline; metatarsi reaching the sternite VII.

Abdomen. Segments I-VIII visible from dorsal view; segments IX-X inverted, urogomphi absent. Tergites I-VII with 6-8 setae on each side of the midline, disposed as in the following: 5-7 setae lined along the posterolateral part and 1 anterior seta close to the midline; tergite VIII with 50-60 setae on each side of the midline; pleurae of segments II-VIII with decreasing number of setae, from 8 to 2 small setae each. Spiracles annular, dorso-laterally positioned in a tergopleural groove. Sternites as in *Platyrhopalopsis*. Male gonotheca (Fig. 26) asymmetrical, not protruding, composed of a medial swollen and multilobed area, partially hidden under sternite VII; female gonothecae (Fig. 27) conical and symmetrical, rounded at the tip.

DISCUSSION

Paussinae pupae have a nearly complete dorsal pubescence: all paussine species lack dorsal pubesence on the mesonotum and those of tribe Paussini (*Platyrhopalopsis* and *Paussus*) also lack pubescence on the head. It seems that the lack of the pupal mesonotal setae is a synapomorphy of the Paussinae and the lack of setae on the head of Paussini, supports the derived position of Paussini within the subfamily.

The examined Ozaenini differ from the Paussini in the arrangement of the setae. In *Pachyteles* and *Physea* (Ozaenini) the setae of the metanotum and the abdominal tergites 1 to 7 are arranged in a single transverse row on each side of the midline (diagonal on metanotum). In contrast, in *Platyrhopalopsis* and *Paussus* (Paussini) the setae form an irregular group on the metanotum, and are arranged in two transverse rows on the abdominal tergites 1 to 7. The posterior row extends from the lateral border almost to the middle of the tergite. The internal end of the anterior row is situated also close to the midline, but it is much shorter than the posterior one. In *Paussus* it is only represented by a single internal seta; in *Platyrhopalopsis* there are about 4 to 5 and they are somewhat irregularly placed. In light of the phylogenetic relationships of the Paussinae based on larval characters (Di Giulio *et al.*, 2003), the complex setation pattern of *Platyrhopalopsis* and *Paussus* can be interpreted as a shared derived character. It represents either a synapomorphic character of the Paussini or a more derived clade within this monophyletic tribe.

The morphology of pupal spiracles differs among Adephaga taxa. Whereas the mesothoracic spiracles are closed in the pupae of Haliplidae, Amphizoidae, Hygrobiidae and Dytiscidae (Ruhnau, 1986), they are well developed in Carabidae. Seven (presumably functional) abdominal spiracles of similar sizes and shapes are present in the pupae of *Carabus* and most Hydradephaga according to the illustrations (Sturani, 1962; Bertrand, 1972). However the 1st abdominal spiracle is larger than the following six in *Clinidium canaliculatum* and *Dyscolus megacephalus*, and the 7th abdominal spiracle is smaller and more weakly sclerotised than the other spiracles in the Paussinae.

The pupal integument of all Paussinae examined have a unique microsculpture. The entire body is covered by a uniform pattern of more or less regularly spaced, small triangular thorn-like sculpticells.

In Carabidae, the last abdominal segments are visible and the 9th tergite often contains remnants of the larval urogomphi, as in *Carabus* and *Dyscolus*. The shape of pupal urogomphi, as well as their setae, seem to be true remaining larval characters. In contrast to the other Carabidae, the last abdominal segments of Paussinae are inverted and more or less invisible. The gonothecae are almost totally visible in Ozaenini while they are partially inverted and the basal part hidden in Paussini.

Another important pupal character in the Paussinae is the extent of the fusion of the abdominal segments. Luna de Carvalho (1951, 1959, 1977) stressed the importance of the number of visible abdominal sternites in paussine pupae. In contrast to four distinguishable sternites in adults, there are 6 sternites visible in the pupae. However, in adult Paussinae the first 3 visible sternites are fused (sternites 2 to 4 – the first one is more or less atrophied in all Adephaga), often with the intersegmental sutures indistinct, so that only 4 ventral plates are seen. The sternites are still separate in the pupae, so that the pupae exhibit 6 distinct ventral plates. This condition clearly shows that the fusion of abdominal segments is an apomorphic character state of the adults, while pupae preserve an ancestral condition of six visible abdominal plates typical of Adephaga.

Perhaps the most important pupal character with respect to phylogenetic implications within the Paussini is the visible segmentation of the antennothecae of *Platyrhopalopsis*. This genus is member of the subtribe Paussina, widely considered to be the most derived clade of the Paussini (Darlington, 1950; Nagel, 1997; Di Giulio *et al.,* 2003). The antennae of adults in this subtribe have only three segments: the scape (1st antennomere), the strongly reduced, ring-like pedicel (2nd antennomere), and a club, which is formed by the fusion of the flagellum (Nagel, 1987, 1997). The pattern of transverse constrictions in the adults of some species indicates a fusion of different groups of articles in different species. However the club of adult *Platyrhopalopsis* is lens-shaped without any trace of articles. In contrast, six or seven articles are apparent in the pupae, as well as a tubercle at the apex of the club, which is absent in the adults, suggesting that a number of 6-7 articles could be the ancestral state for this species. Future studies of the pupae in other Paussina species may reveal more or less antennal segments, which may provide informative characters for inferring relationships within this group.

To conclude, this study suggests that pupae may contain characters useful for phylogenetic reconstruction at different levels. Some characters, such as the unique microsculpture, the inversion of the last abdominal segments and perhaps the reduction in the size of the 7th abdominal spiracle, probably represent apomorphies of the Paussinae. The extent of pubescence is interpreted as a morphocline among Adephaga, with an increased reduction in pubesence in derived taxa. The arrangement of setae and the folding of gonothecae differ between basal and derived Paussinae. Finally, the possibility of recognising distinctly separate abdominal segments and traces of originally separate antennal articles at the pupal stage in taxa with fused metameric parts in the adult stage provides a potential ontogenetic basis for elucidating phylogenetic relationships in this group.

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Chionea austriaca in caves and artificial galleries of Slovenia (Diptera, Limoniidae)

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***Chionea austriaca* in caves and artificial galleries of Slovenia (Diptera, Limoniidae).** - We sampled 54 caves and galleries in north and east Slovenia methodically for ecological data and the invertebrate fauna. The snow fly *Chionea austriaca*, recorded in 37% of the cavities, proved indifferent with regard to most of the abiotic factors, but occurred in significantly higher individual numbers in caves on north and east slopes. The subterranean sojourn of *Ch. austriaca* appears merely weather-mediated. No indications of larval development in the caves were found.

Keywords: abiotic factors - speleobiology - distribution - snow fly.

INTRODUCTION

As their scientific and trivial names imply, snow flies – species of the genus *Chionea* – are usually met on the snow surface where they can easily be noticed. Nevertheless, these wing-reduced and somewhat spiderlike limoniids spend most of their adult lifetime in leaf litter, under logs and stones, in subnivean habitats or in mammal burrows. The larvae are soil-dwelling. Low catchability makes snow flies appear so rare that Byers (1983), for instance, referred to a catch of 29 specimens as a rich yield.

Snow flies have been reported from altitudes up to 2700 m (3500 m in North America: Byers, 1983). *Chionea* (*Sphaeconophilus*) *belgica* (Becker, 1912), and *Ch.* (*S.*) *lutescens* Lundström, 1907, occur also in the colline zone and in lowlands (Grootaert, 1984; Reusch, 1988, 1997; Weber & Weidemann, 1993), whereas the bulk of the *Chionea* species prefer forest sites, or open habitats from the submontane zone upwards (Focarile, 1975).

Chionea austriaca (Christian, 1980), originally described from a Lower Austrian cave, is distributed over western Hungary (Christian, unpubl.) and parts of

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Slovenia and Austria. At the northwestern and western limits of distribution *Ch. austriaca* touches the areas of two closely related species, namely *Ch. belgica* and the widespread *Ch. lutescens* (Christian, in press).

Ecological notes on European *Chionea* species focus on aboveground habitats (e.g. Heim de Balsac, 1934; Nadig, 1943, 1949; Bitsch, 1955; Sömme & Östbye, 1969; Hågvar, 1971; Mendl *et al.*, 1977; Itämies & Lindgren, 1985; Heijerman, 1987). Several authors have casually mentioned the sojourn of snow flies in caves (Strobl, 1900; Peyerimhoff, 1906; Bezzi, 1911; Czerny, 1930; Español Coll, 1955, Strinati & Aellen, 1967; Turquin, 1973; Bourne, 1977, 1979; Christian, 1980; Byers, 1983; Novak & Kuštor, 1983; Novak, 2005). Information about environmental conditions in cavities inhabited by snow flies, however, is anecdotal at the best.

The present paper addresses the abiotic conditions at sampling sites of *Ch. austriaca* in caves and artificial galleries in Slovenia. We want to test our hypothesis that this species is only loosely aligned to macrocaverns.

MATERIALS AND METHODS

During the period 1977-2001, 54 caves and artificial galleries (in the following: caves) in central and northern Slovenia (mapped in Novak, 2005) were ecologically investigated in January, April, July and October according to a standardized scheme. All accessible surfaces of the cave passages like walls, ceiling, speleothems, microhabitats below stones and wood, and water surfaces, were carefully inspected for terrestrial animals. Pitfall traps were set, on average, every 3 m starting at the entrance, and exposed for 47±1 hours. Each trap was baited with 3 g of decomposing meat attached on a wire above the trapping liquid (2 cm of fruit juice with cherry and maraschino essences, and a lacing of detergent). Substrate from the close vicinity of the trap sites was sampled for Tullgren extraction.

Environmental parameters were determined chiefly according to Stewart *et al.* (1974) and Rowell (1997). The distance from a trap to entrance and surface, respectively, and the cross-section of the passage at the trap site were taken from cave maps (Novak, 2005). Illumination was measured using a Lunasix luxmeter. Substrate pH was determined with a combined electrode (91–02 Orion, USA; Orion Ionalyser 407 A) in elutriated fresh samples after 2-4 hrs stirring in an equal volume of distilled water. Substrate carbonate and organic matter contents were established for the dried and pulverized <2 mm fraction; carbonate was quantified by Scheibler calcimetry, ignition loss after heating at 700°C for 1 h. Ground and air temperatures were measured with decimal thermometers (Intos, Croatia). Air humidity was determined with a psychrometer according to August, ground moisture by drying at 105°C to constant weight. Airflow was detected with a hand-held anemometer (Munro IM159) or, when below 0.3 $m \cdot s^{-1}$, derived from the velocity of fog or magnesium smoke (cf. Andrieux, 1970).

Cold hardiness of one male, collected on a south-facing meadow slope at Studence (46°18’53” N, 15°09’51” E, 330 m) on snow, 31.01.2006, was determined in a thermostat chamber THK/V1-2020 (Elelstro, Slovenia). The specimen was enclosed in a glass tube with a scrap of wet paper and cooled down to lethal temperature in 12 hour treats in steps of 1°C/day, with intermediate 12 hour breaks at acclimatization temperature of +8°C.

Voucher specimens of *Ch. austriaca* are deposited in the Slovenian Museum of Natural History (Ljubljana), in the Muséum d'histoire naturelle de la Ville de Genève, and in the Natural History Museum, Vienna.

RESULTS

Three of 14 European *Chionea* species (Oosterbroek, 2005) have been recorded in Slovenia (Oosterbroek & Simova-Tošić, 2003, and own data; Fig. 1). *Ch.* (*Chionea*) *araneoides* Dalman, 1816 was found in the Krma valley (UTM: VM13); *Ch.* (*Sphaeconophilus*) *alpina* Bezzi, 1908 is known from Mt. Grmada (VM61, 640 m), Zdenska jama cave (VL77, 460 m), Dobrepolje (VL77, 450 m), Mačkovica cave (VL47, 480 m) (Simova-Tošić & Sivec, 1977), and the alpine ice cave Ivačičeva jama in Mt. Kredarica at 2435 m a.s.l. (Novak & Kuštor, 1983); the third species, *Ch.* (*S.*) *austriaca* was encountered in numerous caves in central and eastern Slovenia (Table 1). Here we add three snow-surface records of *Ch. austriaca*: Mt. Jesenik (WM13, 688 m), Studence (WM13, 330 m) and Mt. Snežnik (VL54, 1690 m, currently the southernmost locality), and a further cave record: Brezno pod Durcami in Mt. Raduha (VM84, 1840 m, currently the highest record in Slovenia), which was not included in the systematic investigations.

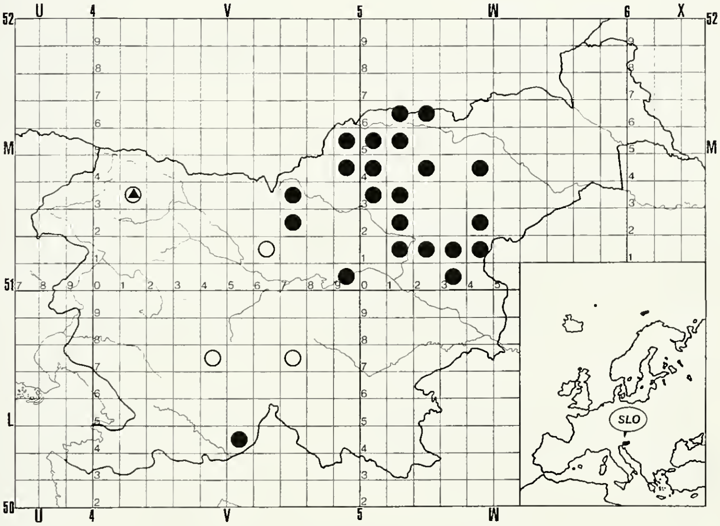

FIG. 1

Records of snow flies in Slovenia: ▲ *Chionea araneoides*, ○ *Ch. alpina* and ● *Ch. austriaca*.

In 20 (37%) of the 54 caves, 38 specimens (11 males, 27 females; sex ratio 29:71) of *Ch. austriaca* were met, at altitudes between 270 and 1515 m (Tab. 1). Tab. 2 compiles values of abiotic factors at effective trapping sites. All specimens were trapped in pitfalls exposed in January. Larvae were neither seen, nor trapped or Tullgren-extracted. Most adults occurred in the entrance zone of the caves during the winter (Fig. 2). Caves opening in northern and eastern slopes were significantly more

TABLE 1: *Chionea austriaca* in caves of Slovenia. No = current number as in Novak, 2005; Cad = cadastral number in the Slovene cave register; Capital letters indicate artificial galleries; UTM code (see Fig. 1); Alt = altitude (m); Bed = bedrock: e = conglomerate, l = limestone, d = dolomite, m = marble, p = pegmatite, s = schists, t = tonalite); Ind, Date = number of individuals and date of collection [ddmmyy].

Cave or gallery	No	Cad	UTM	Co-ordinates (N, E)	Alt	Bed	Ind, Date
Rački pekel	10	465	VM73	46°23'27", 14°43'14"	590	l	1♀, 060179
Zijalka v Dovji Griči	11	376	VM72	46°18'18", 14°40'14"	1515	l	1♂, 4♀, 100179
Jama pri Votli peči	18	3263	VM95	46°32'51", 14°58'33"	400	p	1♀, 120179
Skobirjeva votlica	19	3956	VM94	46°27'45", 14°58'46"	940	d	1♀, 050179
Brdajsova jama	23	3497	VM90	46°07'03", 14°54'02"	651	l	1♂, 3♀, 210179
Objekt pri Žnodru	25	B1	WM05	46°30'34", 15°03'22"	550	l	1♀, 110178
Rdečka jama	26	3488	WM04	46°26'54", 15°03'44"	858	e	1♂, 120178
Lokoviška jama	27	3959	WM03	46°22'03", 15°01'27"	370	l	1♀, 070178
Umetni rov v Bistriškem grabnu	30	U2	WM16	46°38'47", 15°07'56"	480	s	2♀, 150178
Zapečke peči	31	3208	WM15	46°32'49", 15°13'26"	610	l	1♂, 150178
Špegličeva jama	34	3512	WM12	46°17'58", 15°11'55"	400	l	1♀, 090179
Oevirkova jama v Štadlerjevem gozdu	35	5348	WM11	46°12'29", 15°11'11"	320	l	2♂, 2♀, 090179
Jama pod Herkovimi pečmi	37	1849	WM26	46°37'35", 15°16'04"	545	l	2♀, 190178
Jaklova luknja	38	4636	WM24	46°28'56", 15°16'49"	1100	t	1♂, 110178
Fantovska luknja 2	40	3967	WM21	46°12'14", 15°18'35"	480	l	1♂, 4♀, 180179
Jama v kamnolomu pri Suhem	42	4632	WM31	46°08'40", 15°23'55"	500	l	1♂, 18011978
Glija jama	43	84	WM30	46°06'39", 15°26'32"	515	l	1♀, 18011978
Luknja pri Naeeku na Planici	45	2407	WM44	46°28'30", 15°34'13"	730	m	1♂, 200178
Jama v kamnolomu nad Studenicami	46	252	WM42	46°17'51", 15°37'11"	400	l	1♂, 2♀, 170179
Rov	47	U4	WM41	46°09'31", 15°35'43"	270	s	1♀, 170179

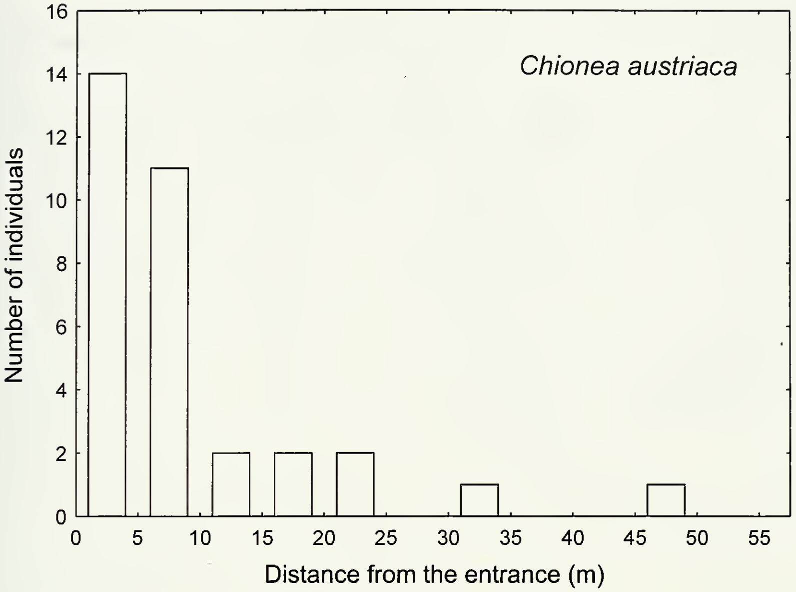

FIG. 2

Yield of *Ch. austriaca* individuals relating to the distance between cave entrance and trap locality.

frequently settled by *Ch. austriaca* as compared to other slopes ($\chi^2 = 24.54$; $P < 0.001$), and hosted significantly more individuals ($\chi^2 = 17.05$; $P = 0.017$) (Tab. 3).

Preference for any kind of bedrock was not observed. In two cases (26 and 38 in Tab. 1) entrances were situated in various types of forests.

By comparing the meteorological conditions in caves with vs. those without *Ch. austriaca* we found that in "*Chionea* caves" the air and ground temperatures were significantly lower, and airflow significantly higher. There were no significant differences regarding relative air humidity and substrate moisture (Tab. 4). Males and females did not differ significantly with respect to any abiotic parameter at the trapping sites ($F_{1,37} = 0.000\text{-}2.614$; $P = 0.11\text{-}0.98$).

In the cold hardiness test the single male of *Ch. austriaca* died at -7°C.

DISCUSSION

Adult *Ch. austriaca* were trapped in caves only during the cold season, in agreement with the period of their occurrence on snow. The temperature demands of *Ch. austriaca* are comparable to those of most other European snow flies (Wojtusiak, 1950; Bourne, 1979), and its supercooling ability – admittedly determined for one specimen only – seems to agree with the values reported for *Ch. araneoides* (mean supercooling point -7.5°C, range -10.5 /-4.5°C: Sömme & Östbye, 1969). A vast ecological range of *Ch. austriaca* is indicated by the large altitudinal range, indifference to bedrock, its occurrence in forested as well as in non-forested areas, and inside caves by tolerance

TABLE 2: January values of abiotic factors at effective trapping sites of *Ch. austriaca*, compared to the extreme values in "*Chionea* caves" and to the mean and extreme values of all the 54 caves (based on 605-617 sampling sites).

	Mean ± s.d. (min-max) at effective trapping sites	**Min-Max in "*Chionea* caves"**	**Mean ± s.d. (min-max) in all the 54 caves**
Distance from entrance [m]	8±10 (0-49)	0-121	31±31 (0-121)
Distance from surface [m]	9±8 (1-40)	0-70	18±14 (0-80)
Passage cross-section [m^2]	5±7 (0?36)	0.2-80	13±31 (0.2-460)
Illumination [lx]	258±169 (0-~10,000)	0-~100,000	194±171 (0-~100,000)
pH	7.9±0.8 (4.3-8.6)	4.3-8.7	8.1±0.6 (2.4-8.9)
CO_3^{-2} [%]	21.4±24.0 (0.0-76.0)	0-96.6	31.9±29.8 (0.0-98.7)
Ignition loss [%]	13.2±15.2 (0.3-52.9)	0.3-85.9	10.7±13.2 (0.3-85.9)
Air temperature [^{0}C]	1.2±3.8 (-5.0-8.9)	-5.0-11.5	3.6±4.4 (-6.0-11.5)
Ground temperature [^{0}C]	1.6±3.3 (-3.0-9.0)	-4.6-12.6	4.1±4.2 (-7.2-12.6)
Relative air humidity [%]	91±12 (65-100)	54-100	95±9 (54-100)
Substrate moisture [%]	18.4±12.0 (0.2-46.7)	0.0-73.6	20.8±14.7 (0.0-87.6)
Airflow [m/s]	0.07±0.04 (0.00-2.00)	0.00-10.00	0.11±0.73 (0.00-10.00)
Soil colour / modus (min-max)	10YR 5/4 (5Y 3/2-7.5YR 5/6)	5YR 5/8-5Y 5/2	10YR4/4 (5YR 3/2-2.5Y 6/4)

TABLE 3: Distribution of *Ch. austriaca* with respect to slope orientation of cave entrances.

Slope orientation	***Ch. austriaca*** **individuals N (%)**	**Caves with** ***Ch. austriaca*** **N (%)**	**All caves N (%)**
N	12 (31.6)	4 (20.0)	10 (18.5)
NE	2 (5.3)	2 (10.0)	3 (5.6)
E	12 (31.6)	6 (30.0)	14 (25.9)
SE	5 (13.2)	3 (15.0)	4 (7.4)
S	4 (10.5)	4 (20.0)	7 (13.0)
SW	0 (0.0)	0 (0.0)	4 (7.4)
W	0 (0.0)	0 (0.0)	10 (18.5)
NW	3 (7.9)	1 (5.0)	2 (3.7)
total	**38 (100)**	**20 (100)**	**54 (100)**

TABLE 4: Selected meteorological parameters of caves with *Ch. austriaca* present vs. absent. January values from all trap sites along the first 10 m (i.e.. those without *Chionea* yield included). Significant differences asterisked *.

	Ch. austriaca **present (N = 103)**	**absent (N = 159)**	$F_{1,260}$	*P*
Air temperature	4.8±2.4 (0.6-9.5)	6.2±2.0 (0.3-11.4)	24.59	<0.001*
Ground temperature	4.7±2.5 (-0.3-11.3)	5.7±2.0 (0.5-11.0)	12.78	<0.001*
Air humidity	94±8 (69-100)	92±22 (43-100)	2.52	0.113
Substrate moisture	23.3±16.1 0.0-65.4	24.8±17.0 (1.1-79.2)	0.52	0.473
Airflow	0.08±0.05 (0.0-10.00)	0.06±0.04 (0.0-5.00)	4.97	0.026*

of wide ranges of illumination, substrate pH, carbonate contents and ignition loss. The conspicuous prevalence of individuals in caves on north and east facing slopes contrasts with the impression that snow flies in open-air habitats do not display any slope orientation preference. Their surface activity, however, is strongly weatherdependent inasmuch heavy frost and wind drive them into more moderate hideaways. So the disproportionately high individual numbers of *Ch. austriaca* in caves opening out on north and east slopes is not a consequence of psychrophily, but rather the result of more frequent chill avoidance migrations there. The highest trapping yield of snow flies in the entrance zone of the caves and in passages of small cross-section supports this conclusion. Lower ground temperature and higher airflow in "*Chionea* caves" may be merely the consequence of the harsh climate conditions on north and east slopes.

Wing reduction of snow flies has been explained as a result of regressive evolution due to temporary exposure to cold and windy weather (Hackman, 1964; Byers, 1961, 1983). This morphological character could lead to consider snow flies as being pre-disposed to life in subterranean habitats (cf. Vandel, 1964; Ginet & Decou, 1982). However, *Ch. austriaca* – like several other European congeners – inhabits macrocaverns facultatively and only temporaryly during its epigean ecophase in the cold season. The fact that maximum density in caves is observed in January, when virtually all females are ready for egg-laying (Christian unpubl.), does not necessarily indicate subterranean oviposition. On the one hand there is no report on larval development of *Chionea* in caves, and on the other hand an extremely long oviposition period (from November to March) was shown for *Ch. araneoides* (Hågvar, 1976), so that females of *Ch. austriaca* – let's assume an adult life span of two months (cf. Byers, 1983) – may lay eggs after they have quitted the cave shelter. Thus, in terms of the classical biospeleological classification (Vandel, 1964), *Ch. austriaca* is best included in the trogloxenes.

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A new genus and species of the spider family Agelenidae from western Sichuan Province, China (Arachnida: Araneae)

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A new genus and species of the spider family Agelenidae from western Sichuan Province, China (Arachnida: Araneae). - *Ageleradix sichuanensis*, a new genus and new species, is reported based on specimens from western Sichuan, China. *Ageleradix* gen. n. is distinguished from the other genera of Agelenidae by having a special sclerite between tegulum and embolus in males, a well-developed posterior plate in the epigynum and a broad copulatory bursa in females. Two species are included in the new genus, the type species and *Ageleradix cymbiforma* (Wang, 1991) comb. n.

Keywords: Taxonomy - *Ageleradix* - *Agelescape* - new combination.

INTRODUCTION

Sichuan Province is located in the Upper Yangtze Valley in the southwest part of China. It covers an area of 569,000 square kilometres and has an estimated population of over 70 million people. Lying along the transition zone between the Sichuan Basin and the Qinghai-Tibetan Plateau, western Sichuan has an unusual geography and weather conditions, which have given rise to a variety of landforms and habitats.

A collection trip to western Sichuan in summer 2004 yielded a very unusual new agelenid species, which is here assigned to the new genus *Ageleradix* gen. n. A detailed description of this genus and its type species, *Ageleradix sichuanensis* sp. n., is given in the following.

MATERIAL AND METHODS

Measurements are given in millimetres. Eye diameters were measured at the widest part. Leg measurements are given as: Total length (femur, patella, tibia, metatarsus, tarsus). Chaetotaxy follows Thaler & Knoflach (1998): v', v'' position pro-, retroventral, l', l'' pro-, retrolateral, d dorsal; subscript a and 2 denote apical position and number of spines, respectively; pairs of spines are given in parentheses,

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whorls of spines in square brackets. Terms used in the text and figure legends mainly follow Levy (1996) and Wang (1997). Abbreviations used in text and figures are: ALE – anterior lateral eye; ALS – anterior lateral spinneret; AME – anterior median eye; C – conductor; CB – copulatory bursa; D – diverticula; E – embolus; FD – fertilization duct; MA – median apophysis; MOQ – median ocular quadrangle; PA – patellar apophysis; PLE – posterior lateral eye; PLS – posterior lateral spinneret; PME – posterior median eye; PMS – posterior median spinneret; PP – posterior plate of epigynum; R – radix; RTA – retrolateral tibial apophysis; S – spermatheca; SC – scape; TP – tegular process.

All type specimens are deposited in the Institute of Zoology, Chinese Academy of Sciences, Beijing (IZCAS) and in the Muséum d'histoire naturelle, Genève, Switzerland (MHNG).

TAXONOMY

Ageleradix gen. n.

TYPE SPECIES: *Ageleradix sichuanensis* sp. n.

SPECIES INCLUDED: Two species are here placed in this new genus: *Ageleradix sichuanensis* sp. n. and *Ageleradix cymbiforma* (Wang, 1991) comb. n. which is transferred from *Agelena*.

ETYMOLOGY: The generic name is derived from the words "Agelena" and "radix"; the gender is feminine.

DIAGNOSIS: In its general appearance (Fig. 1), this new genus resembles two other Palaearctic genera, *Agelena* and *Agelescape*, which construct funnel webs among bushes and in grass. In the shape of their epigynum, *Ageleradix* gen. n. females are similar to those of *Agelescape* by having a scape (Fig. 10), but can be distinguished by having a well-developed posterior plate in their epigynum and a broad copulatory bursa (Figs 10-11). Males can be easily distinguished from those of *Agelena* and *Agelescape* by having a radix between tegulum and embolus, by their basal median apophysis and by a strong and broad conductor (Figs 3-7). The new genus is distinct from *Agelena* by females having a scape extending from the anterior rim of the epigynum (Fig. 10).

DESCRIPTION: Body shape, coloration and eye arrangement as in *Agelena* and *Agelescape* (Fig. 1); body covered with feather-like hairs (Fig. 2); ALE biggest, AME smallest; cheliceral groove with 3 promarginal and 3 retromarginal teeth; epigynum with a plate extending from posterior rim (Fig. 10); spermathecae widely separated from each other; copulatory bursae well-developed (Fig. 11); male palp with small retrolateral tibial apophysis and with indistinct patellar apophysis; tegulum with process; conductor very strong, slightly modified into a shallow concavity housing the distal end of the embolus; embolus originating centrally, with broad base and pointed distal end; radix developed as a partly serrated additional sclerite between tegulum and embolus; median apophysis situated basally on the palpal organ (Figs 3-9).

DISTRIBUTION: Sichuan, China.

***Ageleradix sichuanensis* sp. n.** Figs 1-11

HOLOTYPE: ♂(IZCAS), Jintang Town, Kangding County (30.0° N, 101.9° E), Sichuan Province, China, July 19, 2004.

PARATYPES: 1♂(IZCAS), Yutong Town, Kangding County (30.0° N, 101.9° E), Sichuan Province, China, August 4, 1981. – 6♀ and 6♂(MHNG), Jintang Town, Kangding County, July 18-19, 2004. – 1♂(IZCAS), Changpinggou Valley, Mt Siguniang (31.1° N, 102.9° E), Xiaojin County, August 1, 2004. – 2♀ and 4♂(IZCAS), Waba Village, Geshizha Town, Danba County (30.8° N, 101.9° E), July 30, 2004. – 1♀ and 2♂(IZCAS), Meirengu Town, Danba County, July 31, 2004. – 1♀(IZCAS), Daxue Village, Geshizha Town, Danba County (30.8° N, 101.9° E), July 30, 2004. – 1♂(IZCAS), Geshizha Town, Danba County, July 30, 2004. – 5♂(IZCAS), Kungyu Town (30.5° N, 102.0° E), Danba County, July 30, 2004. All type material was collected in the Sichuan Province by Dr Xiang Xu, Mr Zhengtian Zhang, Mr Yucheng Lin, and Ms Qian Wang.

ETYMOLOGY: The specific name derives from the name of the province in which the types were collected.

DIAGNOSIS: This new species can be distinguished from *A. cymbiforma* by having a scape extending from the anterior rim of epigynum and globular spermathecae in females, and by the evidently different shape of the conductor and the presence of a radix in males.

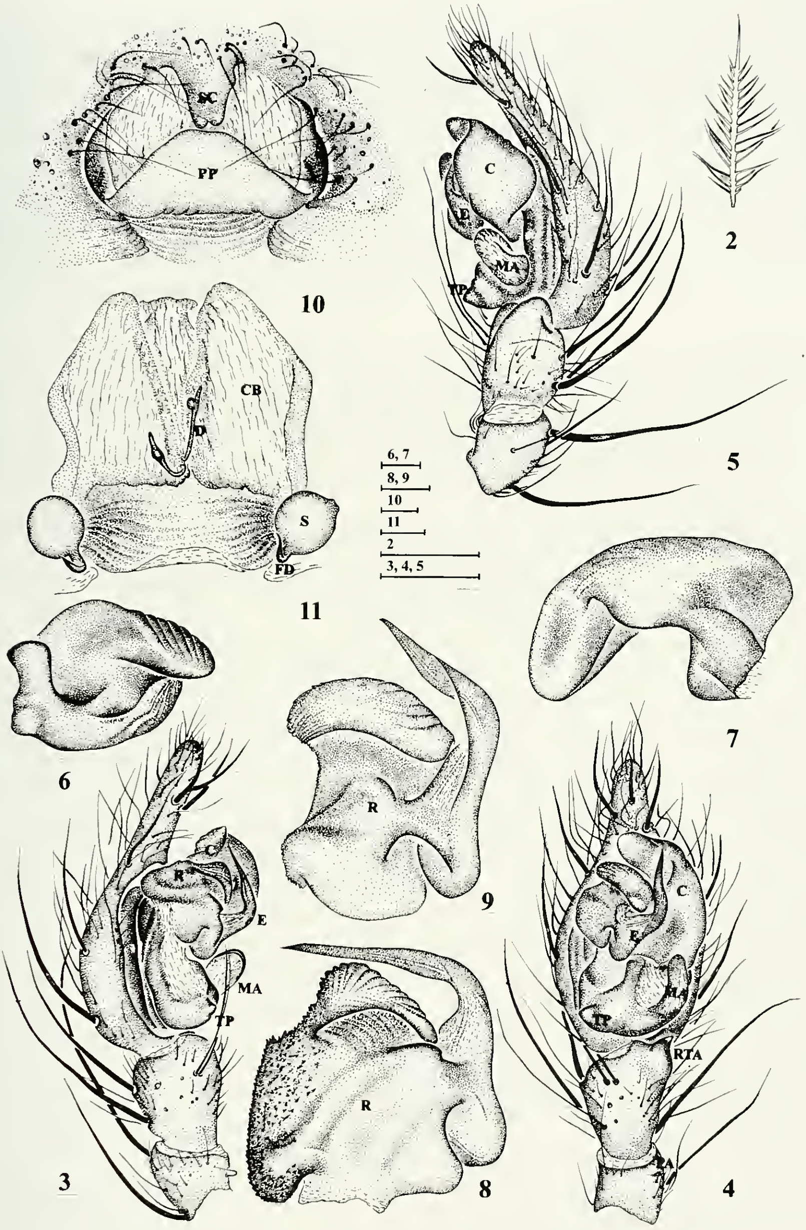
DESCRIPTION OF MALE: Total length 7.64-9.84. Holotype 9.27 long; carapace length 4.00, width 2.91; abdomen length 5.27, width 2.73. Two eye rows strongly procurved; in dorsal view AME in the middle of an open circle formed by the other six eyes. AME 0.12, ALE 0.19, PME 0.15, PLE 0.16; AME-AME 0.05, AME-ALE 0.07, PME-PME 0.10, PME-PLE 0.08; MOQ length 0.36, front width 0.29, back width 0.40; clypeus height 0.17. Body covered with tiny white or grey featherlike hairs (Fig. 2). Carapace brown; head region clearly narrower than thorax region in dorsal view (Fig. 1). Fovea long, longitudinal. Chelicerae red-brown, promargin and retromargin each with 3 teeth on groove. Labium wider than long. Sternum yellow-brown, its distal end slightly inserted into coxa IV. Legs thin and long. Tibiae I-IV with two rows of dorsal trichobothria; metatarsi I-IV and tarsi I-IV with single row of trichobothria dorsally. Chaetotaxy (slightly variable): Femur I d l'' (d l') (l' l''); II/III d (l' l'') d (l' l''); IV d l' d (l' l''). Patella I-IV d l' d_a'. Tibia I (v' v'') l' (v' v'') l' v_a'; II v'' l' (v' v'') l' v_a'; III (d v') (l' l'') v' v'' d (l' l'') (v_a' v_a''); IV (d v') (l' l'') l' (d l'') (l' l'') (v_a' v_a''). Metatarsus I (v' v'') l' (v' v'') [l' v' v'']; II (v' v'') l' (v' v'') [d l' v' v'']; III [d l' l'' v' v''] [d l' l''] (v' v'') [d_2 l' l'' v' v'']; IV [d l' l'' v''] v'' l'' v' l' l'' (v' v'') [v_{2a}' v_{2a}'' l_{2a}' l_{2a}'']. Tarsus I-III 0; IV l' l'' v' l' l''. Leg IV longest; leg formula: IV, I, II, III. Leg measurements: I: 16.64 (4.00+5.18+4.91+2.55); II: 15.73 (3.91+4.73+4.73+2.36); III: 15.28 (3.82+4.55+4.64+2.27); IV: 20.10 (4.82+5.82 +6.55+2.91). Abdomen much longer than wide, sides darker than middle of dorsum (Fig. 1). ALS 0.62 long; basal article of PLS 0.52 long, apical article 0.62 long; AMS, PMS and PLS with conspicuous gland spigots. Male palp with indistinct patellar apophysis; conductor strong, broad, and slightly modified into a shallow concavity; embolus originating centrally, with broad base and pointed distal end; radix partly covered with denticles; tegulum with a cone-shaped process; median apophysis palmate (Figs 3-9).

FIG. 1

Ageleradix sichuanensis sp. n., male from Sichuan, China.

DESCRIPTION OF FEMALE: Colour and leg formula as in male. Measurements very variable. Total length 7.64-8.73. A specimen from Jintang Town, Kangding County 9.27 long; carapace length 3.64, width 2.55; abdomen length 5.09, width 3.14. AME 0.13, ALE 0.18, PME 0.14, PLE 0.16; AME-AME 0.05, AME-ALE 0.07 PME-PME 0.12, PME-PLE 0.10; MOQ length 0.39, front width 0.26, back width 0.36; clypeus heighth 0.13. Chaetotaxy (slightly variable): Femur I d (d l’) (l’ l’’); II-IV d d (l’ l’’). Patella I-IV d l d_a Tibia I (v’ v’’) l’’ l’ (v’ v’’) (d l’); II (d v’’) l’’ v’’ d l’; III/IV (d v’) (l’ l’’) (v’ d) (l’ l’’) v_a’. Metatarsus I/II (v’ v’’) l’ (v’ v’’) [l’ v’ v’’]; III [l’ v’’ v’ v’’] l’ l’’ d v’’ l’ [d_2 l’ l’’ v’ v’’]; IV [d l’ l’’ v’’] v’ l’ v’’ (l’ l’’) (v’ v’’) [l_2’ l_2’’ v’ v’’]. Leg measurements: I: 11.10 (3.00+3.73+2.55+1.82); II: 10.36 (2.91+3.36 +2.45+1.64); III: 10.28 (2.82+3.18+2.73+1.55); IV: 14.18 (3.64+4.27+4.18+2.09). ALS 0.60 long; basal article of PLS 0.45 long, apical article 0.65 long. Epigynal atrium large. Long scape extending over most part of atrium; distal end of scape slightly bifid and almost in contact with triangular plate extending from posterior rim of epigynum. Broad, membranous copulatory bursae bearing a pair of threadlike diverticula; diverticula with a slightly swollen part; copulatory bursae connected internally to a pair of globular spermathecae, to the outside through an atrium; fertilization duct distinct (Figs 10-11).

DISTRIBUTION: Only known from the type locality.



FIGS 2-11

Ageleradix sichuanensis sp. n. (2) Featherlike hair. (3) Left male palp, prolateral view. (4) Same as in 3, ventral view. (5) Same, retrolateral view. (6) Conductor (separated from palpal organ), prolateral view. (7) Same, ventral view. (8) Embolus (separated from palpal organ), prolateral view. (9) Same, ventral view. (10) Epigynum, ventral view. (11) Same, dorsal view. Scale bars: 2, 6-11= 0.1 mm; 3-5= 0.5 mm.

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Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland

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Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland.- A survey of invasive species belonging to the Mysidae in the Rhine and Danube Rivers and adjacent freshwater systems revealed that certain species have invaded the waters of many more countries than previously known. First records of *Hemimysis anomala* G. O. Sars, 1907 are given for Switzerland, Slovakia, Hungary, Croatia and Serbia. The same holds true for *Katamysis warpachowskyi* G. O. Sars, 1893 in Croatia and Serbia, and for *Limnomysis benedeni* Czerniavsky, 1882 in Switzerland. New or first records are also given for *L. benedeni* in the systems of artificial inland waterways of northern Germany, France and Serbia. *L. benedeni* and *H. anomala* are the first representatives of the order Mysidacea (or Mysida according to certain authors) in Switzerland. A single specimen of *Paramysis lacustris* (Czerniavsky, 1882) serves as a first record for the upper Danube in Austria. The observed spreading of *L. benedeni* in inland waterways of France suggests that it probably will soon arrive at the Mediterranean coast, with unknown consequences for indigenous populations of the closely related species in the genus *Diamysis* Czerniavsky, 1882. *H. anomala*, a top invader of continental waters in Europe, could become a potential threat at the ecosystem level if its invasion continues into large lakes, such as those connected with the Rhine system in Switzerland.

Keywords: *Hemimysis anomala* - *Limnomysis benedeni* - *Katamysis warpachowskyi* - *Paramysis lacustris* - invasive aquatic species - Ponto-Caspian invaders - continental Europe - distribution - anthropogenic dispersion - ecological impact.

INTRODUCTION

Up to the mid-20th century, only few range extensions were recorded for mysids in continental waters of Europe. Behning (1938), for example, noticed that *Paramysis ullskyi* Czerniavsky, 1882 penetrated only a few hundred kilometres into the tributaries of the Black Sea, whereas more than 3000 km into the Volga River and its tributaries. He explained the strong differences in distribution, already observed in the 1920s, by

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the more developed inland navigation along the Volga; such navigation may have favoured the dispersal of this mysid and of other peracarids attached to the fouling on ship hulls. Only few later authors adopted this view, which has recently been reconsidered by Tarasov (1996). The next major expansion event was noted in 1946 with the surprising appearance of *Limnomysis benedeni* Czerniavsky, 1882 in the winter harbour of Budapest, almost 1200 km upstream of the previously known distribution limit in the Danube River (Dudich, 1947; Woynárovich, 1955). Such a strong yet rapid displacement of the known limit suggested anthropogenic mechanisms of dispersion. Băcescu (1966) and Mordukhai-Boltovskoi (1979) already pondered why *Limnomysis* dispersed to the upper reach of the Danube, while it inhabited only the lower reach of the Volga River and only a near-mouth confluent in the Don River system.

After having been projected already in the 1930s, the next major change started in the late 1940s with the intentional introduction of mysids into hydropower reservoirs, lakes, and other water bodies in order to enrich the supply of food for fish. From 1948-1965 more than one hundred million mysids, together with a great variety of other invertebrates, were intentionally released into more than 200 water bodies of the former Soviet Union. Our knowledge about these introductions and their outcomes is quite obscure. This is mainly due to the inaccessibility of cryptic literature (citations in Komarova, 1991; Grigorovich *et al.*, 2002) and inadvertent stocking (Pligin & Yemel'yanova, 1989).

During the next decades some of the mysid species showed local secondary spreading from the introduction sites; a few species – essentially the four presented in Fig. 1 – transgressed the large continental watersheds and invaded vast areas of central, northern and western Europe. In the early 1980s it became clear that mysid introductions could have adverse effects at the ecosystem level (Rieman & Falter, 1981; Fürst *et al.*, 1984; Ketelaars *et al.*, 1999), and most of the intentional introductions were stopped. This had no direct effect on the ongoing non-intentional mechanisms of dispersion, which culminated in 1997-1998 with the explosive range expansion of *Hemimysis anomala* G. O. Sars, 1907 and *L. benedeni* in waters of the Rhine system. The present contribution indicates further range expansions of these and additional species in large areas of continental Europe, for the first time also including Switzerland. A critical analysis of invasion histories could help to estimate the potential for future dispersal and possible threats to ecosystems and biodiversity.

MATERIAL AND METHODS

By convention, the river kilometres are numbered in downstream order for the Rhine and its tributaries, but in upstream order for the Danube. Measurements of abiotic parameters were taken as explained in Wittmann (2002). Salinity was calculated from conductivity measurements corrected to 25°C, as a dimensionless equivalent of overall ionic content rather than content of sea salts. Mass occurrence was defined as ≥1000 specimens and, as an additional prerequisite, ≥10 times the average yield of positive samples taken with the same method under comparable conditions.

The diverse sampling methods follow those outlined in Wittmann (2002), with the exception of the following modifications introduced in 2004: the hand nets were optionally attached to a 4.6 m telescopic rod, allowing for sampling from the shore down to 3.5 m depth; the drift net was larger (opening 2872 cm^2, mesh size 500 μm for the anterior 150 cm of length, and 280 μm for the posterior 100 cm) than before and kept in position 10 cm above the substrate by a steel cage. Ten bottle traps were used in 2005, designed essentially according to Odenwald *et al.* (2005); the main difference was that the bottles were tightly attached to 0.5 kg weights in order to throw them, filled with about 1.5 l of water and the bait, several metres from the shore. The bait was commercial tablets for aquarist use («Wels Tabs mit Spirulina» by 'Fa. Product Aquaristik-Terraristik' in Austria, imported from 'Hicari Corp.' in Japan), composed of dried, compressed algae, insects and crustaceans.

The yield obtained with the baited traps confirmed the findings of Odenwald *et al.* (2005) that *Hemimysis anomala* is more effectively trapped than other mysid species (*Limnomysis benedeni* and *Katamysis warpachowskyi* G. O. Sars, 1893). The drift net was useful for currents >0.2 m/s, especially if no or only few stagnant side arms were accessible in a particular river stretch. Drift samples yielded all three above-mentioned species more often than the remaining methods. Drift nets and bottle traps were set up over night.

In 1985-2001 a total of 390 samples containing mysids were taken along the Rhine and Danube Rivers, from the upper reaches down to the deltas, as well as along the coasts of Romania and western Turkey (Black, Marmora, Aegean Seas) and in adjacent freshwaters. Part of these sampling data is available in Wittmann (1995, 2002), Wittmann *et al.* (1999) and Wittmann & Ariani (2000). In 2002-2005 a total of 230 samples were taken at 117 stations in the Rhine and Danube systems and in adjacent waters.

Additional data were obtained from hand net samples taken by B. Csányi during the Cousteau-Expedition 1991 at 50 stations between Danube-km 2786 and km 80. Twelve of these samples contained mysid species. Two samples with *L. benedeni* were studied in the collection of the Biologija Univerza Ljubljana: from the Tisa River in Serbia (26 June 1977, leg. I. B. Sket) and from the Danube at Donji Milanovac in the Carpathian breakthrough (8 Oct. 1984). Ten samples with *L. benedeni* and *Diamysis pengoi* (Czerniavsky, 1882), taken on 21 Aug.-30 Sept. 1924 by V. Pietschmann and O. Koller at Lake Patiu (46.20°N, 28.0167°E, at the River Prut, an affluent of the Danube at km 133) and at six stations from Danube-km 181 down to km 19 of the Chilia branch, were studied in the collection of the Naturhistorisches Museum Wien (Crust. Coll. nos. 5960, 5962, 13397-13408).

In 1985-2004 most of the material was fixed in a solution of 4% formalin in ambient water and later transferred into an aqueous solution of 60% ethanol with 10% diethylene glycol. In 2005 most material was fixed in 96% ethanol in view of future genetic studies. Representative material was deposited in the Muséum d'histoire naturelle de la Ville de Genève and the Naturhistorisches Museum Wien (Crust. Coll. nos. 20685-20704).

RESULTS

Hemimysis anomala G. O. Sars, 1907 Figs 1A, 2

The sampling campaigns in 2004-2005 yielded this species at 19 stations. These are shown in Fig. 2 together with published data from previous campaigns and litera-

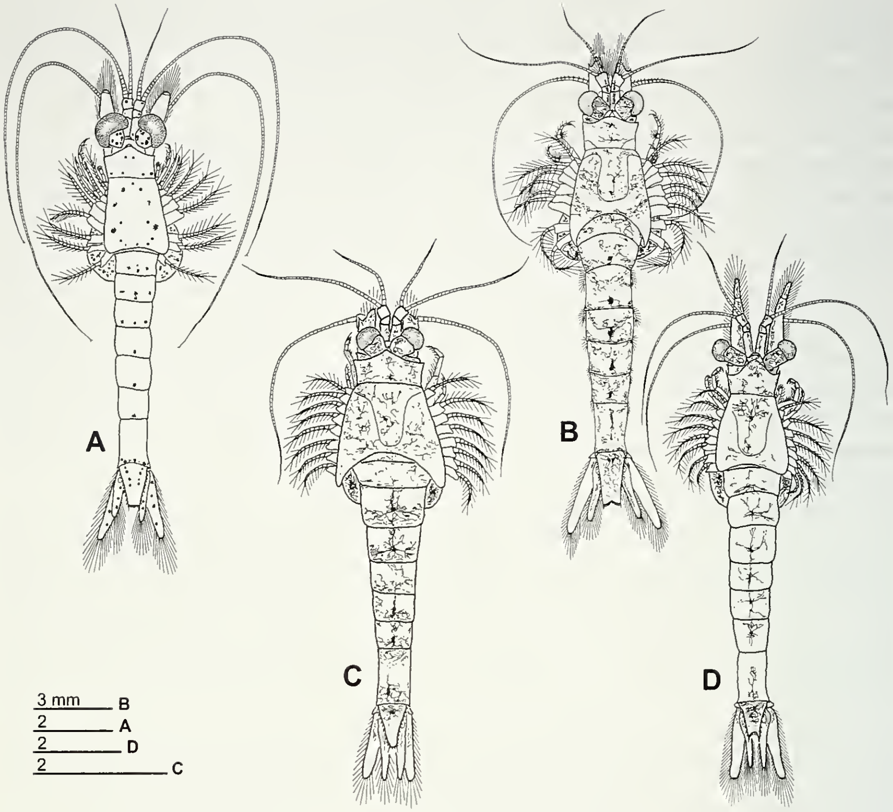

FIG. 1

The currently most expansive mysid species in continental waters of Europe: *Hemimysis anomala* (A), *Paramysis lacustris* (B), *Katamysis warpachowskyi* (C) and *Limnomysis benedeni* (D). Adult females from the Danube River in Vienna (A, C, D) and from the Danube Delta (B). Adults of the four species are macroscopically distinguished by body proportions, and by the size and form of eyestalks and cornea. A, C and D taken from slightly schematized drawings in Wittmann (2002).

ture data. A number of first records were noted in 2005: *H. anomala* was found southwards of the already published range limit in the Rhine system, namely in Strasbourg (km 295) and Basel (km 170). The finding at Strasbourg is represented by a total of seven specimens trapped in five out of seven bottles exposed over night (24/25 Oct. 2005) on the right river bank, in the Port de la Redonne and at the main harbour entrance (48.59372°N, 7.80210°E). The new southern limit of *H. anomala* in the Rhine system is now marked by the harbour of Kleinhüningen (km 170), where a total of five specimens were found in three out of six baited bottle traps exposed over night (47.58757°N, 7.59340°E; 25/26 Oct. 2005; first record for Switzerland). A single specimen of *H. anomala*, trapped at Danube-km 1865 at the entrance of the dock harbour of Bratislava, represents the first record of this species for Slovakia (48.12443°N, 17.15068°E; 16 Sept. 2005). A number of new records fill the large gap along the middle course of the Danube River: the first record for Hungary was taken at the right river bank at km 1578 in Dunaújváros, where 40 specimens were collected by drift net (46.95704°N, 18.95602°E; 28/29 July 2005). A single specimen of *H. anomala* collected by drift net at the right river bank at Danube-km 1333 in Vukovar represents the first record for Croatia (45.35380°N, 19.00383°E; 29/30 July 2005). The first record for Serbia was taken at the right river bank at km 1059 in the impoundment basin in Veliko Gradište, where 1349 specimens were collected by drift net (44.76710°N, 21.51488°E; 30/31 July 2005). This station lies 19 km above the entrance into the Carpathian breakthrough of the river.

Mass occurrences were found at certain stations in turbid waters with varying ionic content, i.e. in the impoundment basin (371 μS/cm) of the Danube River at km 1059 (14 days after the peak of a moderate flood event), in the Mittellandkanal (km 4) at 1600-1630 μS/cm and in the winter harbour of Linz (Danube-km 2132) at 296 μS/cm. Remarkably, the first two of these three stations simultaneously showed a mass occurrence of *Limnomysis benedeni* (see below). The *H. anomala* mass occurrences in the Mittellandkanal and at Linz were local. Inspections of the same Linz harbour site, this time operating the same hand net from a swimming platform in the same way, yielded no *Hemimysis* on 18 June 2004, 1167 specimens on 15 July 2005 and again zero on 14 Aug. 2005. The rich yield was made three days after the peak of a strong flood event, the zero yields during periods of normal water levels. *L. benedeni* collected together with *H. anomala* with the same nets showed a completely different phenology: 16, 294, and 652 specimens, respectively.

In 2004-2005 *H. anomala* was found only in strongly anthropogenic habitats. The measurements of abiotic factors are integrated in Table I. The 19 positive sampling stations showed massive structures for shore or river bank stabilization, such as large stones, boulders, concrete or steel. Additional structures included vegetation, such as algal cover on hard substrate or loose stands of submerged macrophytes. Hand net samples taken during the day contained *Hemimysis* at only six stations where the animals were found between large stones or boulders in ≤1.5 m depth (≤3.5 m examined). A slightly higher abundance in shallow water was revealed by 36 positive bottle traps exposed over night at ten stations in 0.6-3.5 m depth.

Limnomysis benedeni Czerniavsky, 1882 Figs 1D, 2

The records of this species yielded by the Cousteau-Expedition 1991 and own excursions in 1985-2005 in the Rhine and Danube systems, and in waters of western Turkey, are given in Fig. 2, together with available literature data. The Cousteau-Expedition captured this species on the banks of the Danube River at kms 2112, 1533, 1070, 954, 877, 851, 624, 506, 496 and 296. Own sampling in 2004-05 yielded this species at 92 stations. The following first records were taken in 2005: the species was found southwards of the already published range limit on the Rhine River and in its parallel, artificial side arm Grand Canal d'Alsace, at four stations between Breisach (km 225) and Basel (km 170). Hand net collecting in the harbour of Kleinhüningen in Basel (47.58740°N, 7.59142°E) yielded the first record of the order Mysidacea for Switzerland. Hundreds of *Limnomysis* specimens were found there during two inspections (10 July and 26 Oct. 2005), with maximum densities in 0.2-1.0 m depth among

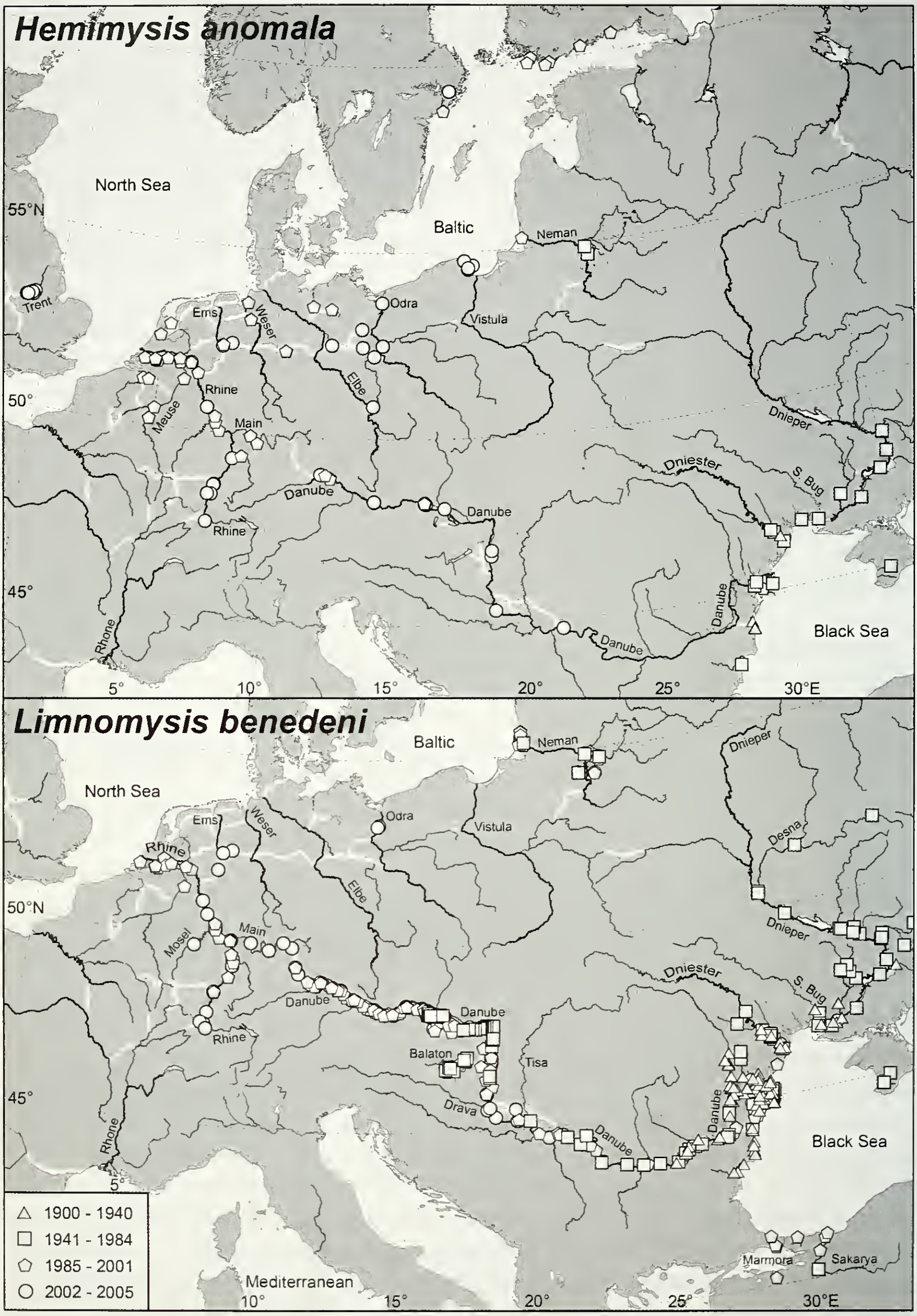

FIG. 2

Distribution of *Hemimysis anomala* and *Limnomysis benedeni* in the Rhine-Danube system and other waters. Overlapping symbols are arranged with the older records on top, so that the

the filiform, green algae covering vertical concrete and steel walls. Eight stations further upstream in the river and in Lake Constance (Bodensee) contained no mysids. Also, a westward range expansion in and from the Rhine system was noted by findings in the Mosel River at Riol (49.79697°N, 6.79727°E), Canal de la Marne au Rhin at Strasbourg (48.59133°N, 7.78302°E), Canal du Rhône au Rhin at Niffer (47.71270°N, 7.50190°E) and at Mulhouse (47.75442°N, 7.34880°E). *L. benedeni* was found for the first time in navigation channels of NW Germany: Mittellandkanal at km 4 and km 35, and Dortmund-Ems-Kanal at km 48. The only mysid species found in the Ems-Jade-Kanal was the marine euryhaline species *Praunus flexuosus* (O. F. Müller) in the brackish reach (S = 26-31) at km 70-71. Regarding the Danube system, first records of *L. benedeni* are here given for the Drava River at km 20 in Croatia, for the Tisa River 9 km above mouth into the Danube River (collection material from 1977) in Serbia, and for the DTD-Channel-System that connects (among others) the Tisa and Danube in Serbia (record in the Veliki Kanal at Srbobran, 45.54040°N, 19.78738°E).

Mass occurrences were found at certain stations in turbid waters with varying ionic content, i.e. in the Mittellandkanal (km 4) at 1600-1630 μS/cm, in the Neusiedler See at 3580 μS/cm, in Lake Balaton (811 μS/cm) and in the impoundment basin (351-371 μS/cm) of the Danube River at km 1059 (14 days after the peak of a moderate flood event). The first three of these mass occurrences were local, while the impoundment basin was not tested in this regard.

In 2004-2005 *L. benedeni* was found in a broad range of habitats from near-natural to strongly anthropogenic. The measurements of abiotic factors are integrated in Table I. Maximum densities of *Limnomysis* were observed among vegetation, with a preference for stands in only 0.3-1.0 m depth; nonetheless, *L. benedeni* was also present down to the greatest depth sampled (4 m). Very high densities were found among brush-like plant structures, such as cover of long, filiform algae on hard substrates or fine roots of *Salix* trees, or in dense stands of submerged macrophytes or in flooded terrestrial weeds. Densities were generally lower on and in the space between stones and over soft substrate. A few animals even lived on bare walls of wood, concrete or steel. As observed by snorkelling during the day, the animals swam a few cm from the substrate or were in direct contact with it. Hand net collecting and horizontal surface tows from boats showed that part of the population kept a greater distance from the substrate during the night, with a few specimens swimming up to the surface.

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expansion history can be traced from the symbols indicating different periods. White lines indicate man-made canals, black lines rivers. Original records (in part covered by superimposed symbols) are from waters of the Rhine-Danube system, channel systems in France and north-western Germany, and from waters of western Turkey. Literature records are from Salemaa and Hietalahti (1993), Eggers *et al.* (1999), Kelleher *et al.* (1999), Wittmann *et al.* (1999), Tittizer *et al.* (2000), Borcherding (2001), Haesloop (2001), Grigorovich *et al.* (2002), Rehage & Terlutter (2002), Wittmann (2002), Zettler (2002), Rudolph & Zettler (2003), Lundberg & Svensson (2004), Arbaciauskas (2005), Horecký *et al.* (2005), Janas & Wysocki (2005), Michels (2005), Müller *et al.* (2005), Dumont (2006), Holdich *et al.* (2006) and additional literature cited in these publications.

Katamysis warpachowskyi G. O. Sars, 1893 Figs 1C, 3

The sampling campaigns in 2004-2005 yielded this species at 21 stations. These are given in Fig. 3 together with published data from previous campaigns and literature data. This species was found only in the Danube system, where the following new records were noted: on 16 June 2004, one adult female was taken with hand net close to the fish-ladders, immediately below the impoundment weir of Greifenstein (48.3495°N, 16.2465°E) at river-km 1949 in Austria. This finding shifted the known distributional limit of *K. warpachowskyi* by only 13 km further upstream. This was within the same impoundment basin in which the species had already been detected three years earlier (Wittmann, 2002). A number of new records fill the large gap along most of the middle course of the Danube: the first record for Croatia was nine specimens of *K. warpachowskyi* sampled by hand net in the yachting harbour of Vukovar at river-km 1333 (45.35313°N, 19.00408°E; 29 July 2005). The first records for Serbia were one specimen taken with the hand net at the right river bank near Veliko Golubinje (44.46675°N, 22.17268°E) in the Carpathian breakthrough at km 986, followed by eight specimens taken with the drift net in the impoundment basin at Veliko Gradište at km 1059, and then 46 specimens with the hand net in the winter harbour of Kovin at km 1109 (all three samples on 30/31 July 2005).

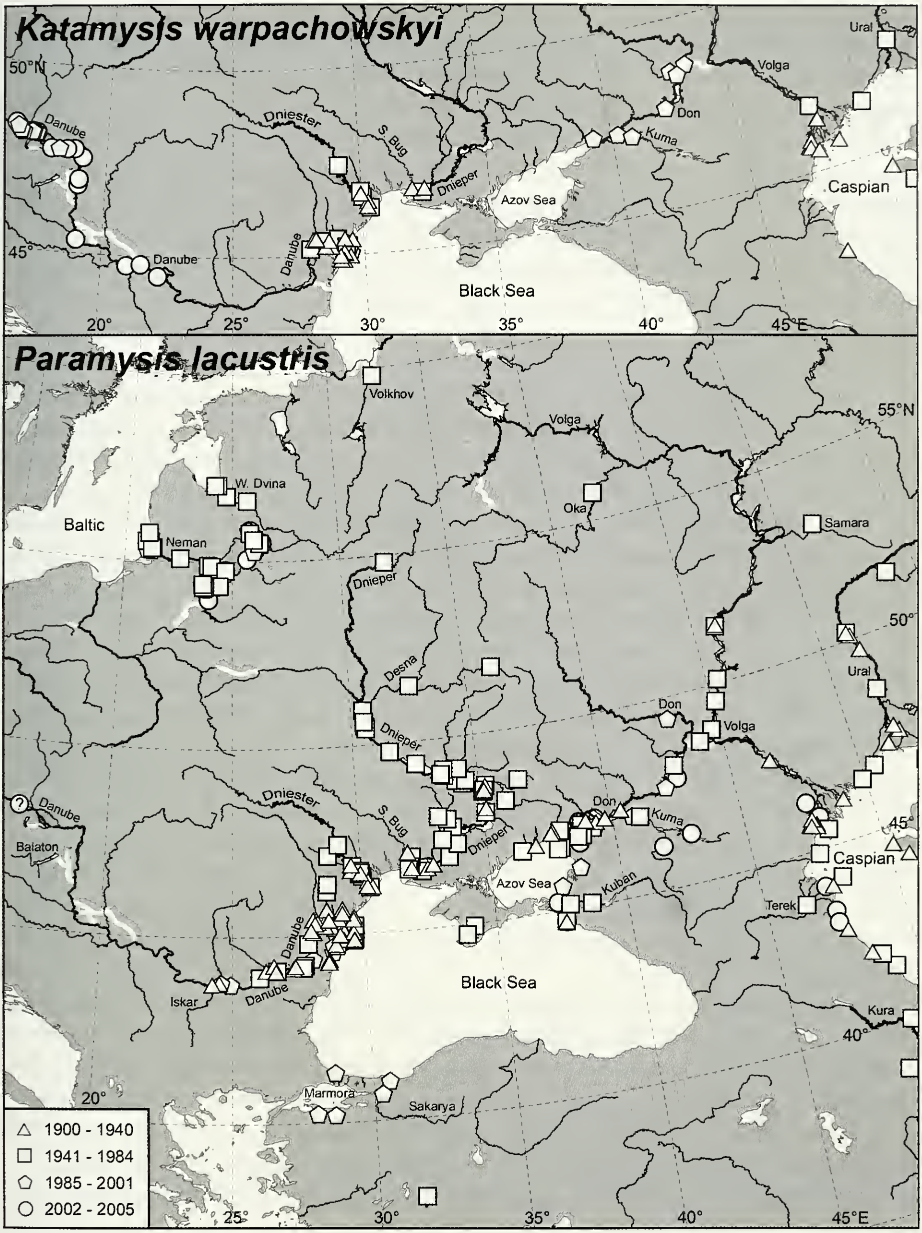
In 2004-2005 *K. warpachowskyi* was found in a broad range of habitats from near-natural to strongly anthropogenic. The measurements of abiotic factors are integrated in Table I. Maximum densities of *Katamysis* were observed on boulders, large stones and on coarse to soft substrates with plant debris, with a preference for stands in ≥1.5 m depth, but also present in 0.2-1.5 m. This species was also found between submerged macrophytes, between flooded terrestrial weeds and in accumulations of stones and shells. In most hand net samples, *K. warpachowskyi* occurred together with *Limnomysis benedeni* and the snail *Viviparus acerosus* (Bourguignat, 1862). Generally, the drift net and bottle traps yielded only small numbers of *Katamysis*. No mass occurrences were recorded for this species.

Paramysis spp. Figs 1B, 3

The records of *P. lacustris* (Czerniavsky, 1882) yielded by the Cousteau-Expedition 1991 and by own excursions in 1985-2005, in the Danube system, are given in Fig. 3, together with available literature data. The Cousteau-Expedition collected *Paramysis* species only in the lower reach of the Danube River. A total of 13 specimens of *P. lacustris* were taken at km 624, km 595, km 489 and km 296. Only fragments of two individuals of *P. intermedia* Czerniavsky, 1882 were sampled at km 624 and km 595. The sampling campaigns of 1985-1998 yielded *P. lacustris* in the Predelta (Lake Sinoe), in the main river branches of the Danube and in a great number of lakes, side arms and canals of the Danube Delta (325-3020 μS/cm). The excursion to western

FIG. 3

Distribution of *Katamysis warpachowskyi* and *Paramysis lacustris* in the tributary system of the Black Sea and other waters. Overlapping symbols are arranged with the older records on top, so that the expansion history can be traced from the symbols indicating different periods. White



lines indicate man-made canals, black lines rivers. Original records (in part covered by superimposed symbols) are from waters of the Danube system and of western Turkey. Literature records are from Băcescu (1940, 1954), Mordukhai-Boltovskoi (1964, 1979), Pligin and Yemel'yanova (1989), Komarova (1991), Tarasov (1996), Daneliya (2001, 2003), Arbaciauskas (2002), Grigorovich *et al.* (2002), Wittmann (2002), Gruszka *et al.* (2003), Audzijonyte (2006) and additional literature cited in these publications.

Turkey in July 1988 showed the presence of this species in a total of five lakes (Fig. 3) near the coasts of the Marmora Sea (Uluabat Gölü, Kus Gölü) and the Black Sea (Durusu Gölü, Sapanca Gölü, Akgöl). All these lakes contained clearly freshwater in the conductivity range of 270-500 μS/cm at surface temperatures of 27-30°C. One immature female of *P. lacustris* surprisingly appeared in a hand net sample taken by snorkelling in stands of *Myriophyllum* in 1.5 m depth in the almost isolated (see 'Discussion') backwater Alte Donau in Vienna (at height of Danube-km 1930; 48.24213°N, 16.42132°E; 10 June 2004). Despite great efforts, no further specimens belonging to this species could be found in waters along the upper and middle reaches of the Danube in 2004-2005.

DISCUSSION

Range expansion history of *Hemimysis anomala*: This species has populated vast areas of continental Europe, originating from an exclusively Ponto-Caspian range in the early 20th century. Indigenous populations were found in the salinity range of 0-18 (Table I), living over hard substrate or algal vegetation along the shores of the Caspian Lake, and the Black and Azov Seas. Before human interventions, the species was known as an essentially estuarine or 'marine' (in terms of NW Black Sea salinities) animal, penetrating not more than 40-60 km into the lower reaches of rivers. Băcescu *et al.* (1971) pointed it out as the only mysid species of Caspian origin occurring in the open Black Sea. Before 1998 the records of *H. anomala* in the Danubian range were restricted to the delta up to 34 km distance from the Black Sea (Băcescu, 1954; Popescu, 1963; most later records are merely citations of these two papers). This was essentially confirmed by own sampling in the delta, where *H. anomala* was rare and only taken in 1995 at mile 13.6 of the Sulina branch, and in 1998 at km 68 of the Sfintu Gheorghe branch (Wittmann *et al.*, 1999). Due to artificial deepening of the Sulina branch, a distinct influence of saline waters invading up to km 80 inland from the sea were reported during the drought season in August-September (Bondar, 1983). Thus the 'original' Danubian range of this species fitted well to the distribution of an essentially estuarine species (Băcescu, 1954) that only marginally penetrates into freshwater.

H. anomala started its range expansion in 1957 as an invader of European brackish and freshwaters by intentional introduction into an impoundment basin of the Dnieper River in the course of fisheries management (Pligin & Yemel'yanova, 1989). The main aim was that this photophobic species would enrich the spectrum of fish food in deep impoundment basins. This actually worked: *Hemimysis* established populations in up to 20-50 m depth (Zhuravel, 1960). This approach was pursued in other reservoirs and lakes of the former Soviet Union (Grigorovich *et al.*, 2002). From impoundment basins in tributaries of the Baltic Sea the species spread into brackish coastal waters of Lithuania, Finland, Sweden and Poland (Razinkovas, 1996; Arbaciauskas, 2002; Lundberg & Svensson, 2004; Janas & Wysocki, 2005). From there it invaded more western Baltic tributaries, together with the River Odra (Gruszka *et al.*, 2003), the system of navigation channels in northern Germany (Eggers *et al.*, 1999; Rehage & Terlutter, 2002; Zettler, 2002; Rudolph & Zettler, 2003; Müller *et al.*, 2005) and, again westwards, tributaries of the North Sea (Elbe and Weser systems; Haesloop, 2001; Horecký *et al.*, 2005). Additional, so far unpublished records from waters connected with the channel system in north-eastern Germany were kindly communicated by E. Rudolph (Havel): Spree River at the village of Radinkendorf, 52.21133°N, 14.27235°E, 24 Dec. 2004, leg. Wulf (Lamitsch), and Havel River at the village of Bahnitz, 52.49717°N, 12.40410°E, 2 Sept. and 1 Nov. 2005, leg. Rudolph.

In 1997-1998 *H. anomala* showed an explosive range expansion by appearing in vast areas of the Rhine-Main-Danube system, ranging from brackish and freshwaters in the Rhine Delta, to the middle Rhine, the rivers Main and Neckar, and the upper Danube. Already in 1999 this species was reported in the Westerschelde estuary in Belgium (Verslycke *et al.*, 2000). Shortly thereafter, in 2000, it appeared at two stations in the middle reach of the Meuse River (Usseglio-Polatera & Beisel, 2003). In June 2005 (four months before my findings reported above) it appeared for the first time in the north-east of France (Dumont, 2006). Due to an unknown introduction, the species surprisingly appeared in 2005 in waters of the Trent River in the English Midlands (Holdich *et al.*, 2006).

Even if certain populations may have been overlooked in earlier years, the speed of range expansion clearly points to anthropogenic dispersion by navigation, as also pointed out below for *Limnomysis benedeni*. The extent and speed of the invasions by both species were probably favoured by the opening of the Main-Danube-Channel in 1992. From the currently available data for *H. anomala* one cannot definitely conclude whether the invaders of 1997-1998 originated from Baltic populations and transgressed this channel from north to south, or if they came from the Black Sea (Danube Delta) and transgressed the channel from south to north (see discussions in Kelleher *et al.*, 1999; Wittmann *et al.*, 1999; Bij de Vaate *et al.*, 2002; Müller *et al.*, 2005). Multiple immigrations cannot be excluded (Müller *et al.*, 2005). Future genetic studies could be helpful to clarify such questions.

With the anthropogenic appearance in the upper Danube in 1998 (Wittmann *et al.*, 1999) a very large gap of records between km 1933 and km 68 became obvious, covering the entire middle and the lower reaches of the river, and part of the delta. A total of 37 hand net and drift net samples taken by me in 2001-2004 at 20 stations between km 1931 and km 1722 yielded *Hemimysis* only at km 1931. In accordance with this, Košel *et al.* (2003) reported only *L. benedeni* and *Katamysis warpachowskyi* but no *H. anomala* for the fauna of Slovakia. Possibly there was a disjunction in the Danubian distribution of *H. anomala* over a few years. A substantial part of the gap was closed in 2005 by the above-presented first records for Slovakia, Hungary, Croatia and Serbia. As in *L. benedeni*, a further upstream (southwards) expansion was noted in 2005 when *H. anomala* was recorded from the French (Dumont, 2006) and the Swiss reach of the Rhine for the first time. Most of these findings were made in harbours, pointing to a possible anthropogenic dispersion by navigation.

The present paper is the first to demonstrate the mass occurrence of *H. anomala* in rivers. The first hypothesis is that these mass occurrences were local and short-lived, possibly caused by flood events that had displaced the mysids by passive drift and/or by active avoidance of strong currents, so that the animals accumulated in more calm zones (harbour at Danube-km 2132, or deep and wide impoundment basin at km 1059). This will be the subject of future research.

RANGE EXPANSION HISTORY OF *LIMNOMYSIS BENEDENI*: As in the preceding species, *L. benedeni* also populated vast areas in continental Europe, starting from an essentially Ponto-Caspian distribution in the early 20th century. Indigenous populations were found in the salinity range of 0-14 (Ovčarenko *et al.*, 2006; Table I), with the greatest population densities in the oligohaline range (0.5-5), but the greatest number of populations in freshwater. Mass occurrences were only found at pH > 7.7. A favourable development in alkaline waters is also indicated by findings of Szalontai *et al.* (2003) that the oxygen consumption of juvenile *Limnomysis* is lower at pH 8.4 than at pH 5.4. The animals mainly dwelled among vegetation in stagnant and slow-flowing waters in the tributary systems of the Caspian Lake and the Black and Azov Seas. Own sampling in July 1988 revealed several populations in streams and lakes belonging to the drainage systems of the Marmora Sea and the Black Sea in western Turkey (Fig. 2). In most large Ponto-Caspian river systems this species penetrated several hundred kilometres beyond the oligohaline reach of the mouth area. The Danubian distribution once extended from the saline mixing zone in the Black Sea up to river-km 460. In any case, the primary distribution did not extend into the former cataract stretch between km 941 and km 1040 in the Carpathian breakthrough.

L. benedeni started its range expansion as an invader of European freshwaters in 1946, when it surprisingly appeared in the winter harbour of Budapest at Danube-km 1644 (the erroneous indication in Dudich, 1947: Tab. 1, was corrected by Woynárovich, 1955; now there is a bridge at this point, today's harbour entrance is at km 1642). During the following five decades *L. benedeni* expanded its distribution in the Danube upstream to the beginning of the Main-Danube-Channel at Kelheim in a series of small (1-173 km) steps. By incorporating additional literature and data from collections, the list given by Wittmann *et al.* (1999) is here updated. Fourteen stations are currently known: km 1683 (year 1949), km 1787 (<1953), km ≈1872 (<1954), km 1911 (1973), km 1919 (1982), km 1920 (1983), km 2093 (1986), km 2112 (1991), km 2132 (1992), km 2214 (1993), km 2228 (1994), km ≈2320 (1995), km 2376 (1997), km 2410 (1998). *Limnomysis* transgressed the Main-Danube-Channel probably shortly before 1997 and thereafter colonized vast areas of the Rhine system, probably in downstream direction, in about 1997-1998. Already in 1998 a further upstream (southwards) expansion was noted by the appearance of *Limnomysis* in the French reach of the Rhine (Wittmann & Ariani, 2000). Most of the observed upstream expansions probably reflect passive transport by ships. Specimens of this species were found on the outside hull of ships, and also inside, particularly in rest water (bilge water) and in cooling-water filters (Reinhold & Tittizer, 1998; Wittmann *et al.*, 1999; Bij de Vaate *et al.*, 2002). The new records, presented above for the Mosel River, the upper Rhine and the navigation channels in France, all came from navigable courses and therefore potentially reflect passive transport by navigation.

L. benedeni was intentionally introduced mainly in the 1950-1960s in eastern Europe, in order to enrich the supply of food for fish. These operations started in 1948 with the release of mysids into a hydropower reservoir of the Dnieper River, followed during the next decades by a great number of other waters in the former Soviet Union (Grigorovich *et al.*, 2002), particularly in Lithuania (Arbaciauskas, 2002), and in Hungary (Lake Balaton; Woynárovich, 1955). Introduction of *Limnomysis* into Lake

Aral (Kazakhstan and Uzbekistan; Mordukhai-Boltovskoi, 1979) was possibly due to inadvertent stocking (Aladin *et al.*, 2003). From introduction sites along tributaries of the Baltic Sea *L. benedeni* spread into coastal waters (Olenin & Leppäkoski, 1999; Arbaciauskas, 2002) and other tributaries, including the waters of the Odra system in Poland (Michels, 2005). The new records presented above for navigation channels in north-western Germany may originate from a (north-) eastwards expansion of populations from the Rhine system, although a westwards expansion from Baltic tributaries appears possible as well.

RANGE EXPANSION HISTORY OF *KATAMYSIS WARPACHOWSKYI*: In most large Ponto-Caspian river systems *Katamysis* originally penetrated up to 200 km into rivers of the Black Sea, or 120 km into those of the Caspian Lake. Black Sea populations were found in a salinity range of only 0-5, with the optimum in freshwater; Caspian populations showed a broader range (0-14; Table I). A similar difference was also observed in *Paramysis lacustris* (Table I). In 2000 *K. warpachowskyi* surprisingly appeared in waters of the Don system (Fig. 3), from where it had never been reported before. According to Daneliya (2001), this may indicate a recent immigration from the Volga River via the Volga-Don navigation channel, which was completed in 1951-1952. Deliberate introductions were of little importance for the distribution of this species. In 1956 it was released into the Dubossary reservoir (Dediu, 1966), upstream of its previously known distribution range in the Dniester River. For more details on the distribution, ecology, bionomics and possible modes of dispersion of *K. warpachowskyi*, see Wittmann (2002).

In 2001 this species was surprisingly detected at km 1936, more than 1700 km upstream of its previously known limit of distribution in the Danube (Wittmann, 2002). So far it has not transgressed the limits of the watersheds belonging to its exclusively Ponto-Caspian range. With the new record at km 1949 in 2004 the upper limit shifted by only 13 km and thus remained within the same impoundment basin. This was not surprising, because the comparatively rheophilic *K. warpachowskyi* is considered to be capable of swimming against the water currents observed along the banks of this impoundment basin under normal hydrological conditions.

Within the same month (Oct. 2001) an already differentiated distribution was found along the Austrian, Slovakian and Hungarian reach, down to km 1769 (Wittmann, 2002). This campaign was continued in 2004 with sampling down to Danube-km 1722, in the side arm Kis Duna (47.76335°N, 18.69988°E; 23 June 2004) near its flow back into the main river, and in 2005 down to km 986 in the Carpathian breakthrough, yielding the first records for Croatia and Serbia. In no case was a lower limit documented by negative downstream samples, because the species was always present at the lowest station examined. Extrapolating this, it seems likely that before 2005 a continuous population range already existed from kms 1936-1949 down to the delta. The absence of this species in samples taken at 26 stations in the Hungarian and Austrian reach in 1997-1998, as well as in samples of preceding campaigns (Nesemann *et al.* 1995; Wittmann, 1995), including the Cousteau-Expedition 1991, suggest that the middle and upper reaches of the Danube were colonized within a few years before 2001.

Table I. Hydrological and physicochemical parameters at sampling stations of four Ponto-Caspian mysid species[a].

Samples selected / parameter	*Hemimysis anomala*			*Limnomysis benedeni*		
	m ± S.D.[b]	range	n	m ± S.D.[b]	range	n
All samples:						
Depth (m)	4.037 ± 5.422	0-60	103	1.452 ± 1.166	0-10	479
Water current (m/s)	0.152 ± 0.222	0.0-0.81	98	0.106 ± 0.194	0.0-1.5	443
Temperature (°C)	17.21 ± 4.47	2-28	78	19.38 ± 4.79	0-31	353
Salinity	2.140 ± 4.209	0.1-18.0	87	0.594 ± 1.659	0.0-14.0	345
Conductivity (μS/cm)	3792 ± 6947	279-29200	87	1215 ± 2774	195-22300	345
pH	7.866 ± 0.503	6.35-8.65	63	7.970 ± 0.599	5.54-9.57	267
Carbonate hardness (°d)	8.642 ± 0.975	6-12	60	9.209 ± 3.455	3-30	191
Oxygen content (mg/l)	7.197 ± 1.422	3.99-10.80	63	7.922 ± 1.994	3.75-18.10	263
Turbidity (NTU)[c]	28.61 ± 26.29	5-137	63	34.17 ± 41.44	1-274	266
All regions, drift samples excluded:						
Water current (m/s)	0.031 ± 0.078	0.0-0.35	69	0.073 ± 0.148	0.0-1.0	406
All sample types, samples in the Caspian Lake excluded:						
Salinity	1.475 ± 3.317	0.1-18.0	82	0.480 ± 1.274	0.0-14.0	340
Conductivity (μS/cm)	2697 ± 5486	279-29200	82	1025 ± 2139	195-22300	340

Samples selected / parameter	*Katamysis warpachowskyi*			*Paramysis lacustris*		
	m ± S.D.[b]	range	n	m ± S.D.[b]	range	n
All samples:						
Depth (m)	2.011 ± 1.570	0-10	84	3.908 ± 4.896	0-48	122
Water current (m/s)	0.146 ± 0.283	0.0-1.5	74	0.061 ± 0.122	0.0-0.5	83
Temperature (°C)	17.72 ± 4.61	0-27	77	19.82 ± 5.54	0-30	70
Salinity	0.919 ± 2.915	0.1-13.8	74	1.909 ± 3.269	0.0-13.8	82
Conductivity (μS/cm)	1738 ± 4828	279-22873	74	3451 ± 5450	270-22873	82
pH	7.693 ± 0.729	6.13-9.35	54	8.344 ± 0.625	7.42-9.42	24
Carbonate hardness (°d)	9.294 ± 3.437	5-25	51	9.889 ± 2.374	8-16	18
Oxygen content (mg/l)	8.359 ± 1.972	3.99-16.99	54	7.401 ± 1.979	5.01-12.17	23
Turbidity (NTU)[c]	30.02 ± 42.81	1-272	54	43.30 ± 49.97	1-194	23
All regions, drift samples excluded:						
Water current (m/s)	0.122 ± 0.282	0.0-1.5	67	0.051 ± 0.109	0.0-0.5	80
All sample types, samples in the Caspian Lake excluded:						
Salinity	0.159 ± 0.413	0.1-5.0	68	1.179 ± 1.956	0.0-8.0	75
Conductivity (μS/cm)	475 ± 721	279-8800	68	2242 ± 3338	270-13800	75

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[a] data sources as in Figs 1, 2

[b] mean ± standard deviation

[c] nephelometric turbidity units

RANGE EXPANSION HISTORY OF *PARAMYSIS* SPP.: In the large Ponto-Caspian river systems *P. lacustris* originally penetrated about 200-600 km into the Danube, Dnieper, Don and Ural Rivers, and about 900 km into the Volga. Almost the same penetration distances were found for *P. intermedia*, with the remarkable difference that it reached as far as about 2000 km from the Caspian Lake into the Kama River, a northern tributary of the Volga. In the Caspian Lake *P. lacustris* showed a more continuous distribution in estuarine waters to freshwaters along the west coast (Fig. 3), while the distribution in the more saline Black Sea showed a distinct maximum at coastal stretches influenced by the freshwater input of large rivers. As shown in the 'Results', *P. lacustris* was found in freshwater lakes of western Turkey, where it locally occurs together with *Limnomysis benedeni* (Figs 2, 3). It is remarkable that *P. lacustris* was also found in Lake Beizehir (Băcescu 1948, 1966) in the Anatolian highland. The salinity range of *P. lacustris* was 0-14 (Table I); the range was 0-12 for *P. intermedia*.

In 1936 the upper limit of the known distribution of *P. lacustris* and *P. intermedia* in the Danube system was in the Orlea swamps (Lake Potelu) that drain into the river at km 644 (Băcescu, 1940). In 1991 this limit again coincided for both species and was still close to the previous position, downstream of the mouth of the Iskar River at km 624, as derived from the material of the Cousteau-Expedition.

In 2004 the single specimen of *P. lacustris* (see 'Results') surprisingly was recorded at the height of Danube-km 1930 in an almost isolated backwater. This backwater is connected with an artificial side arm of the river solely by an underground pipe and pumping station for stabilization of the water level. This was 1286 km upstream from the nearest documented population (Lake Potelu), or 620 km upstream from the nearest confluence with the drainage system of an introduction site (Lake Balaton). Due to its relatively isolated position, this single specimen does not provide definite evidence of a viable population of *P. lacustris* unless further material is found, and is therefore indicated with a question mark in Fig. 3. This species, along with *P. intermedia*, already had disappointed previous expectations of existing populations: according to Băcescu (1966 and pers. comm.) and Băcescu *et al.* (1971), *Paramysis* stocks were taken from Lake Olţina (drainage into Danube at km 338) and transplanted into Lake Balaton (drainage at km 1497) by Hungarian fishery biologists. A first attempt was made with *P. intermedia* in 1955 and a second one with both species in 1964 (*P. lacustris* indicated as *P. kowalewsky* in Băcescu, 1966). Despite long-term monitoring by the biological station at Tihany (e.g., Ponyi *et al.*, 1971) and the detailed study of Muskó & Leitold (2003) on the distribution of malacostracans in Lake Balaton, no *Paramysis* species were ever reported from this lake. Own sampling in 1983, 1997, 1998 and 2005 always yielded *Limnomysis benedeni*, but no *Paramysis* species. The same result was achieved by three hand net samples taken by L. Forró and H. Nesemann at different stations in Lake Balaton in 1990-1991 (Nesemann *et al.*, 1995).

Both species did not survive the first winter after introduction into the Rybinsk reservoir in the most northern reach of the Volga, 2900 km from the Caspian Lake (Slynko *et al.*, 2002). By contrast, introduction of *P. intermedia* into hydropower reservoirs in the middle reach of the Volga in 1957-1966 was successful (Borodich & Havlena, 1973). Extensive successful introductions of *P. lacustris* and *P. intermedia* were carried out in vast areas of the Ukraine, Crimea Peninsula, Uzbekistan, Kazakhstan and Kirgizstan, particularly to the lakes Aral, Balkhash and Issyk-Kul (Mordukhai-Boltovskoi, 1979; Komarova, 1991; Grigorovich *et al.*, 2002; Aladin *et al.*, 2003). Following release into water reservoirs and lakes draining into the Baltic Sea, *P. lacustris* established itself in a great number of waters of Lithuania (Arbaciauskas, 2002). It was also introduced in reservoirs of the Western Dvina (= Daugava), from where it subsequently spread into coastal lakes of Latvia (Gasiunas, 1972); additional introductions include the Volkhov reservoir that drains into Lake Lagoda (Zhuravel, 1969). A secondary spread, subsequent to introduction, was reported for *P. lacustris* populations in the Neman, Western Dvina, Dnieper and Volga Rivers. In the 1960s this species appeared in the Gulf of Finland (Jansson, 1994; not shown in Fig. 3 due to missing details on location).

MODES AND FACTORS OF DISPERSION: Van der Velde *et al.* (2000) listed the success factors for crustacean invaders, most of which were also relevant for mysids. Unintentional introductions of mysids were mainly referred to navigation, particularly transport in ballast water, in cooling-water filters and on the outside wall of ships; construction of waterways and inadvertent stocking were also reported to be of major importance.

Jazdzewski & Konopacka (2002) argued that the massive invasion of Ponto-Caspian species in central to western Europe may have been facilitated by the increasing ionic content in large rivers caused by industrial und agricultural pollution during recent decades. This may be relevant for the invasions by the more (*Hemimysis anomala*) or less (*Limnomysis benedeni*) halophilic mysids, but needs to be differentiated for the Rhine and Danube Rivers: after several decades of increase, the ionic content distinctly decreased in these river systems over the last 1-2 decades (Weilguni & Humpesch, 1999; Van der Velde *et al.*, 2000). According to Kelleher *et al.* (2000) and Van der Velde *et al.* (2000), the improved water quality of the Rhine may have facilitated the establishment of certain invaders. This is supported by own observations in the Danube, where the appearance of *H. anomala* in 1998 and *Katamysis warpachowskyi* in 2001 preceded the re-establishment of the stenoecious, indigenous snail *Theodoxus danubialis* (C. Pfeiffer, 1828) in 2004 (9 Sept., six snails sampled with drift net (!), together with *L. benedeni*; at river-km 1933 in Vienna), after four decades without positive records of the snail in the Austrian reach of the main river. In the 1930s this snail was common along river banks in Vienna, became rare in the 1950s, and was declared as already extinct for Austria by Reischütz (1981), but has persisted in a relict population in the Leitha River, a tributary of the Danube (Frank, 1982). When sampling for neozoans in 2005, hundreds of *Theodoxus* were seen on stones and concrete walls along the banks of the Danube in Vienna. The Austrian reach of the Danube has been subject to intensive faunistic studies since the 1930s (e.g., Vornatscher, 1938; Moog *et al.*, 1994), clearly confirming that all currently observed mysid species are neozoans rather than re-established indigenous faunal elements, such as the *Theodoxus* snails.

Simberloff & Von Holle (1999) and Ricciardi (2001) explained part of the success of Ponto-Caspian invaders by "invasional meltdown", i.e. that preceding invasions could facilitate subsequent invasions. Accordingly, the zebra mussel *Dreissena polymorpha* (Pallas, 1771) as a primary invader provided substrate, food and shelter for subsequent invaders. In the case of mysids, such interactions may be complex and require detailed future studies: *K. warpachowskyi* was repeatedly found in accumulations of stones and shells and thus may profit from empty *Dreissena* shells as shelter; adult *H. anomala* are strong predators of small crustaceans and may profit from the mass occurrence of the invasive amphipod *Chelicocorophium curvispinum* (G.O. Sars, 1895) as food in the Rhine and Danube systems. On the other hand, *L. benedeni*, *K. warpachowskyi* and the juveniles of *H. anomala* are mostly micro-herbivores: their food supply may be reduced by strongly enhanced plankton clearance rates (Ojaveer *et al.*, 2002) due to invasions by *D. polymorpha*.

The mysid invaders *H. anomala*, *L. benedeni* and *K. warpachowskyi* have in common that they are euryhaline and often found in great densities in harbours

(Wittmann, 2002). Ports are considered to be distribution hubs of invertebrates (Ricciardi & Rasmussen, 1998). The strong increase of traffic along European waterways during the last decades could partially explain the observed acceleration of mysid invasions.

EFFECTS AT THE ECOSYSTEM LEVEL: Detrimental effects from introductions or invasions of Mysidae species in continental waters have been reported for a number of species, particularly *Hemimysis anomala*, *Mysis diluviana* Audzijonyte & Väinölä, 2005, *M. relicta* Lovén, 1862, *Neomysis mercedis* Holmes, 1896 and *Paramysis lacustris*. Damage at the ecosystem level was mainly related to overgrazing of zooplankton and subsequent effects (Rieman & Falter, 1981; Fürst *et al*., 1984; Koksvik *et al*., 1991; Ketelaars *et al*., 1999; Haskell-Presenter, 2004) and to out-competing of native species by invaders (Arbaciauskas, 2002, 2005; San Francisco Bay Institute, 2004). In particular the top invader *H. anomala* is the focus of great concern due to its high expansion potential in combination with potential mass occurrences and due to its role as a predator of zooplankton. This species is essentially omnivorous with increasing percentage of zooplankton consumption with increasing body size (Borcherding *et al*., 2006). One important prerequisite for mass occurrences is deeper water, because the photophobic mysids are pelagic during the night and inhabit the dark zone or the bottom during the day, where they are more protected from predation by visually oriented fish.

Limnomysis benedeni and *Katamysis warpachowskyi* are essentially microherbivorous filter feeders with a small portion of their diet composed of invertebrates. This leaves them a more marginal role in the food web as compared to the two *Mysis* species and to *H. anomala*. *L. benedeni* and *K. warpachowskyi* are also more benthic than these species. Accordingly, Wittmann & Ariani (2000) and Wittmann (2002) did not expect strong detrimental effects by *L. benedeni* and *K. warpachowskyi*. No strong impact on the zooplankton community was observed after the invasion of *L. benedeni* in the backwater Alte Donau in Vienna (Wittmann & Ariani, 2000). After a first occurrence in 1993 the population densities of *Limnomysis* peaked in 1996-2000, as revealed by hand net collecting along the shore. This peak was followed by a marked reduction in 2002-05, concurrent with increased water transparency in the course of successful restoration measures.

The above-cited data suggest that mass occurrence is an important prerequisite for potential environmental damage by mysids. The mass occurrences here reported for *H. anomala* and *L. benedeni* were local and/or short-lived. This was not directly observed for the occurrence in drift samples, but mass occurrences would have been short-lived effects of flood events there as well (discussed above).

FUTURE PROSPECTS: Upon first detection of *Limnomysis benedeni* in the French reach of the River Rhine, Wittmann & Ariani (2000) speculated that the range expansion of this species could continue into the system of navigation channels in France, from where the mysid could spread along the Rhône River down to the Mediterranean coast. With the above-presented new records from several navigation channels, the first part of this prediction has become true earlier than expected. If its range expansion continues at the same speed, *Limnomysis* could reach the Mediterranean coast within a few years, with unknown consequences. The indigenous populations of the closely related genus *Diamysis* Czerniavsky, 1882, represented by a number of species in brackish to freshwater bodies all around the coasts of the Mediterranean, could be particularly affected.

If the diffusion of *Hemimysis anomala* along the Rhine system continues, it may enter Lake Constance (Bodensee) and, in the long term, also other deep lakes in Switzerland and neighbouring countries. This could represent a threat to the lake ecosystems in that it leads to overgrazing of zooplankton. Similarly, the Ponto-Caspian gammarid amphipod *Dikerogammarus villosus* (Sowinsky, 1894), a recent invader of Lake Geneva (Bollache, 2004), is expected to spread into other lakes and to seriously threaten the biodiversity in European freshwater ecosystems.

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Les *Phlyctimantis* et *Kassina* du Cameroun (Amphibia, Anura, Hyperoliidae)

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The *Phlyctimantis* and *Kassina* of Cameroon (Amphibia, Anura, Hyperoliidae). - The Cameroonian batrachofauna includes one species of *Phlyctimantis* and five species of *Kassina*, which are reviewed in this paper. *Phlyctimantis* have been found in only five 10 minutes side squares; the discussion of the status of the southernmost population shows that all known Cameroonian populations must be referred to *P. boulengeri*. In the genus *Kassina*, *K. maculosa* and *K. decorata* were tentatively synonymised by authors. Although they share a great number of morphological characters, they exhibit constant differences in cephalic and dorsal maculation and occupy different distribution areas. Thus, distinction at specific level appears to be the most appropriate status for these taxa. A new species, *Kassina wazae*, is described; it superficially resembles *K. senegalensis* but differs by several distinctive features, as vocal sac, lateral head maculation, presence of a small tarsal tubercle. For each species, many original data on distribution, ecology and phonocenosis are given. Finally, attention is drawn on the unexpected lack of a true forest-species of *Kassina* in the Cameroonian fauna.

Keywords: Africa - Cameroon - batrachology - systematics - ecology.

INTRODUCTION

Parmi les rainettes africaines (famille des Hyperoliidae) une vingtaine d'espèces se distinguent par les caractères de leur têtard et de l'appareil vocal des mâles, sans équivalents dans le reste de la famille. Cet ensemble est actuellement divisé en cinq genres très proches, dont le principal est *Kassina*. La plupart des espèces ne correspondent pas à la notion habituelle de « rainette » car elles ont la particularité de vivre sur le sol, ou en tout cas de peu s'élever sur la végétation, et cela même lorsqu'elles sont forestières. Toutefois, dans le genre *Phlyctimantis*, le comportement et l'habitus sont ceux des rainettes: on peut admettre que ce genre est resté proche de la souche d'où sont dérivés les autres Hypéroliens « kassinoïdes » (Laurent, 1976; Drewes, 1984).

Au Cameroun, les représentants des genres *Phlyctimantis* et *Kassina* sont peu nombreux, mais restent pourtant assez mal connus. Il a donc semblé utile de rassembler ici des données inédites concernant leur systématique, leur chorologie et leur étho-écologie.

MATÉRIEL ET MÉTHODES

Les spécimens sur lesquels est basé ce travail ont été récoltés la nuit, en général par repérage auditif des mâles en cours d'activité vocale. Dans un but pratique, toutes les données relatives à l'ensemble du matériel étudié ont été regroupées dans un même tableau synoptique (Tab. 1): – nombre de mâles (M) et de femelles (F), – numéro de

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TABLEAU 1. Principales données relatives au matériel étudié (juvéniles non compris). Précisions dans le texte sous « Matériel et méthodes ».

Espèce Populations	Nombre de spécimens	Numéro de collection	Localité	Coordonnées de la maille	Altitude	Date de capture
Ph. boulengeri						
Ouest						
	4 M	78.052-055	Fainschang	9°20’-30’ x 5°30’-40’	≈ 200	14.IV.78
Sud						
	4 M	87.001-004	Tom	10°30’-40’ x 2°20’-30’	≈ 450	02.1.87
K. maculosa						
Centre						
	4 M	70.739-742	Olembé	11°40’-50’ x 4°10’-20’	≈ 460	17.IX.70
	3 M	71.482-484	Foulasi (Obala)	11°30’-40’ x 4°00’-10’	≈ 540	19.IV.71
	3 M	71.1051-1053	Elomzok	11°30’-40’ x 4°10’-20’	≈ 500	13.IX.71
	6 M, 1 F	71.1073-1077; 71.1143-1144	Elomzok / Minkama	11°30’-40’ x 4°10’-20’	≈ 500	13.IX.71
	2 M	71.1068-1069	Binguela	10°20’-30’ x 3°40’-50’	≈ 700	14.IX.71
	4 M	72.655-658	Foulasi (Obala)	11°30’-40’ ≈ 4°00’-10’	≈ 540	12.IX.72
	2 M	75.303-304	Elomzok	11°30’-40’ x 4°10’-20’	≈ 500	15.X.75
	2 M	83.013-014	Yambassa / Bombato	11°10’-20’ x 4°20’-30’	≈ 400	29.IX.83
Ouest						
	2 F	70.432-433	Nsoung	9°40’-50’ x 4°50’-5°	≈ 1400	19.III.70
	4 M	71.737-738; 71.910-911	Dschang	10°00’-10’ x 5°20’-30’	≈ 1400	24.V.71
	1 M	79.048	Niamboya (Yimbéré)	11°30’-40’ x 6°10’-20’	760	24.VI.71
Mt Cameroun						
	2 M, 1 F	81.146-148	Bonianango	9°10’-20’ x 4°00’-10’	≈ 550	11.VII.81
Adamaoua						
	2 M	81.088-089	Hourso Manang	13°10’-20’ x 7°20’-30’	900	20.V.81
	1 M	81.109	Ndjaouro Ndekaou	13°00’-10’ x 7°20’-30’	900	20.V.81
	3 M	82.095-097	Mbella Assom	12°50’-13° x 6°30’-40’	≈ 900	20.V.82
K. decorata						
Ouest						
	10 M, 1 F	71.683-692; 71.801	Santchou	9°50’-10° x 5°10’-20’	≈ 700	24.V.71
	1 M	71.1120	Santchou	9°50’-10° x 5°10’-20’	≈ 700	22.IX.71
	2 M	72.301-302	Lac Manengouba	9°40’-50’ x 5°00’-10’	≈ 2000	29.III.72
Adamaoua						
	12 M	71.957-964; 71.1005-1008	Sadolkoulaye	13°50’-14° x 7°10’-20’	≈ 1200	29.VI.71
	1 M	71.1011	Ngaoundéré Vina	13°40’-50’ x 7°10’-20’	≈ 1100	02.VII.71
	6 M, 1 F	73.245-249; 73.306-307	Sadolkoulaye	13°50’-14° x 7°10’-20’	≈ 1200	28.IV.73
	1 M, 2 F	73.397-399	Wakwa	13°30’-40’ x 7°10’-20’	≈ 1200	23.VI.73
	16 M, 2 F	81.229-246	Sadolkoulaye	13°50’-14° x 7°10’-20’	≈ 1200	17.V.81

TABLEAU 1 (suite).

Espèce Populations	Nombre de spécimens	Numéro de collection	Localité	Coordonnées de la maille	Altitude	Date de capture
K. senegalensis						
Sud						
	1 M	70.132	Nanga Eboko	12°20'-30' x 4°40'-50'	≈ 600	VIII.70
	1 M	70.752	Elomzok / Minkama	11°30'-40' x 4°10'-20'	≈ 500	05.X.70
	1 M	71.1054	Elomzok	11°30'-40' x 4°10'-20'	≈ 500	13.IX.71
	1 M	71.1078	Elomzok / Minkama	11°30'-40 x 4°10'-20'	≈ 500	13.IX.71
	1 M	71.1134	Elomzok / Minkama	11°30'-40' x 4°10'-20'	≈ 500	04.X.71
	1 M, 1 F	73.244; 73.300	Sadolkoulaye	13°50'-14° x 7°10'-20'	≈ 1200	28.IV.73
	3 M	77.083-085	Elomzok	11°30'-40' x 4°10'-20'	≈ 500	07.X.77
	1 M	81.067	Bélel	14°20'-30' x 7°00'-10'	≈ 1540	16.V.81
	1 M	81.068	Sadolkoulaye	13°50'-14° x 7°10'-20'	≈ 1200	17.V.81
	3 M	81.110-112	Ndjaouro Ndekaou	13°00'-10' x 7°20'-30'	900	20.V.81
	1 F	82.198	Lipel	12°50'-13° x 6°30'-40'	≈ 900	20.V.82
	1 M	83.015	Yambassa / Bombato	11°10'-20' x 4°20'-30'	≈ 400	29.IX.83
	1 M	84.001	Ebebda	11°10'-20' x 4°20'-30'	380	21.III.84
	1 M	86.025	Makouopnsap	11°00'-10' x 5°10'-20'	≈ 650	18.III.86
Nord						
	2 M	71.940;71.1002	Réserve Bénoué	13°40'-50' x 8°00'-10'	≈ 400	28.VI.71
	9 M	72.532-540	Badjouma	13°30'-40' x 9°20'-30'	≈ 250	20.VII.72
	1 M	72.562	Dogba	14°10'-20' x 10°40'-50'	≈ 400	12.VII.72
	1 F	72.546	Koza (Jiller)	13°50'-14° x 10°50'-11°	≈ 450	15.VII.72
	1 M, 1 F	72.597-598	Mokolo	13°50'-14° x 10°50'-11°	≈ 700	15.VII.72
	1 M	73.326	Garoua / Pitoa	13°20'-30' x 9°20'-30'	≈ 180	01.VII.73
	3 M, 1 F	73.375-378	Salak	14°10'-20' x 10°20'-30'	≈ 420	03.VII.73
	5 M	75.364-368	Mora / Waza	14°20'-30' x 11°10'-20'	≈ 300	14.VII.75
	1 M	81.107	Karna	13°30'-40' x 7°40'-50'	500	21.V.81
K. wazae						
	6 M	75.358-363	Mora / Waza	14°20'-30' x 11°10'-20'	≈ 300	14.VII.75
K. cassinoides						
	3 M	71.941-942; 71.1003	Réserve Bénoué	13°40'-50' x 8°00'-10'	≈ 400	28.VI.71
	4 M	73.321-324	Garoua / Pitoa	13°20'-30' x 9°20'-30'	≈ 180	01.VII.73
	1 M, 1 F	73.451-452	Mbé	13°30'-40' x 7°50'-8°	580	13.VII.73
	2 M	75.176-377	Boki	13°30'40' x 8°40'-50'	320	17.VII.75

collection de l'auteur, – localité d'origine, telle qu'elle est reportée sur les étiquettes de collection (en général, village proche du point de capture), – coordonnées géographiques de la maille de dix minutes de côté où se situe le point de capture, – altitude, – date de capture.

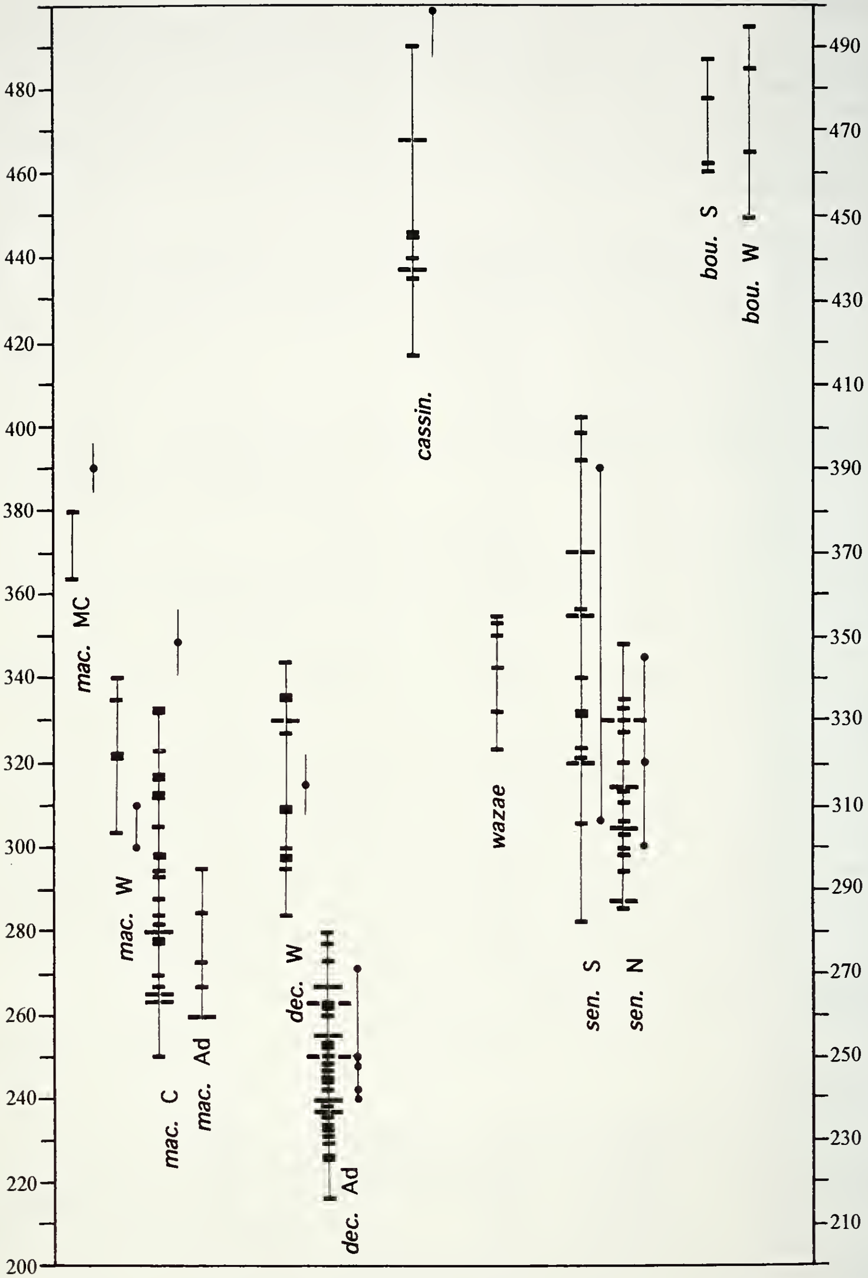


FIG. 1

Valeurs de L chez les *Phlyctimantis* et *Kassina* du Cameroun. Rectangles: mâles; cercles: femelles. Abréviations: mac: *K. maculosa*; dec: *K. decorata*; cassin: *K. cassinoides*; sen: *K. senegalensis*; bou: *P. boulengeri*; MC: Mont Cameroun; Ad: Adamaoua; C: centre; N: nord; S: sud; W: ouest.

Pour tenir compte de la variation géographique qui affecte la plupart des espèces traitées, les données des tableaux I et II et de la figure 1 sont réparties en grands ensembles de populations (par exemple, « *decorata* Adamaoua » ou « *senegalensis* Sud ») qui sont définis dans les parties relatives à chaque taxon.

Le matériel comprend 168 individus adultes. Ce chiffre est relativement faible car, pour diverses raisons, les régions de savanes ont été relativement peu prospectées, alors que les *Kassina* sont surtout savanicoles. Cet inconvénient devrait être compensé par le fait que tous les spécimens, sauf trois, proviennent de captures personnelles et que l'environnement dans lequel ils ont été trouvés est donc connu avec une précision satisfaisante.

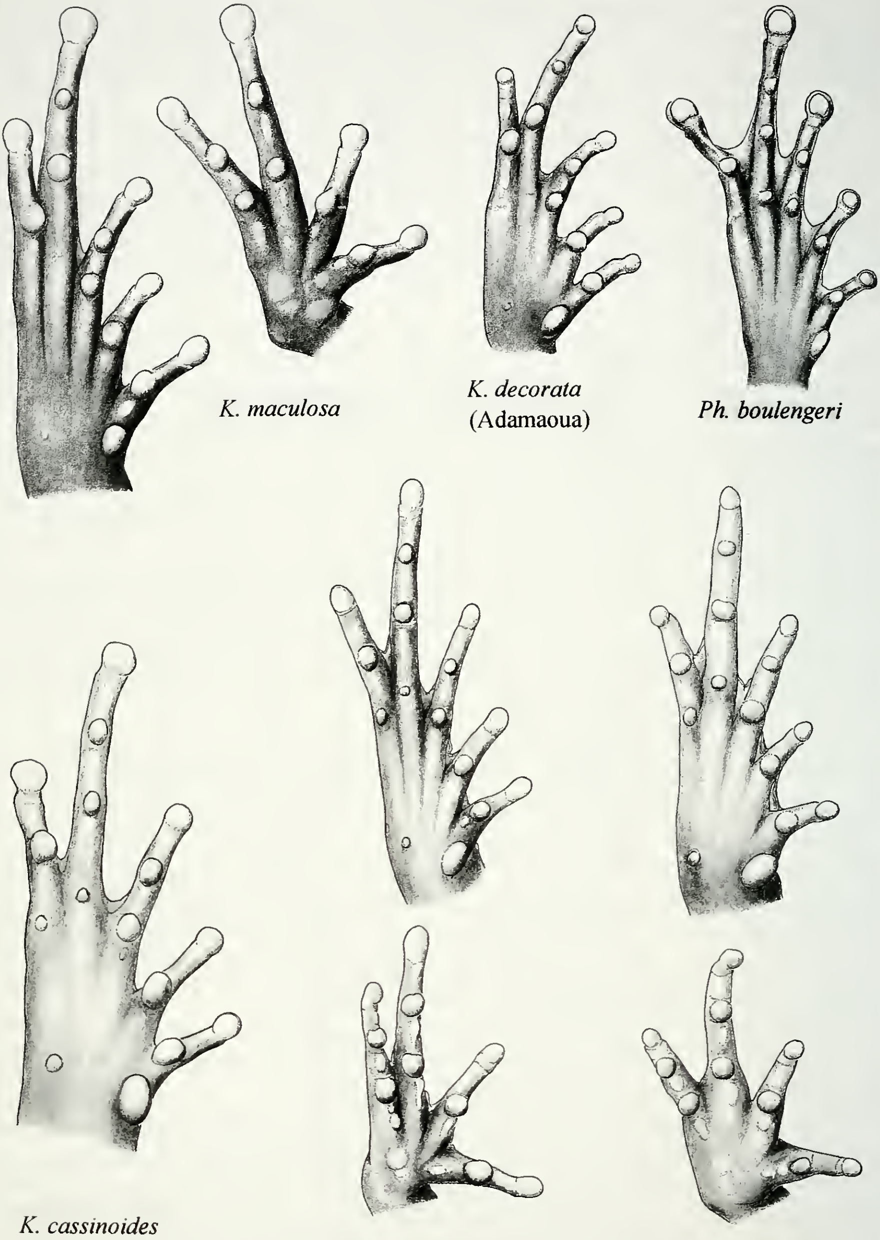
Les mensurations ont été faites au pied à coulisse, en dixièmes de mm. La longueur (L) a été mesurée du bout du museau à l'entrejambe (et non à l'anus), l'animal étant maintenu bien à plat (il est souvent incurvé vers le bas). Les autres données morphométriques ont été rapportées à L et exprimées en pourcentage: – largeur de la tête au niveau des tympans (T), – longueur de l'avant-bras, du coude à la base du pouce (AB), – longueur de la cuisse, de l'entrejambe au genou (C), – longueur de la jambe, du genou au talon (J), – longueur du pied, du talon à l'extrémité de l'orteil IV (P). Dans tous les cas où un matériel suffisant était disponible, les valeurs de C et J se sont révélées égales ou, en proportion semblable, légèrement supérieures l'une à l'autre. C'est donc le rapport C+J / L qui a été retenu. Il n'a pas été tenu compte des données morphométriques céphaliques, qui n'ont montré qu'un intérêt diagnostique limité chez les espèces étudiées. Le tableau II synthétise les principaux résultats des 947 mensurations effectuées et des 611 rapports calculés.

Dans le genre *Kassina*, certains éléments de la maculation – parfois restés méconnus –, sont très significatifs au plan taxonomique. Une place importante leur sera accordée, aussi bien dans le texte que dans les illustrations. Tous les dessins ont été faits à la chambre claire, les spécimens étant en milieu liquide. Ce dernier point est *très important* car, à sec, le contour des macules peut être difficile à percevoir; c'est la seule méthode qui permette le « décryptage » de la maculation chez certaines espèces si les spécimens ont été fixés en livrée nocturne, sombre et peu contrastée (voir plus loin). De nombreux dessins de maculation ont été donnés car c'est le meilleur moyen d'en montrer à la fois la variation et les traits fondamentaux.

Pour faciliter la comparaison entre les différentes espèces, la figure 1 synthétise toutes les données relatives à la taille (valeurs de L). Dans le même but, les dessins de pieds et de mains ont été regroupés dans la figure 2.

Les distributions sont représentées sur des cartes quadrillées à 10 minutes sexagésimales. On trouvera plus de précisions sur les méthodes de cartographie utilisées pour l'étude de la batrachofaune camerounaise dans un travail antérieur consacré à ce sujet (Amiet, 1983). L'orthographe des noms de lieux est celle figurant sur les feuilles au 1 / 200 000 de la couverture cartographique du Cameroun. Dans les parties relatives à la distribution et à l'écologie des espèces, les données phytogéographiques et climatiques sont empruntées aux travaux fondamentaux de Letouzey (1968, 1985) pour les premières, et de Suchel (1972, 1988) pour les secondes.

Les appels d'individus appartenant à tous les taxons ont été enregistrés mais, mon matériel bio-acoustique n'étant pas exploitable pour le moment, les vocalisations



K. maculosa

K. decorata
(Adamaoua)

Ph. boulengeri

K. cassinoides

K. senegalensis

K. wazae

FIG. 2

Face plantaire du pied (tarse non compris) et face palmaire de la main chez les *Phlyctimantis* et *Kassina* du Cameroun. Figures à la même échelle, sauf *P. boulengeri*, réduit de moitié. Remarquer la disposition des orteils V et IV, ainsi que l'absence de tubercules sous-articulaires proximaux sous les mêmes orteils, chez *K. maculosa* et *K. decorata*.

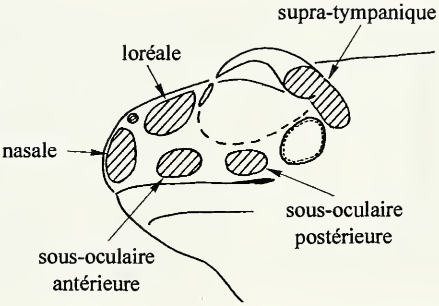


FIG. 3
Représentation schématique des macules céphaliques latérales dans le genre *Kassina*. Voir aussi les Figs. 9, 12 et 13.

ne seront pas utilisées dans un but taxonomique. Elles serviront néanmoins pour préciser les périodes d'activité vocale ainsi que les répartitions. Dans ce dernier cas, tous les enregistrements susceptibles de prêter à confusion ont été écartés.

Le présent travail n'a pas pour objectif de présenter des monographies des différentes espèces concernées. Pour les mieux connues, les descriptions se limiteront aux points les plus remarquables.

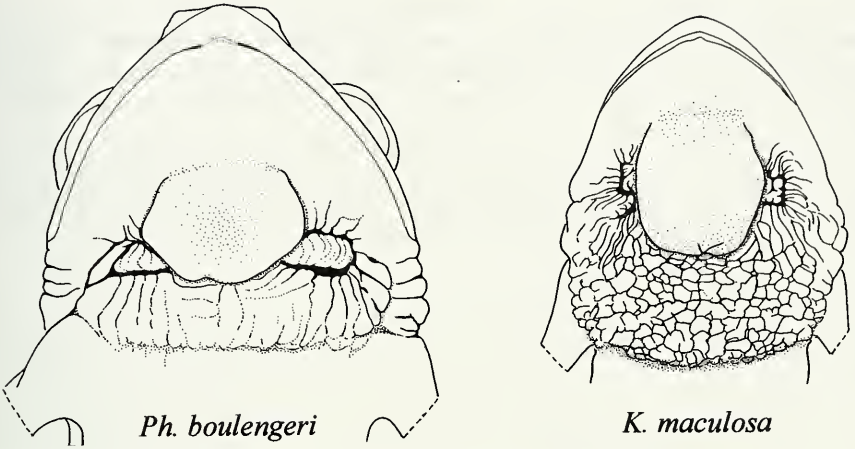
Pour alléger le texte et les tableaux, les noms des auteurs et les dates de description des espèces n'ont pas été mentionnés. On les trouvera ci-après, genres et espèces étant classés par ordre alphabétique: *Afrixalus fulvovittatus* (Cope, 1861 « 1860 »), *A. paradorsalis* Perret, 1960, *A. vittiger* (Peters, 1876), *A. weidholzi* (Mertens, 1938), *Amnirana albolabris* (Hallowell, 1856), *Astylosternus diadematus* Werner, 1898, *Bufo maculatus* Hallowell, 1855 « 1854 », *B. regularis* Reuss, 1834, *B. steindachneri* Pfeffer, 1893, *B. xeros* Tandy, Tandy, Keith & Duff Mac Key, 1976, *Chiromantis rufescens* (Günther, 1869 « 1868 »), *Hemisus guineensis* Cope, 1865, *Hildebrandtia ornata* (Peters, 1878), *Hoplobatrachus occipitalis* (Günther, 1859 « 1858 »), *Hydrophylax galamensis* (Duméril & Bibron, 1841), *Hyperolius adametzi* Ahl, 1931, *H. adspersus* Peters, 1877, *H. balfouri viridistriatus* Monard, 1951, *H. bolifambae* Mertens, 1938, *H. bopeleti* Amiet, 1979, *H. cinnamomeoventris* Bocage, 1866, *H. concolor* (Hallowell, 1844), *H. igbettensis* Schiøtz, 1863, *H. kuligae* Mertens, 1940, *H. pardalis* Laurent, 1947, *H. platyceps* (Boulenger, 1900), *H. sylvaticus nigeriensis* Schiøtz, 1967, *H. tuberculatus* (Mocquard, 1897), *H. viridiflavus aureus* Perret, 1966, *H. viridiflavus pallidus* Mertens, 1940, *Kassina arboricola* Perret, 1985, *K. cassinoides* (Boulenger, 1903), *K. cochranae* (Loveridge, 1941), *K. decorata* (Angel, 1940), *K. fusca* Schiøtz, 1967, *K. lamottei* Schiøtz, 1967, *K. maculosa* (Sternfeld, 1917), *K. schioetzi* Rödel *et al.*, 2002, *K. senegalensis* (Duméril & Bibron, 1841), *Leptopelis aubryi* (Duméril, 1856), *L. calcaratus* (Boulenger, 1906), *L. nordequatorialis* Perret, 1966, *L. viridis* (Günther, 1869 « 1868 »), *Phlyctimantis boulengeri* Perret, 1966, *P. leonardi* (Boulenger, 1906), *Phrynobatrachus auritus* Boulenger, 1900, *P. natalensis* (Smith, 1849), *P. cf. werneri* (Nieden, 1910), *Phrynomantis microps* Peters, 1875, *Ptychadena aequiplicata* (Werner, 1898), *P. bibroni* (Hallowell, 1845), *P. floweri* (Boulengeri, 1917), *P. oxyrhynchus* (Smith, 1849), *P. perreti* Guibé & Lamotte, 1958, *P. pumilio* (Boulenger, 1920), *P. schubotzi* (Sternfeld, 1917), *P. stenocephala* (Boulenger, 1901), *P. straeleni* (Inger, 1968), *P. trinodis* (Boettger, 1881). *P. trinodis* (Boettger, 1881).

REMARQUES SUR QUELQUES CARACTÈRES D'INTÉRÊT TAXONOMIQUE

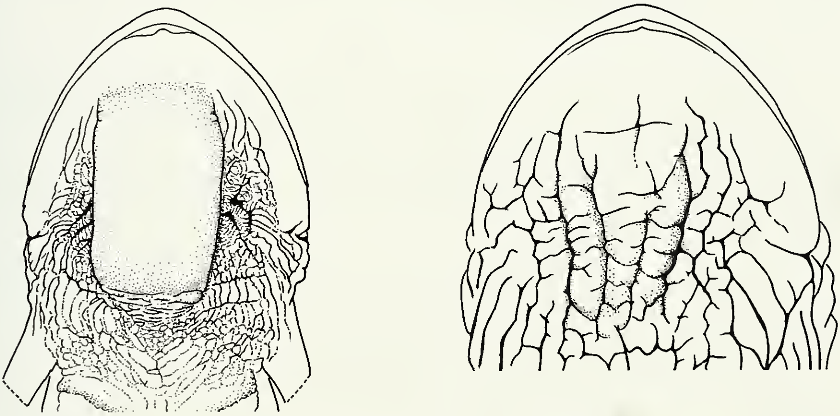
Il est d'abord nécessaire de s'arrêter sur certaines particularités plus ou moins négligées dans les descriptions antérieures, et dont il sera fait état à plusieurs reprises par la suite.

TABLEAU 2. Données morphométriques relatives au matériel étudié. Abréviations: voir « Matériel et méthodes ». Pour chaque série de valeurs, de haut en bas: nombre de spécimens mâles (M) et femelles (F) mesurés, valeur maximale, valeur minimale, **moyenne**, écart-type.

	K maculosa Mt Cameroun	*K. maculosa* Ouest	*K. maculosa* Adamaoua	*K. maculosa* Centre	*K. decorata* Ouest	*K. decorata* Adamaoua	*K. senegalensis* sud	*K. senegalensis* nord	*K. wazae*	*K. cassinoides*	*P. boulengeri* sud	*P. boulengeri* ouest
L	2 M, 1 F	5 M, 2 F	6 M	26 M, 1 F	13 M, 1 F	36 M, 5 F	17 M, 2 F	23 M, 3 F	6 M	10 M, 1 F	4 M	4 M
	390	340	295	333	344	280	403	348	355	500	487	495
	364	300	260	250	284	216	282	285	323	417	460	449
	378	**318,7**	**273,3**	**292,3**	**314,9**	**248**	**345,8**	**314**	**340,2**	**453**	**471,8**	**473,5**
	13,1	15,3	14,2	25,3	18,7	15,1	34,8	17,7	12,6	25,4	13	20,6
T / L	2 M, 1 F	5 M, 2 F	6 M	26 M, 1 F	13 M, 1 F	36 M, 5 F	17 M, 2 F	23 M, 3 F	6 M	10 M, 1 F	4 M	4 M
	37,3	38	37,3	39,3	38,3	43,3	36,5	36,9	34,2	39,8	36,5	34
	31,3	33,2	33,3	31,9	32,8	32,9	28,8	30	32,8	31,6	34,2	33
	33,9	**35,5**	**34,5**	**35,1**	**35,2**	**37,3**	**33,4**	**32,6**	**33,8**	**35,4**	**35**	**33,6**
	3,1	1,6	1,6	2	1,4	2,5	1,9	2	0,6	2,6	1	0,5
AB / L	2 M, 1 F	5 M, 2 F	6 M	13 M,	13 M, 1 F	12 M, 2 F	12 M	13 M	6 M	10 M, 1 F	4 M	4 M
	31,6	29,3	27,1	30,6	29,6	28,8	26,1	22,7	25,5	24,2	18,6	20,4
	28,9	25,4	24,2	25,5	25,6	23,2	20	19,1	18,9	20,4	22	22,6
	29,8	**27,3**	**26,1**	**28,1**	**27,5**	**25,8**	**23,5**	**21,2**	**21,1**	**22,7**	**20,8**	**21,7**
	1,6	1,2	1,1	1,6	1,3	2	1,7	1,5	2,7	1,3	1,5	1
C+J / L	2 M, 1 F	5 M, 2 F	6 M	26 M, 1 F	13 M, 1 F	36 M, 5 F	17 M, 2 F	23 M, 3 F	6 M	10 M, 1 F	4 M	4 M
	79,6	84,8	77,1	84,9	82,2	76,6	75,6	71	67,7	73,8	97	89,6
	73,6	71,1	65,3	72,2	68,7	64,8	62,8	55,5	60,6	56,5	86,6	80,1
	76	**77,1**	**72**	**78,6**	**77,4**	**70,3**	**70**	**64,9**	**64,5**	**69,2**	**89,6**	**86,8**
	3,2	5,6	4	3,8	4,2	3	4,5	3,8	3,2	5,2	5	4,5
P / L	2 M, 1 F	5 M, 2 F	6 M	26 M, 1 F	13 M, 1 F	36 M, 5 F	17 M, 2 F	23 M, 3 F	6 M	10 M, 1 F	4 M	4 M
	69,7	68,3	61,8	68,8	68,4	65	60,2	54,2	49,5	57	72	66,8
	68,7	58,2	54,9	58,9	59,9	49,4	50,1	34,9	47,9	45,9	62,6	63,3
	69,3	**62,8**	**58,8**	**64**	**63,4**	**56,4**	**55,3**	**49,4**	**49,1**	**52,8**	**67,2**	**65**
	0,5	4,2	2,5	2,9	2,8	3,6	3,3	3,9	0,6	3,6	4	1,6



Ph. boulengeri *K. maculosa*



K. senegalensis *K. cassinoides*

FIG. 4

Aspect de la région gulaire chez les mâles de *Phlyctimantis* et *Kassina*. Sac vocal de type 1: *P. boulengeri*, *K. maculosa* et *K. senegalensis*. Sac vocal de type 2: *K. cassinoides* (voir aussi, pour ce type, la Fig. 13).

LIVRÉES SOMBRES ET LIVRÉES CLAIRES

Chez les *Phlyctimantis* et *Kassina*, contrairement aux *Hyperolius*, il n'y a ni phases ni morphes mais, comme chez eux, il y a une forte variabilité de la livrée en fonction des conditions ambiantes. Bien que ces variations soient, globalement, nycthémérales, on peut de façon plus concrète parler de « livrée sombre » et de « livrée claire ». La première est marquée par un assombrissement général de la pigmentation, entraînant une forte atténuation des contrastes; elle se développe la nuit, mais aussi le jour chez des animaux maintenus à l'obscurité et dans une ambiance humide. La livrée claire s'accompagne d'un renforcement du contraste entre les macules et la coloration de fond; ce contraste atteint son maximum si l'animal est soumis à un fort éclairement, ce qui ne doit pas être souvent le cas dans les conditions naturelles, la phase de repos ne paraissant pas se dérouler à découvert. Heureusement, si l'observation des macules peut être difficile en livrée sombre (*cf.* ci-dessus: « Matériel et méthodes »), ni la forme ni la disposition de celles-ci ne sont affectées. Fait à première vue inattendu, chez les *Kassina* et les *Phlyctimantis* la *face ventrale*, y compris la région gulaire des mâles, s'éclaircit ou s'assombrit en même temps que la face dorsale.

Il résulte de ce qui précède que des spécimens de collection pourront donner une impression fort différente suivant qu'ils ont été sacrifiés en livrée diurne ou nocturne et que, en les comparant, il faut toujours avoir ce phénomène présent à l'esprit.

MACULATION CÉPHALIQUE LATÉRALE

Chez les *Kassina*, les côtés de la tête portent des macules de forme et de taille variables mais de *situation constante*: – macules supra-tympaniques, – macules sous-oculaires postérieures, – macules sous-oculaires antérieures, – macules loréales, – macules nasales (Fig. 3). La fusion, la disparition ou l'extension de certaines de ces macules conduisent à des « patterns » spécifiques, fait qui paraît avoir échappé jusqu'ici aux descripteurs (voir Figs. 9, 12 et 13).

APPAREIL VOCAL

Drewes (1984) a décrit en détail l'appareil vocal des *Kassina* et genres voisins, et en a montré la profonde originalité. Parmi les espèces représentées au Cameroun, il a étudié essentiellement *K. senegalensis*. Cette espèce offre en effet un « modèle » largement répandu. Il en existe un autre, un peu différent, propre à deux des espèces de la faune camerounaise. Les caractéristiques principales de ces deux types sont les suivantes (Fig. 4 et Pl. II, Fig. e).

– Type 1. La partie médiane épaissie du tégument gulaire, ou glande gulaire, est bien développée, non déprimée ni sollonnée à sa surface, et présente un contour rectangulaire, elliptique ou plus ou moins arrondi.

De chaque côté se trouvent des fossettes fortement pigmentées, au fond desquelles se distinguent des replis constitués par un tégument plus mince, non granuleux, de coloration noirâtre. Quand le sac vocal est gonflé, ce tégument se déplisse et dessine deux aires très foncées contrastant avec la couleur plus claire du reste du sac (Pl. II, Fig. d).

Chez les espèces camerounaises, ce type est représenté chez *Phlyctimantis boulengeri*, *Kassina maculosa*, *K. decorata* et *K. senegalensis*.

– Type 2. La glande gulaire est relativement petite, rétrécie vers l'arrière, plus ou moins concave et/ou sillonnée.

Il n'y a pas de dépressions de part et d'autre de la glande gulaire, mais le tégument, épais, forme des plis très contournés, séparés par de profonds sillons. Ce système complexe de plis permet un fort accroissement de la surface du tégument quand le sac vocal se gonfle.

Ce type est représenté chez une espèce nouvelle décrite plus loin ainsi que chez *K. cassinoides*, dont la glande gulaire est particulièrement réduite et mal différenciée. La disparition des aires noires du sac vocal chez ces espèces affaiblit les interprétations (très anthropocentriques) de la « fonction » de ces macules, évoquées par Drewes (1984).

Dans les deux cas précédents, comme l'a bien vu ce dernier (*op. cit.*), la partie du tégument affectée par le gonflement du sac vocal s'étend largement vers l'arrière. La limite postérieure de la partie gonflable apparaît sous la forme d'un pli ou d'un bourrelet pectoral, allant de la base d'un bras à l'autre.

AUTRES CARACTÈRES SEXUELS SECONDAIRES

Sur la face interne de l'avant-bras, les mâles de *Kassina* sont munis d'un empâtement glandulaire, parfois légèrement saillant, qui s'étend presque jusqu'au poignet. Chez les *Phlyctimantis* cette zone glandulaire est reportée sur les doigts I, II et III. Dans les deux cas, ces formations se reconnaissent par leur absence de pigmentation.

Un caractère propre aux femelles des *Kassina*, et généralement omis par les auteurs, réside dans l'aspect du tégument ventral. Chez toutes les espèces, il est lisse sous la gorge, mais cette texture peut s'étendre plus ou moins loin vers l'arrière: région pectorale chez *K. maculosa* et *K. decorata*, deux tiers antérieurs de la région abdominale chez *K. senegalensis*, et presque les trois quarts chez *K. cassinoides*. Il faut remarquer que ce caractère se retrouve chez les *mâles* de deux espèces d'Afrique de l'Ouest, *K. schioetzi* et *K. cochranae*, dont le centre de la région pectorale est lisse (Rödel *et al.*, 2002).

Phlyctimantis boulengeri Perret, 1986

HISTORIQUE

Contrairement à l'Afrique de l'Ouest et à l'est de la République démocratique du Congo, les localités camerounaises où des représentants du genre *Phlyctimantis* ont été trouvés sont peu nombreuses et dispersées. Cette constatation paraît pouvoir être étendue aux pays limitrophes.

Dans une publication de 1978, suite à la redécouverte de *P. leonardi* à Fainchang, dans la région de Mamfe, j'ai fait le point sur les localités signalées auparavant au Cameroun: plusieurs citations, entre 1911 et 1940, concernent un étroit secteur côtier à la base du versant sud du Mont Cameroun; une autre citation, la première pour le territoire camerounais (1908), concerne une localité proche de Kribi, Londji, elle aussi en situation littorale. A l'inverse des précédentes, la localité de Fainchang se situe largement à l'intérieur des terres (environ 180 km de la côte), mais à basse altitude, dans un secteur se rattachant, au point de vue climatique et phytogéographique, à la Plaine littorale.

Grâce au petit matériel frais (5 mâles) recueilli à Fainchang, un complément de description a pu être donné, avec en particulier une comparaison entre les caractères chromatiques des spécimens camerounais (en livrée diurne et en livrée nocturne) et ceux décrits par Schiøtz (1967) à partir de son matériel de Côte d'Ivoire (Amiet, 1978).

Quelques années plus tard, Perret (1986) a publié une mise au point sur le genre *Phlyctimantis* dans laquelle il établit que les syntypes ayant servi à la description originale de *P. leonardi* par Boulenger (1906) forment une série hétérogène. S'appuyant sur un matériel de provenances diverses (de la Côte d'Ivoire au Gabon), il scinde l'espèce de Boulenger en deux: – l'une, *P. leonardi*, définie d'après du matériel gabonais et supposée exister jusqu'en RDC, – l'autre, *P. boulengeri* n. sp., avec un des spécimens de Fainchang comme holotype et répandue depuis le Cameroun jusqu'à la Côte d'Ivoire. Les descriptions de Perret font ressortir deux caractères discriminants principaux: – la taille, de 1 cm en moyenne plus grande chez *leonardi* que chez *boulengeri*, – une « peau dorsale finement verruqueuse » chez *boulengeri*, alors que le tégument dorsal est « lisse ou très finement chagriné » chez *leonardi*; accessoirement, *P. boulengeri* est distingué aussi par sa maculation jaune plus apparente et son tympan mieux marqué.

En 1987, j'ai trouvé un site de reproduction de *Phlyctimantis* à Tom, village proche de la frontière équato-guinéenne. Cette localité a le grand intérêt d'être plus proche du Gabon que les localités connues jusqu'alors: la *terra typica* de *P. leonardi*, Ndjolé, est à environ 260 km à vol d'oiseau, soit une centaine de km de moins que Fainchang.

Une autre station de *Phlyctimantis* a été trouvée en 1991 par Ch. P. Blanc dans la Plaine littorale, au NE de Campo, à une cinquantaine de km au sud de l'ancienne localité de Londji.

La présence de *Phlyctimantis* près de la frontière sud du Cameroun pouvait laisser supposer que les deux espèces reconnues par Perret seraient présentes sur le territoire. Comme on va le voir, la comparaison des spécimens de Fainchang et de Tom ne confirme pas cette hypothèse.

COMPARAISON DES SPÉCIMENS DE FAINCHANG ET DE TOM

Le matériel utilisé est modeste, 4 mâles pour chacune des localités, mais 1°) ces individus ont été capturés en pleine activité vocale et ont donc des caractères sexuels secondaires pleinement développés, 2°) ils constituent des échantillons homogènes car, dans chaque localité, ils ont été pris au même endroit et la même nuit. Dans ce qui suit, l'accent sera mis sur les caractères qui, d'après Perret (*op. cit.*), permettent de séparer *boulengeri* de *leonardi*.

Taille, proportions, habitus: comme le montrent la figure 1 et le tableau II, il n'y a pas de différence de taille notable entre les individus des deux échantillons. Il en est de même pour les proportions des différents segments des membres. La morphologie céphalique, la palmure, les disques digitaux ne fournissent pas non plus de caractères distinctifs. Pourtant, les individus de Fainchang ont un aspect plus robuste, alors que ceux de Tom paraissent plus graciles, mais il est difficile d'accorder à cette différence d'apparence une valeur discriminante de niveau spécifique.

Tégument: dans ma description des spécimens de Fainchang j'ai, pour la première fois, signalé l'existence d'un relief tégumentaire: « Le tégument dorsal est apparemment lisse, garni en fait d'infimes verrucosités éparses ». Le terme « verrucosités » me paraît à présent imprécis. Le tégument dorsal forme de petites excroissances mousses, arrondies ou plus ou moins étirées, irrégulièrement dispersées et peu apparentes (elles ne se voient plus sur les spécimens fixés), qui peuvent effectivement être qualifiées de verrues. Mais, en plus de ces petites verrues, parfois sur elles mais aussi entre elles, il y a d'infimes spinules coniques, cornées, blanchâtres, telles qu'on peut en observer par exemple chez les *Hyperolius* du groupe d'*H. nasutus* (Amiet, 2005). Ces aspérités sont présentes sur toute la face supérieure du corps, de la tête et des membres, et même, encore plus petites, sur les reliefs du tégument gulaire.

Chez les spécimens de Tom, le tégument dorsal paraît plus lisse, les petites verrues se localisant sur le dessus des membres. Les aspérités cornées, en revanche, sont aussi nombreuses que chez les individus de Fainchang.

Dents vomériennes: elles sont bien développées (encore plus que chez *Kassina cassinoides*) chez les individus des deux localités.

Caractères sexuels secondaires: (1) La glande gulaire, assez petite (de l'ordre de 6 à 8 mm de large), a un contour pentagonal, hexagonal ou subcirculaire; postérieurement, elle forme un repli qui paraît libre mais est en fait relié par un raphé au reste du tégument gulaire. Le disque est flanqué de deux dépressions où apparaissent, sous forme de gros plis, les aires noires rétractées du sac vocal (et non « les sacs vocaux », comme je l'ai écrit par erreur dans mon article de 1978). Chez certains individus, il y a un pli pectoral assez peu marqué (Fig. 4). (2) Contrairement aux *Kassina*, les aires glandulaires des membres antérieurs ne sont pas situées sur les avant-bras mais sur le face supérieure des doigts I, II et, de façon plus limitée, III. (3) Faute de spécimens femelles, il n'est pas possible de dire si les petites aspérités cornées tégumentaires sont propres aux mâles, mais cela est probable. Cette hypothèse est confortée par le fait qu'elles manquent chez trois juvéniles de Tom, et qu'elles sont peu développées chez le plus petit des mâles adultes de la même localité.

Aucun des caractères précédents ne diffère de façon notable entre les individus des deux localités.

Pigmentation: à première vue, les spécimens de Fainchang s'opposent par leur teinte très foncée, sur les faces dorsale et ventrale, à ceux de Tom, beaucoup plus clairs. Quoique très apparente, cette différence n'a pas de valeur discriminante : elle est due seulement au fait que les premiers ont été fixés alors qu'ils étaient en livrée nocturne, alors que les seconds l'ont été en livrée diurne. En réalité, il n'y a pas de différence substantielle entre la coloration des individus de Fainchang et de Tom. Dans les deux cas, il n'y a plus aucune trace d'une maculation dorsale « structurée », mais simplement quelques petites taches foncées irrégulièrement dispersées et, chez certains individus, des « ombres » correspondant à des macules loréales et supra-tympaniques. Les bandes jaunes et noires alternées des membres postérieurs montrent, dans les deux échantillons, une variabilité individuelle qui empêche de les utiliser comme caractères distinctifs.

DISTRIBUTION, ÉCOLOGIE

Sur la carte Fig. 5 ont été reportées les localités camerounaises, anciennes et récentes, où des *Phlyctimantis* ont été signalés; de plus, toutes les mailles où j'ai relevé au moins cinq espèces d'Anoures (souvent beaucoup plus, jusqu'à la cinquantaine) ont été barrées d'une ligne diagonale, ce qui permet de mieux apprécier la distribution en fonction de la « pression d'investigation » sur les différentes régions du territoire. Deux faits en ressortent: – 1°) la grande dispersion des sites peuplés par des *Phlyctimantis*, qui ne paraît pas pouvoir être imputée seulement à une insuffisance des prospections; – 2°) leur localisation à basse altitude, dans la Plaine littorale ou à ses abords immédiats, contrastant avec leur absence sur le Plateau sud-camerounais (à peu près circonscrit par la courbe de niveau de 600 m).

Les localités où la présence de *Phlyctimantis* a été relevée ont en commun: – une température moyenne annuelle élevée, de l'ordre de 24° à 26°5 C, en relation avec leur faible altitude; – une importante quantité de précipitations, de 2 m par an à 9 m (au pied du Mt Cameroun); – une végétation climacique correspondant à la forêt ombrophile de type atlantique (ou biafréen). Ces facteurs peuvent conditionner l'aire d'ensemble sur le territoire, mais n'expliquent pas sa discontinuité.

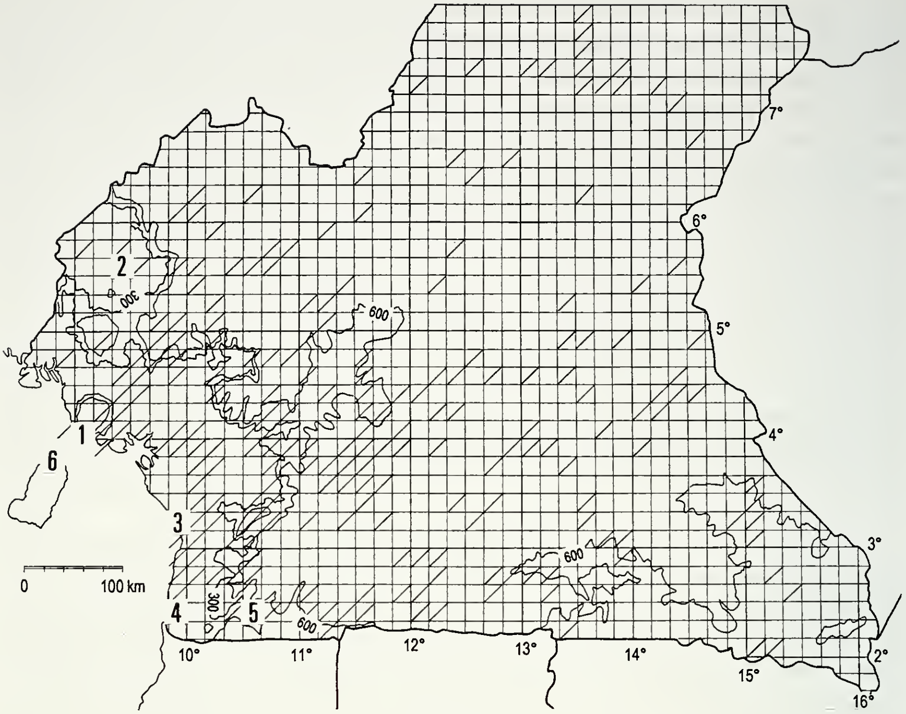


FIG. 5

Carte du Cameroun au sud du 8ème parallèle montrant les localités où *P. boulengeri* a été observé. 1: Isongo et Mubenge (= Mowange, = Mubange); 2: Fainchang (= Fineschang, = Fainschang); 3: Londji (= Longji); 4: Campo; 5: Tom. En 6 a été ajoutée la localité équato-guinéenne de Punta Frailes (= Punta Europa). Pour 1, 3 et 6, les récolteurs et auteurs sont mentionnés dans Amiet, 1978.

Dans la localité de Fainchang, le 14 avril 1978, une douzaine de mâles étaient actifs dans une raphiale inondée après de fortes pluies. Ils étaient accompagnés de centaines d'*H. bolifambae*, de nombreux *H. concolor* et *Afrixalus paradorsalis* et de quelques *Hyperolius sylvaticus nigeriensis*. Le site de reproduction de Tom était différent: un grand étang découvert, entouré de buissons sur lesquels étaient perchés les mâles, estimés à une cinquantaine. Bien que la station ait été visitée au tout début de janvier, donc en saison sèche, l'activité vocale était intense et il n'a pas été possible de faire un relevé des espèces compagnes, difficiles à repérer dans la « masse sonore » produite par les *Phlyctimantis*. Dans les environs proches pouvaient être entendus *Afrixalus fulvovittatus*, *Hyperolius platyceps*, *H. pardalis* et *H. tuberculatus*. Dans les deux stations, la nature des sites de reproduction et les espèces compagnes témoignent du caractère *parasylvicole* des *Phlyctimantis*, ce qui confirme les observations de Largen & Dowsett-Lemaire (1991) au Congo et de Rödel & Ernst (2001) en Côte d'Ivoire.

Il est cependant surprenant que, contrairement aux autres espèces parasylvicoles, très « expansionnistes », les populations de *Phlyctimantis* restent aussi localisées et disséminées[1]. Cette situation est d'autant plus paradoxale que – 1°) l'aire de répartition du couple *P. leonardi – P. boulengeri* est immense, allant du centre de la cuvette congolaise au Libéria; – 2°) dans leurs rares stations camerounaises, les populations paraissent florissantes à en juger par le nombre de mâles actifs. Pour parachever ce tableau, il faut souligner que les sites de reproduction ne montrent aucune particularité notable: dans la région de Fainchang, une dizaine de formations marécageuses partageant les mêmes caractéristiques et présentant des peuplements identiques ont été prospectées, mais une seule hébergeait des *Phlyctimantis*.

Discussion

La comparaison qui précède a montré qu'il n'y a pas de différence notable entre les mâles des populations de Fainchang et de Tom. Leur taille relativement faible et leurs aspérités tégumentaires conduisent, si l'on suit les critères distinctifs définis par Perret (1986), à les placer sous le nom de *P. boulengeri*.

Cependant, cette attribution n'est pas entièrement satisfaisante pour les raisons suivantes.

1°) A Tchissanga, dans le bassin du Kouilou (Congo), Largen et Dowsett-Lemaire ont trouvé une importante population d'un *Phlyctimantis* qu'ils ont rapporté à *P. leonardi*. Ils indiquent toutefois que « The relative small size of these males (snout-vent length 45-50 mm) does, however, cast some doubt on Perret's contention that *leonardi* is a significantly larger species than *boulengeri* » (Largen & Dowsett-Lemaire, 1991). De plus, comme me l'a indiqué M. Largen (comm. épist.), les 8 mâles de cette localité « have the dorsum densely beset with minute asperities... ».

2°) Cet autre critère distinctif que constituent les aspérités tégumentaires devrait de toute façon être précisé. Il faudrait en particulier savoir si elles existent chez les femelles de *P. boulengeri*, ce qui n'est pas explicitement indiqué dans la description. Au cas où il s'agirait d'un caractère propre aux mâles, ne disparaît-il pas en dehors des périodes de reproduction ? Sans réponse à ces questions, le critère tégumentaire n'apparaît pas totalement fiable.

3°) Entre les localités de Tom (*P. boulengeri*) et de Ndjolé (*terra typica* de *P. leonardi*), il n'y a pas d'obstacle géographique ou écologique majeur, ni de limite biogéographique reconnue, qui puissent expliquer le remplacement d'une espèce par une autre. Il est possible que des localités intermédiaires abritent des populations de *Phlyctimantis* et des recherches complémentaires seraient nécessaires pour comprendre les rapports spatiaux entre *P. leonardi* et *P. boulengeri* dans l'intervalle d'environ 260 km qui sépare Tom de Ndjolé.

4°) Les grands mâles de Bélinga (Gabon) sur lesquels Perret a fondé sa redescription de *P. leonardi* proviennent d'une localité plus « continentale » que celles de Tom, Ndjolé et Tchissanga. Au Congo, *P. leonardi* a été cité de la Sangha (Guibé, 1946, in Largen & Dowsett-Lemaire, 1991). En RDC, la même espèce, d'après Laurent (1976), s'avance jusqu'au cœur de la cuvette congolaise. On peut se demander si ces

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[1] Un cas un peu similaire est celui d'*Hyperolius bopeleti*, qui paraît propre aux formations forestières dégradées ou à couvert discontinu et ne peuple pourtant qu'une étroite bande côtière: *cf.* Amiet (1979).

populations sont bien conspécifiques des populations établies dans les régions plus littorales.

Il subsiste donc un certain nombre d'incertitudes et d'interrogations au sujet des *Phlyctimantis* d'Afrique centrale. Elles confèrent un caractère provisoire à l'attribution des populations camerounaises à *P. boulengeri*.

Le problème de *Kassina maculosa* (Sternfeld, 1917) et de *K. decorata* (Angel, 1940)

HISTORIQUE

K. maculosa a été décrite en 1917 par Sternfeld, sous le nom de *Megalixalus maculosus*, sur deux spécimens provenant de l'Ubangi, dans l'actuelle République démocratique du Congo.

En 1940, Angel a décrit, sur une unique femelle provenant du cratère du Mt Manengouba, au Cameroun, un *Megalixalus decoratus* dont Laurent & Combaz (1950), après examen du type, ont montré l'appartenance au genre *Kassina*.

Ni Angel ni Laurent et Combaz n'ont tenté un rapprochement entre les deux espèces[2]. Perret (1966) semble être le premier a l'avoir envisagé. Pour désigner ses spécimens du Cameroun, il utilise le nom « *decorata* » et écrit: « Ne pouvant apporter la preuve de la synonymie de *decorata* avec *maculosa* (Sternfeld) je conserve pour l'instant l'espèce d'ANGEL du Cameroun mais je soupçonne l'existence d'une seule espèce... ».

Peu après, Schiøtz (1967), évoquant *K. decorata* et *K. maculosa*, mentionne que « Perret (in litt.) has informed me that he regards the two last mentionned species as only subspecifically distinct from each other ». Dans son travail sur les rainettes d'Afrique (1999), il reprend cette opinion: « there do not seem to be any convincing arguments for separating *K. decorata* and *K. maculosa* at the specific level... ».

Dans leur révision très documentée des « spotted *Kassina* » d'Afrique de l'Ouest, Rödel, Grafe, Rudolf & Ernst (2002) ont été amenés à discuter le cas de ces espèces, apparentées aux trois espèces qu'ils reconnaissent dans leur territoire d'étude. Ils écrivent que « According to Perret (1966) and Schiøtz (1999) *K. decorata* (Angel, 1940) is a synonym of *K. maculosa* (Sternfeld, 1917) », substituant ainsi une forme affirmative à la tournure dubitative des auteurs cités. Néanmoins, ils indiquent ensuite qu'ils utilisent les deux noms « because they have been used in the literature, and because our acoustic analyses showed remarkable variation ». En fait, dans la suite du travail, il n'y a pas de comparaison entre les appels des deux espèces. Les auteurs donnent les résultats de l'analyse des appels de neuf *K. decorata* du Cameroun (enregistrés par Françoise Dowsett-Lemaire) et relèvent que, sur plusieurs points, ils diffèrent de ceux des trois espèces faisant l'objet de leur révision; en ce qui concerne *K. maculosa*, ils évoquent seulement le sonagramme d'un individu du Cameroun publié par Schiøtz (1999), en mentionnant qu'il ressemble à l'appel de *K. decorata* mais que, faute d'échelle sur l'axe y, une comparaison avec leurs analyses n'est pas possible.

En ce qui concerne l'origine des données bio-acoustiques relatives à *K. maculosa* et *K. decorata*, les précisions suivantes doivent être apportées. 1°) Le sonagramme

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[2] Laurent et Combaz citent « *M. maculatus* Sternfeld » pour préciser que cette espèce a été « reléguée dans la synonymie de *K. senegalensis* » par Mertens (1941). On peut supposer que « *maculatus* » correspond ici à un lapsus pour « *maculosus* ».

de *K. maculosa* publié par Schiøtz (1999) a été obtenu à partir d'un de mes enregistrements, réalisé à Obala, au nord de Yaoundé. 2°) Les enregistrements de *K. decorata* analysés par Rödel *et al.* (2002) ont été effectués par Françoise Dowsett-Lemaire près du Lac Edib, dans l'ouest du Cameroun, et attribués à *K. decorata* par C. Wilde (F. Dowsett-Lemaire, comm. pers.). Il faut relever que, à l'époque où ont été faites ces identifications, une forte incertitude régnait quant à la séparation des taxons et à leur dénomination.

Elles sont cependant probablement valables car, après avoir procédé à l'étude de mon matériel préservé, il m'apparaît qu'il y a au Cameroun deux entités distinctes, reconnaissables uniquement par leur maculation: chez l'une, celle-ci correspond à ce que Angel a décrit chez *K. decorata*, alors que chez l'autre elle correspond à la description de *K. maculosa*. Il a été impossible de trouver d'autres caractères morphologiques nets pour les séparer (les appels n'ont pas paru discriminants sur le terrain). Dans ce qui suit, avant d'en discuter le statut taxonomique, ces *Kassina* seront désignées comme « *Kassina* type *decorata* » et « *Kassina* type *maculosa* ».

DESCRIPTION

Caractères communs aux deux types: tégument dorsal lisse sur la tête et une partie de la région médio-dorsale, avec des granulations, souvent étirées longitudinalement, à l'arrière et sur les côtés du dos ; ces excroissances, peu denses et peu saillantes, sont plus ou moins marquées, peut-être en fonction des conditions ambiantes lors de la fixation (et peut-être aussi du mode de préservation). Tégument de la région loréale, des côtés de la tête et des flancs sub-lisse, passant par de fines granulations au tégument ventral. Celui-ci fortement réticulé-granuleux, les granulations de contour polygonal et en général plus longues que larges; pas de zone lisse médio-pectorale (différence avec *K. cochranae*). Chez les femelles, la gorge et la région pectorale sont lisses. Tégument des membres lisse, sauf sous les cuisses, où il est granuleux.

Membres antérieurs remarquablement grêles et longs (plus que chez les autres *Kassina* et, de façon générale, que chez les autres Hypéroliens); doigts minces et déliés, terminés par des pelotes non dilatées ou dilatées, mais en ce cas plus longues que larges et sans sillon périphérique; tubercules sous-articulaires très saillants; des excroissances surnuméraires sous les doigts; aucune palmure interdigitale (Fig. 2).

Pied (Fig. 2) long et étroit, avec l'orteil V *étroitement accolé* à l'orteil IV, jusqu'à hauteur du tubercule sous-articulaire distal; un rudiment de palmure entre les orteils III et IV[3]; pelotes adhésives non ou modérément dilatées aux orteils IV et V, sans sillon périphérique; tubercules sous-articulaires bien saillants mais, sauf exception, pas de tubercule proximal aux orteils V et IV, et donc un seul tubercule visible à l'orteil V et deux à l'orteil IV. La disparition des tubercules sous-articulaires basaux et la fusion partielle des deux orteils externes ne semblent pas avoir été signalés jusqu'ici chez ces *Kassina*. Entre les tubercules sous-articulaires, de longues excroissances d'aspect similaire.

Sac vocal des mâles de type 1: épaississement médian (glande gulaire) lisse, plus long que large, à bords rectilignes et parallèles; de part et d'autre, fossettes de rétraction du sac bien apparentes, pigmentées de noir; limite postérieure de la partie

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[3] C'est apparemment par erreur que Sternfeld (917) écrit « Zehen mit halber Schwimmhaut » (« orteils palmés jusqu'à mi-hauteur »), ce qui avait déjà intrigué Mertens (1940).

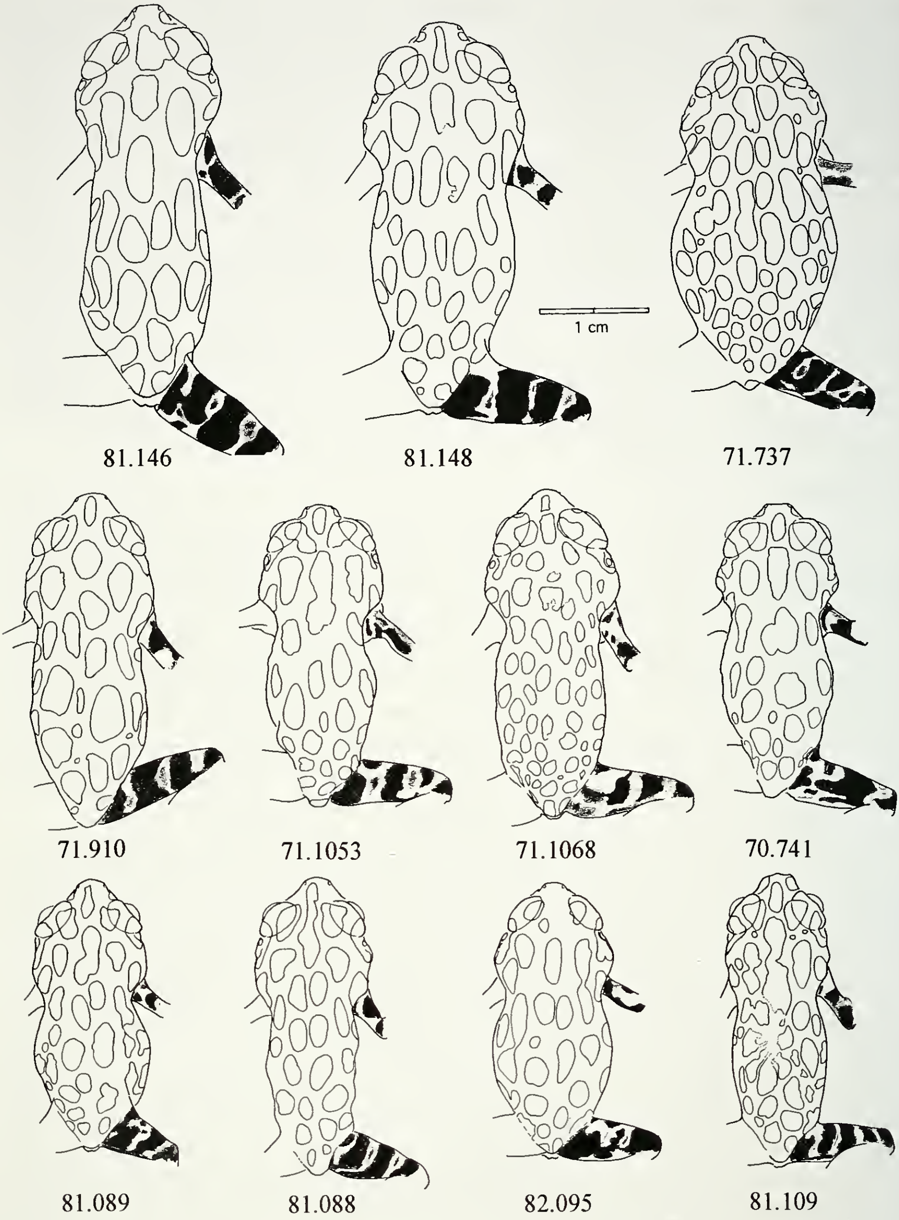


FIG. 6

Maculation du dos, du bras et de la cuisse chez *K. maculosa*. Dessins à la chambre clair limités au contour pour les macules dorsales. Les numéros de collection permettent de retrouver l'origine géographique des spécimens en se reportant au tableau 1.

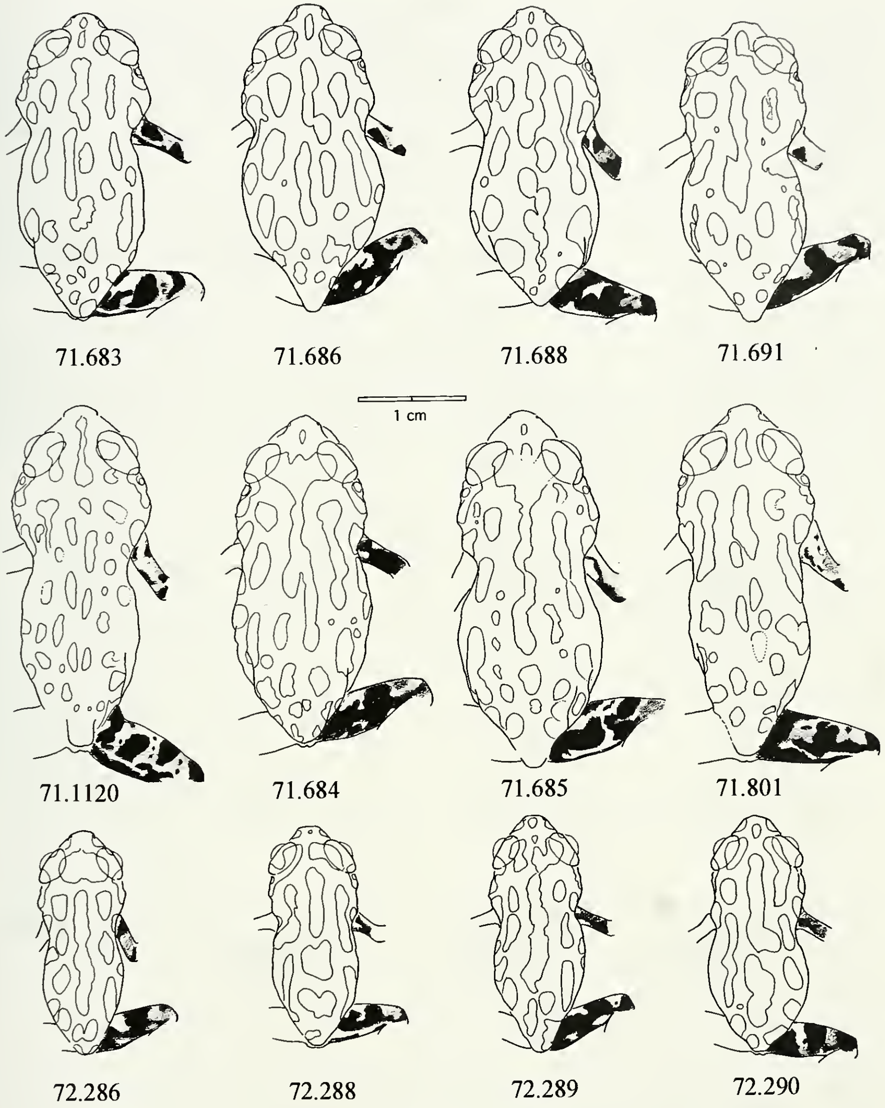


FIG. 7

Maculation du dos, du bras et de la cuisse chez *K. decorata*. Dessins à la chambre claire limités au contour pour les macules dorsales. Les spécimens des rangées supérieure et moyenne proviennent de la Plaine des Mbos (Santchou, *cf.* Tab. 1), ceux de la rangée inférieure sont des juvéniles du cratère du Manengouba (non référencés dans le Tab. 1).

gonflable généralement marquée par un pli interbrachial. Face interne des avant-bras des mâles avec une zone glandulaire étirée, légèrement saillante.

Livrée dorsale constituée de macules foncées sur un fond plus clair, les macules étant *toujours* entourées d'un *fin liséré* jaunâtre ou blanchâtre. Il y a une forte différence entre la livrée sombre, de tonalité générale brun-noirâtre, où les macules et

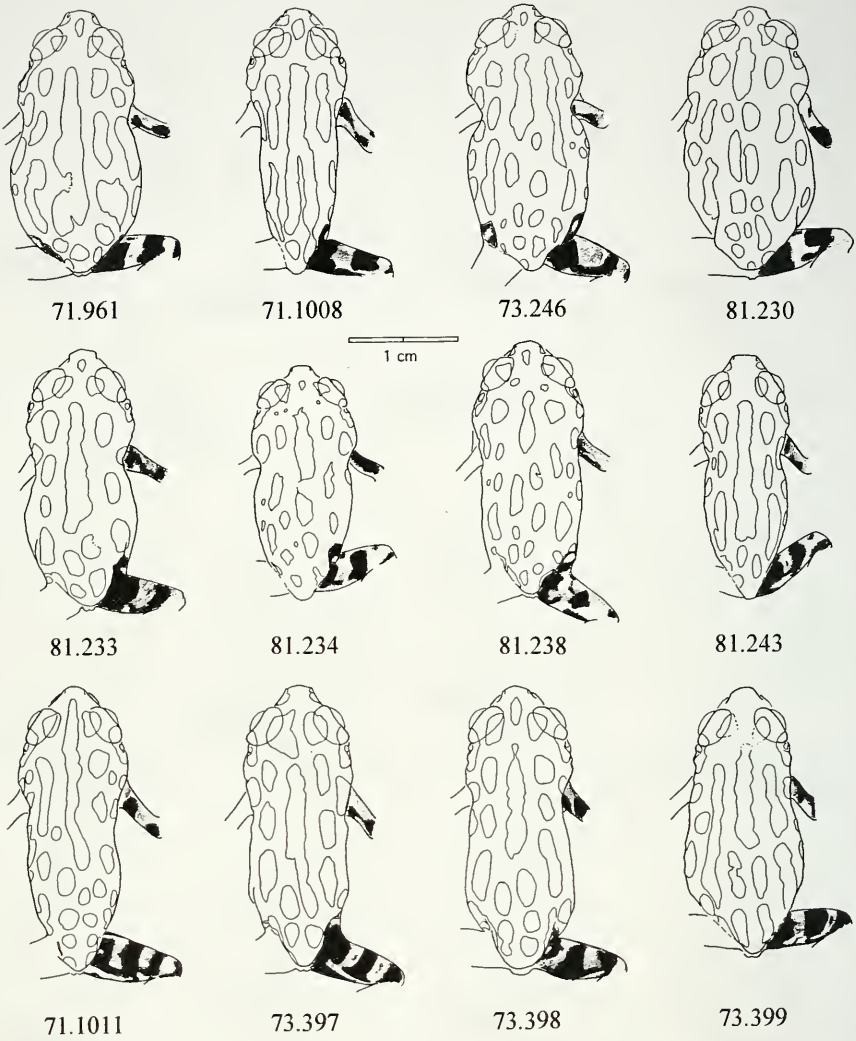


FIG. 8

Maculation du dos, du bras et de la cuisse chez *K. decorata*, populations de l'Adamaoua (voir Tab. 1 pour les localités et dates de capture des spécimens). Dessins à la chambre claire limités au contour pour les macules dorsales.

leur liséré sont à peine discernables, et la livrée claire, montrant un fort contraste entre les macules et le fond, le liséré très apparent donnant alors une impression de taches ocellées. Cette différence entre les deux livrées est beaucoup plus marquée que chez les autres *Kassina* locales (voir plus haut pour les conditions d'observation de la maculation sur des spécimens à livrée sombre).

Chez les deux types, toutes les macules céphaliques latérales sont présentes, les sous-oculaires non fusionnées, la nasale et la loréale fusionnées ou non (Fig. 9). Pas de taches paires occipitales (différence avec *K. arboricola*).

Face ventrale en général pigmentée seulement sous la gorge des mâles, sous la forme d'un assombrissement presque uniforme ou de mouchetures plus ou moins concentrées en macules diffuses. Le reste de la face ventrale, clair (blanchâtre en alcool), peut être voilé, en livrée sombre, par un fin réseau de chromatophores enserrant les granulations tégumentaires.

Membres plus ou moins régulièrement barrés de sombre sur fond clair. Les régions inguinales et axillaires et les parties des membres postérieurs non visibles lorsque ceux-ci sont repliés sont marbrées de jaune vif et de noir sur le vivant, de blanc et de noir sur les spécimens préservés en alcool.

Livrée de type maculosa: il peut y avoir, dans la région occipitale, une macule étirée longitudinalement, mais la majorité des macules ont un contour plutôt elliptique et sont moins de deux fois plus longues que larges. Leur nombre et leur taille varient beaucoup, y compris à l'intérieur d'une même population et il est difficile d'y déceler une répartition en rangées longitudinales (Fig. 6 et Pl. I, Fig. b). La macule supra-tympanique ne se prolonge pas en arrière du tympan (Fig. 9).

Sauf quelques exceptions, la maculation des cuisses est constituée de bandes *transverses* foncées alternant avec des bandes claires.

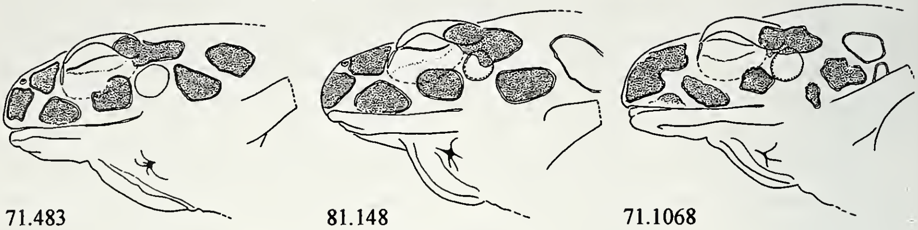
Livrée de type decorata: plusieurs macules dorsales sont très étirées longitudinalement. Elles ont tendance à former des alignements: deux latéro-dorsaux et une bande médio-dorsale qui, assez souvent, se dédouble dans sa moitié postérieure (Fig. 7 et 8 et Pl. I, Figs. a, c et d). Dans les cas extrêmes, la livrée peut évoquer celle de *Kassina* « à bandes » comme *K. senegalensis*. La maculation céphalique offre un bon caractère distinctif: en général, la macule supra-tympanique se poursuit vers le bas *en contournant le tympan* (Fig. 9).

La maculation des cuisses est souvent irrégulière et tend à se disposer en marbrures étirées *longitudinalement*.

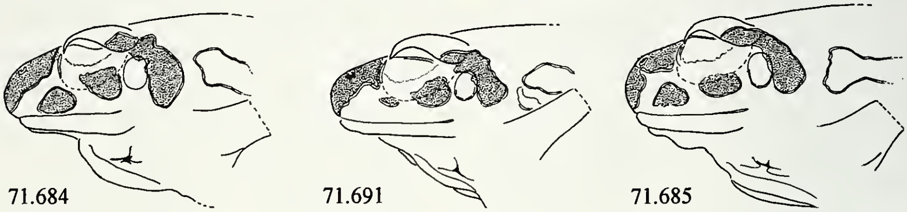
DISTRIBUTION, VARIABILITÉ

Kassina *type* maculosa: son aire camerounaise prolonge vers l'ouest celle qu'elle occupe dans le nord de la RDC, d'où proviennent les types de *K. maculosa* (*cf.* carte *in* Schiøtz, 1999). Dans l'état actuel des connaissances, elle atteint à l'ouest du Cameroun les régions de Dschang et de Kumbo (si, comme il est probable, les trois mâles de Kakar signalés par Mertens, 1940, se rapportent à la même forme) mais ne pénètre pas au Nigeria. Comme, sur ce territoire, aucune *Kassina* similaire n'est connue, il y a entre les populations camerounaises les plus occidentales et les espèces apparentées d'Afrique de l'Ouest, une énorme lacune de distribution, de l'ordre de 1200 km, difficilement explicable. La limite nord de répartition au Cameroun coïncide probablement avec la retombée septentrionale du Plateau de l'Adamaoua, tandis que vers le sud elle colonise les régions les plus « secondarisées » de la zone forestière (voir ci-après). L'absence de pointages dans un vaste secteur du Cameroun, en gros la moitié est du Plateau sud-camerounais, est sûrement imputable à une insuffisance des prospections.

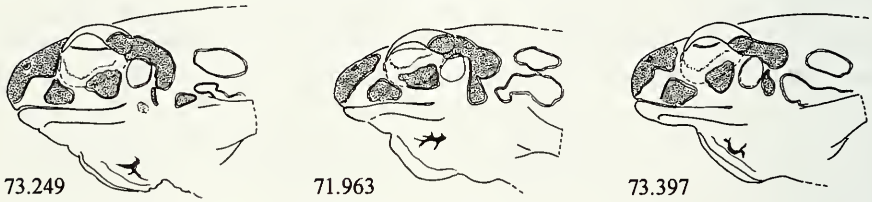
Dans son aire camerounaise, l'espèce varie peu, sauf en ce qui concerne la taille, apparemment plus faible dans les populations de l'Adamaoua. Une exception doit être faite pour les populations du Mont Cameroun. L'existence d'une *Kassina* y est



K. maculosa



K. decorata Ouest



K. decorata Adamaoua

Fig. 9

Exemples de maculation céphalique latérale chez *K. maculosa* et *K. decorata*. Remarquer, chez cette dernière, la forme caractéristique de la macule supra-tympanique.

connue depuis longtemps car Köhler en avait obtenu une femelle et un juvénile au-dessus de Mubenge, versant sud, vers 920 m (spécimens d'abord identifiés comme *K. senegalensis* par Mertens, 1940). La femelle et les deux mâles que j'ai trouvés à Bonianango, versant est, vers 620 m, proviennent de la seule petite population repérée, malgré plus d'une vingtaine de sorties de nuit, sur le pourtour du Mont Cameroun.

Ces spécimens se distinguent nettement par: – leur grande taille (Tab. 2 et Fig. 1), – leur habitus élancé (mais les dessins de la Fig. 6 représentent des individus peut-être émaciés après une période de captivité), – l'élongation des pieds (valeurs de P/L supérieures à celles de toutes les autres *Kassina* mesurées, et dépassées seulement par un spécimen de *Phlyctimantis*!), – la pigmentation plus dense de la gorge (grosses taches ocellées chez les mâles, quelques macules arrondies chez la femelle), – la coloration plus vive du pied (Pl. I, Fig. b). Ces individus font penser à *K. arboricola* (*cf.* photos *in* Perret, 1985, et Rödel *et al.*, 2002) mais s'en distinguent par la pigmentation foncée moins étendue sur la face ventrale des mâles et, surtout, par l'absence de la double tache occipitale caractéristique de cette espèce.

Kassina *type* decorata: elle n'est connue que de deux secteurs distants d'environ 360 km (Fig. 10): – Mont Manengouba et Plaine des Mbos, à l'ouest du Cameroun, – région de Ngaoundéré, sur le Plateau de l'Adamaoua. Il est possible que son aire de répartition soit à la fois plus étendue et moins largement bipolaire, mais on peut d'ores et déjà admettre qu'elle est beaucoup plus restreinte que celle de *Kassina* type *maculosa*.

Les caractéristiques morphologiques des populations du Mont Manengouba et de la Plaine des Mbos, spatialement très proches et même peut-être en continuité, sont semblables. En revanche, les populations de l'Adamaoua sont nettement différentes par : – leur nanisme (chez le plus grand individu de l'Adamaoua, la taille est inférieure à celle du plus petit individu de l'Ouest: Fig. 1 et Tab. 2), – leurs membres postérieurs proportionnellement plus courts (Tab. 2), – les pelotes des doigts et des orteils non dilatées. Les deux premiers caractères se retrouvent, mais nettement moins marqués, chez les *Kassina* de type *maculosa* de l'Adamaoua.

ECOLOGIE, CYCLE D'ACTIVITÉ VOCALE, PHONOCÉNOSES

Kassina *type* maculosa: son habitat optimal paraît correspondre aux savanes humides de type guinéen, parsemées de buissons et de boqueteaux et parcourues de galeries forestières. Elle peut y être localement abondante, comme l'ont montré les prospections dans le secteur Obala - Bafia, au nord et au nord-ouest de Yaoundé. Sur l'Adamaoua et sur les reliefs de la Dorsale camerounaise, où la végétation herbacée est encore plus largement dominante (savanes soudano-guinéennes plus ou moins arborées de l'Adamaoua, secteurs densément cultivés et déboisés des pays bamoun et bamiléké), *Kassina* type *maculosa* peut atteindre environ 1500 m d'altitude, voire 2000 m si les spécimens de Kakar se rapportent à ce type.

Elle peut aussi, plus localement, se comporter en espèce parasylvicole. Elle pénètre en effet dans la zone forestière, où elle « descend » plus ou moins vers le sud comme le font d'autres espèces primitivement savanicoles telles que *Bufo regularis* ou *Hoplobatrachus occipitalis*. Dans ses stations intra-forestières, elle n'occupe que des zones à végétation très « secondarisée » et, à en juger par le faible nombre de mâles actifs, elle n'y est représentée que par de petites populations dispersées.

Sur les sites de reproduction, les mâles peuvent émettre leurs appels depuis des buissons, où ils sont capables de s'élever jusqu'à environ 1,5 m en « empoignant » les rameaux, mais aussi depuis des touffes de graminées; dans ce dernier cas, ils peuvent grimper sur les chaumes et les feuilles, ou simplement se poster sur la partie supérieure des touradons.

L'activité vocale des mâles débute aux premières pluies, quand les collections d'eau commencent à se remplir. Suivant leur situation géographique, les populations sont soumises à un climat à une ou deux saisons pluvieuses. Le premier cas correspond, en gros, à l'Adamaoua et à la plus grande partie de la Dorsale camerounaise, alors que le second correspond au Plateau sud-camerounais: il y a alors deux périodes d'activité vocale, l'une en fin mars - avril, l'autre en septembre - octobre.

La comparaison de relevés effectués dans 11 sites à végétation graminéenne dominante (région d'Obala, Plateau bamiléké et Adamaoua) et dans 5 sites à végétation secondaire de la zone forestière (région de Yaoundé - Mbalmayo) donne un aperçu des phonocénoses auxquelles participe *K.* type *maculosa*. Dans le premier cas, les espèces

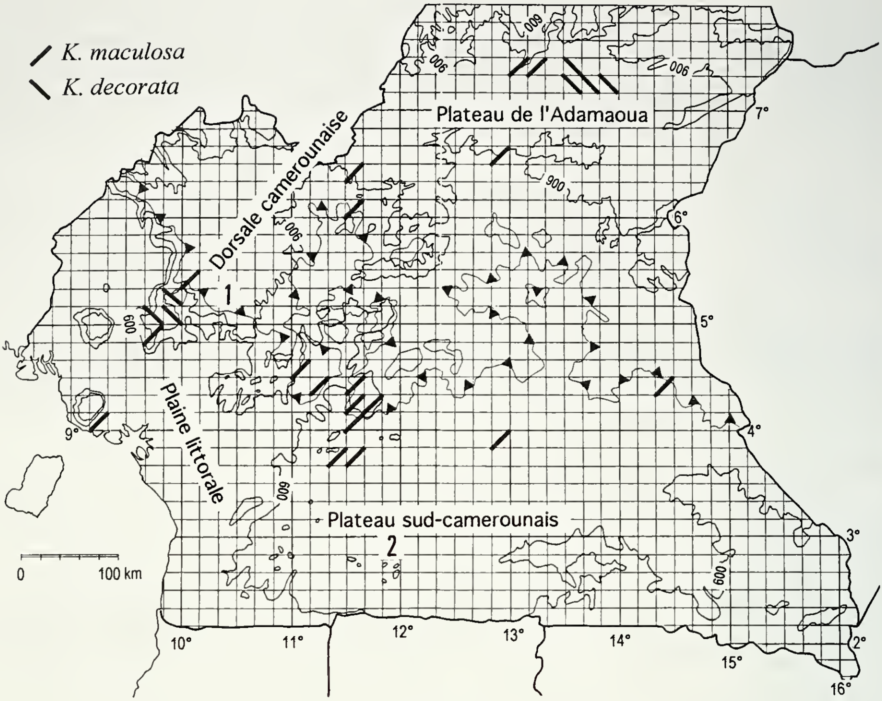


FIG. 10

Carte du Cameroun au sud du $8^{\text{ème}}$ parallèle montrant la répartition des mailles où ont été repérées *K. maculosa* et *K. decorata*. La limite forêt – savane est symbolisée par la ligne avec triangles (pointés vers la savane). Les chiffres correspondent aux localités de Perret (1966): Bangwa (1) et Sangmélima (2).

vocalement actives auxquelles elle est le plus souvent associée (40% des sites ou plus) sont: *Afrixalus fulvovittatus* (100% des sites), *Hyperolius balfouri viridistriatus* (91%), *Kassina senegalensis* (63,6%), *Phrynobatrachus natalensis*, *Hoplobatrachus occipitalis*, *Hyperolius tuberculatus* (54,5%), *Leptopelis nordequatorialis*, *Hyperolius igbettensis*, *Bufo regularis*, *B. maculatus* (45,5%). Cette combinaison d'espèces est tout à fait caractéristique des savanes humides guinéennes et soudano-guinéennes. Dans les sites intra-forestiers, les espèces-compagnes les plus fréquentes constituent un bon échantillonnage du peuplement parasylvicole: *Afrixalus fulvovittatus* (100% des sites), *Hyperolius tuberculatus*, *H. adspersus*, *Amnirana albolabris*, *Ptychadena perreti* (60%), *Bufo maculatus*, *Chiromantis rufescens*, *Hyperolius cinnamomeoventris*, *H. platyceps*, *H. pardalis*, *Afrixalus paradorsalis* (40%).

Les individus trouvés à la base du versant est du mont Cameroun partageaient les abords d'un ruisseau coupé par un barrage avec un mélange d'espèces comprenant des parasylvicoles typiques (*Leptopelis aubryi*, *Afrixalus paradorsalis*, *Hyperolius concolor*, *H. kuligae*, *H. bolifambae*) mais aussi des sylvicoles qui, dans cette région très arrosée, subsistent dans les brousses luxuriantes remplaçant la forêt (*Astylosternus diadematus*, *Leptopelis calcaratus*, *Ptychadena aequiplicata*, *Phrynobatrachus auritus*).

Kassina *type* decorata: les trois secteurs où ont été trouvées des *Kassina* de type *decorata* offrent des conditions d'habitat différentes et seront donc traités séparément .

– Mont Manengouba: c'est un volcan inactif dont le fond est une plaine herbeuse, large de 3 km dans son plus grand diamètre et située à environ 2000 m d'altitude. Les points d'eau sont constitués par deux lacs occupant des cratères secondaires et par une zone marécageuse pouvant se transformer en étang au plus fort de la saison pluvieuse. A l'exception des parois rocheuses, boisées, les pentes environnantes sont couvertes de prairies pâturées par des troupeaux de zébus et des chevaux. Je n'ai pas pu faire de sorties de nuit dans ce site mais trois sorties diurnes (29.III.72, 17-19.IV.76 et 22-23.III.81) m'ont permis d'y trouver: *Bufo sp.* (apparenté à *B. villiersi*?), *Amnirana albolabris* (têtards de grande taille, à l'époque pêchés pour la consommation locale!), *Phrynobatrachus cf. werneri*, *Hyperolius adametzi* et, à chacune des sorties, des *Kassina*, en général juvéniles, abritées sous des pierres. A partir des points d'eau du fond du cratère, ces *Kassina* peuvent s'élever sur les pentes dominantes, au moins jusque vers 2200 m d'altitude.

– Plaine des Mbos: il s'agit d'un fossé d'effondrement, formant une vaste plaine à fond plat entre le Plateau bamiléké au nord et le mont Manengouba au sud. Son altitude est de 700 à 720 m. La végétation est constituée par une mosaïque complexe de savanes humides et de massifs boisés, à caractère souvent marécageux, et de cultures vivrières. La batrachofaune est peu diversifiée, constituée pour l'essentiel de quelques espèces euryéciques et parasylvicoles, qui peuvent être représentées par des populations extrêmement abondantes.

Dans la nuit du 24 mai 1971, des dizaines de mâles formaient un chœur continu dans une prairie inondée. Beaucoup chantaient en partie immergés, prenant appui sur des mottes de terre ou des débris végétaux (comportement qui n'a jamais été observé chez *K.* type *maculosa*). Quatre ans plus tard, à un jour près (25.V.75), seuls quelques appels ont été entendus.

– Adamaoua oriental: l'essentiel du matériel recueilli dans l'est de l'Adamaoua provient de la localité de Sadolkoulaye, située à 35 km à l'est de Ngaoundéré. Le site a été visité, de nuit, les 29.VI.71, 5.VII.71, 28.IV.73 et 17.V.81. Sur un substrat cuirassé absolument plan est établie une prairie qui, en saison des pluies, se transforme en un petit lac herbeux peu profond. Des milliers de Batraciens s'y reproduisent et, au plus fort de la période d'activité vocale (mai-juin) y créent un vacarme assourdissant. Les *Kassina* sont représentées par *K. senegalensis* (grande forme de l'Adamaoua, voir ci-après) et par une *Kassina* naine à pattern *decorata*. Cette dernière, extrêmement abondante, peut faire des chœurs ininterrompus, comme dans la Plaine des Mbos. Les espèces participant à la phonocénose sont *Hoplobatrachus occipitalis*, *Ptychadena pumilio*, *P. straeleni*, *Hyperolius balfouri viridistriatus* (lui aussi de petite taille), *H. igbettensis* et *Afrixalus fulvovittatus*.

De vastes prairies marécageuses d'aspect semblable existent plus près de la ville de Ngaoundéré. Au sud de celle-ci, près de Wakwa, la même *Kassina* naine a été trouvée, en compagnie ou à proximité de *Ptychadena pumilio*, *Hyperolius b. viridistriatus*, *H. viridiflavus aureus*, *Afrixalus fulvovittatus* et *A. weidholzi*.

DISCUSSION

Il faut d'abord relever que la livrée de type *maculosa* correspond bien à la figure que donne Sternfeld (1917) dans sa description de *Megalixalus maculosus*, de même qu'il y a une parfaite concordance entre la livrée de type *decorata* et la description très précise faite par Angel (1940) de la livrée de son *Megalixalus decoratus*. Sans se référer directement à la description d'Angel, mais à celle de Perret (1966), Mertens (1968) évoque aussi une bande vertébrale chez ses 3 ex. de *Kassina* du lac Manengouba, qu'il nomme cependant *K. maculosa*.

En l'absence de caractères morphologiques discriminants autres que la maculation, l'interprétation taxonomique des *Kassina* de type *maculosa* et de type *decorata* pose un problème difficile, apparemment sans équivalent dans la batrachofaune camerounaise. Pour tenter de le résoudre, les données biogéographiques suivantes doivent être prises en compte.

1°) Même si des recherches ultérieures montrent que la forme à pattern *decorata* est plus largement répandue que nous ne le savons à présent, il y a de très fortes probabilités pour qu'elle soit absente au moins dans la moitié ouest du Plateau sud-camerounais, dont la batrachofaune est bien connue. Les aréotypes des deux formes sont donc différents.

2°) Néanmoins, les aires de répartition se recoupent en partie, dans l'Ouest et l'Adamaoua, où sont localisées les populations de type *decorata*.

3°) Les populations des deux formes sont étroitement contiguës mais, dans l'état actuel des connaissances, ne s'interpénètrent pas. La situation, plus précisément, est la suivante. (1) Dans l'Ouest, si on admet que les populations de type *decorata* du mont Manengouba et de la Plaine des Mbos représentent un « foyer » unique, on constate que des individus parfaitement caractérisés de la forme *maculosa* sont présents 4 km au sud (Nsoung) et 20 km au nord (bord du Plateau bamiléké) et « encadrent » donc ce foyer de la forme *decorata*. (2) Sur l'Adamaoua, il y a environ 40 km à vol d'oiseau entre les populations de type *decorata* de Wakwa et celles de type *maculosa* de Hourso Manang.

Il est difficile d'imaginer que la forme *decorata* représente une simple morphe, qui resterait localisée en quelques points d'une aire par ailleurs occupée par la seule morphe *maculosa*. Le statut de sous-espèce ne paraît pas non plus satisfaisant en raison de la proximité spatiale des deux formes et de l'intrication de leurs aires de répartition. Les données biogéographiques suggèrent une « imperméabilité génétique » entre les *Kassina* des deux types, situation à laquelle correspondrait plutôt une séparation de niveau spécifique.

Deux problèmes connexes doivent aussi être pris en considération. 1°) Que représentent les populations de *Kassina* à pattern *decorata* de l'Adamaoua par rapport à celles de l'Ouest, séparées par environ 360 km à vol d'oiseau? La découverte de populations géographiquement intermédiaires pourrait montrer qu'elles correspondent aux extrémités d'un cline. Dans le cas d'une bipolarité effective, deux possibilités devraient être envisagées: (1) disjonction d'une aire auparavant continue occupée par une *Kassina* de type *decorata*, ou (2) acquisition indépendante d'un pattern identique (convergence) par des populations différant par leur taille et les proportions de leurs membres postérieurs. Un statut subspécifique conviendrait pour la première éventualité alors que la seconde impliquerait une distinction de niveau spécifique. 2°) Un problème similaire se pose pour les *Kassina* de type *maculosa* du Mont Cameroun. Le hiatus de distribution est moindre, de l'ordre de 115 km, mais les nombreuses prospections effectuées dans la région intermédiaire montrent qu'elles constituent très probablement un isolat. Des recherches complémentaires seraient cependant nécessaires avant de décider si elles représentent une sous-espèce, voire une espèce, endémique du Mont Cameroun.

La discussion qui précède montre la complexité du problème posé par ces *Kassina*, et l'importance du travail de terrain qui reste à accomplir pour mieux en préciser les données... sans être sûr de le résoudre, car il est possible que les méthodes morphologiques traditionnelles trouvent ici leurs limites. Le maintien du *statu quo* représente une solution trop « réunisseuse » (il est difficile d'admettre que les individus du Mont Cameroun, mesurant près de 4 cm, et ceux de la région de Ngaoundéré, dont la taille est de l'ordre de 2,5 cm, soient placés sous un même nom spécifique). Celle consistant à distinguer deux espèces divisées chacune en deux sous-espèces, voire à distinguer quatre espèces, est insuffisamment étayée dans l'état actuel des connaissances. *Pour le moment*, la solution la plus équilibrée paraît donc être de considérer les *Kassina* à pattern *decorata* et les *Kassina* à pattern *maculosa* comme deux espèces distinctes. On peut en donner les diagnoses suivantes.

K. maculosa: la plupart des macules dorsales sont sub-circulaires ou elliptiques et ne forment pas d'alignements nets; la macule supra-tympanique ne se recourbe pas vers le bas; la maculation des cuisses est généralement transverse.

K. decorata: les macules dorsales sont au moins deux fois plus longues que larges, disposées suivant trois lignes principales, la médiane formant très souvent une bande continue; macule supra-tympanique incurvée vers le bas; marbrures des cuisses en général longitudinales.

Spécimens de référence

Cinq spécimens de *K. maculosa* sont déposés au Muséum d'Histoire naturelle de Genève sous les numéros MHNG 2680.45 à 2680.49; 5 spécimens de *K. decorata* « ouest » sont déposés dans la même institution sous les numéros 2680.35 à 2680.39 et 5 de *K. decorata* « Adamaoua » sous les numéros 2680.40 à 2680.44.

Kassina senegalensis (Duméril & Bibron, 1841)

Historique

K. senegalensis, espèce-type du genre, a d'abord été trouvée près du Lac Galam, au Sénégal. Les recherches ultérieures ont montré qu'il s'agit d'un des Amphibiens savanicoles les plus largement répandus puisque son aire de répartition atteint la Somalie et l'Afrique australe (*cf.* carte *in* Schiøtz, 1999). Toutefois, comme le souligne Schiøtz (*ibid.*), il est possible que plusieurs espèces différentes, actuellement confondues sous *K. senegalensis*, peuplent certaines parties de cette aire immense. En tout cas, les populations du Cameroun ne diffèrent pas ostensiblement de celles d'Afrique de l'Ouest (Schiøtz, 1967; Rödel, 2000) ou de celles du nord-est de la RDC (Inger, 1968), que ce soit par leur aspect ou par leurs vocalisations.

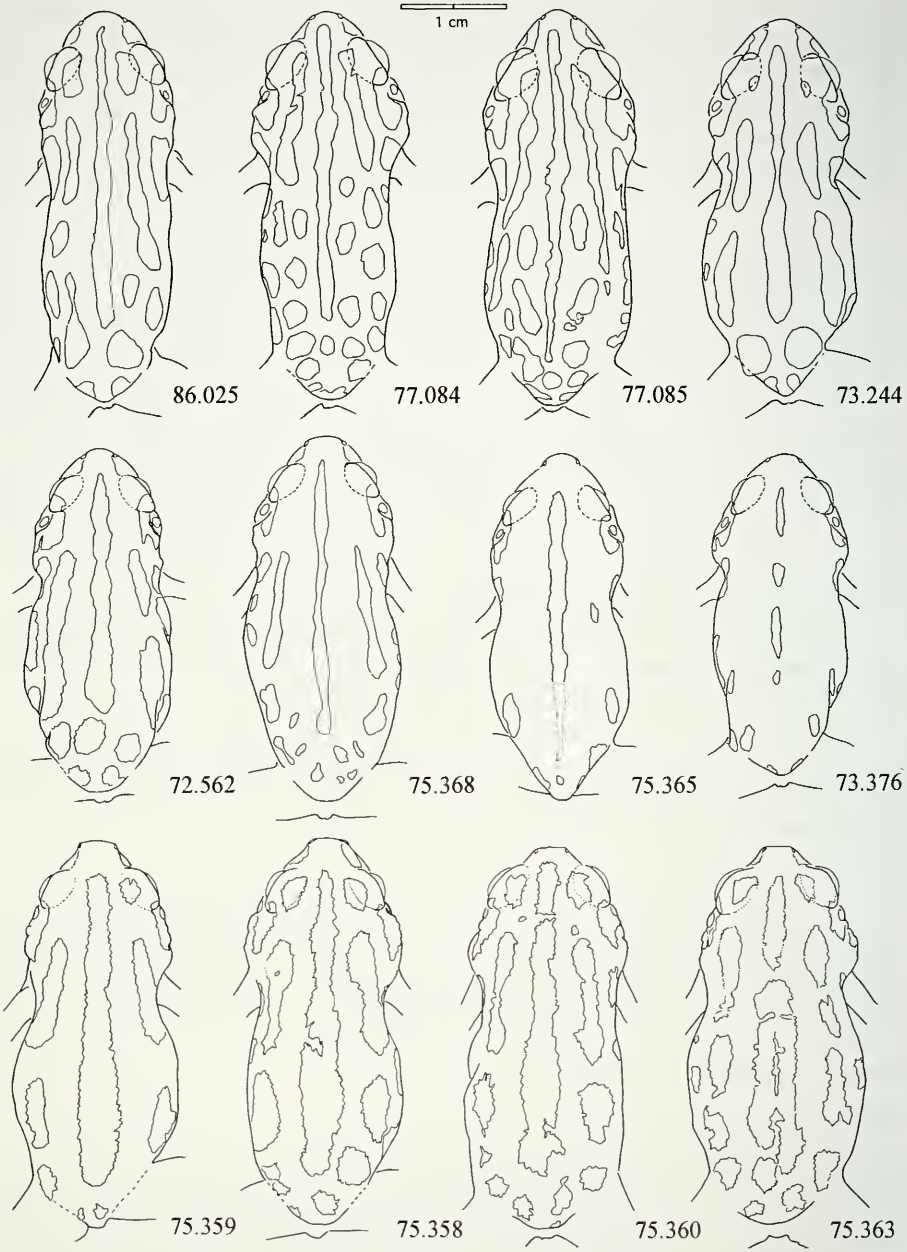
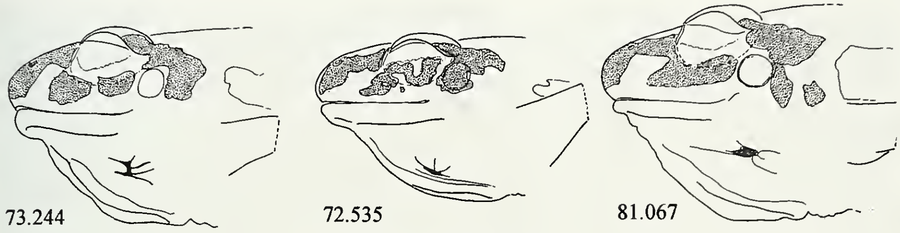


FIG. 11

Maculation dorsale chez *K. senegalensis*, populations méridionales (rangée supérieure) et septentrionales (rangée moyenne), et chez *K. wazae* (rangée inférieure). Pour les localités et dates de capture des spécimens figurés, se reporter aux numéros correspondants dans le tableau 1. Remarquer le contour finement dentelé des macules chez *K. wazae*.



K. senegalensis

K. cassinoides

FIG. 12
Exemples de maculation céphalique latérale chez *K. senegalensis* (remarquer les sous-oculaires, fusionnées ou non) et chez *K. cassinoides* (grande extension de la supra-tympanique et fusion de toutes les macules).

COMPLÉMENTS DE DESCRIPTION

Cette espèce est trop connue pour qu'une redescription soit nécessaire. Seuls les points suivants doivent être mentionnés. – 1°) Les macules sous-oculaires peuvent être soit séparées (63 % des individus étudiés), soit fusionnées (37 %); la macule loréale est fusionnée à la macule nasale; entre les premières et les secondes, un espace de la même teinte que le fond, de forme plus ou moins quadrangulaire, est généralement très apparent (Fig. 12). – 2°) L'appareil vocal externe, bien étudié par Drewes (1984), est du type 1: glande gulaire très développée (c'est, relativement, la plus grande chez les *Kassina* camerounaises), de forme rectangulaire ou elliptique, fossettes de rétraction des aires noires du sac vocal bien visibles, un gros pli interbrachial (Fig. 4 et Pl. II, Fig. e). – 3°) Chez la femelle, comme l'ont signalé Schmidt & Inger (1959), la face ventrale est presque lisse dans ses trois-quarts antérieurs. – 4°) D'après Perret (1966) les dents vomériennes sont présentes. Dans mon matériel, elles ne sont bien développées que chez 4 individus sur 45 (8,8 %), absentes chez 30 / 45 (66,6 %) et très petites, masquées par la muqueuse buccale, chez 11 / 45 (24,4 %).

DISTRIBUTION, VARIABILITÉ

La distribution au Cameroun de *K. senegalensis* (carte Fig. 14) offre un raccourci de ce qu'elle est à l'échelle de l'Afrique: elle s'étend vers le sud jusqu'à la limite de la zone forestière, dont elle contourne au plus près les sinuosités. Vers le nord, elle atteint le domaine sahélo-soudanien.

Dans cette bande, large d'environ 900 km, l'espèce montre une certaine variabilité, qui a conduit à séparer ici des populations « nord » et « sud » (Tab. 1 et 2,

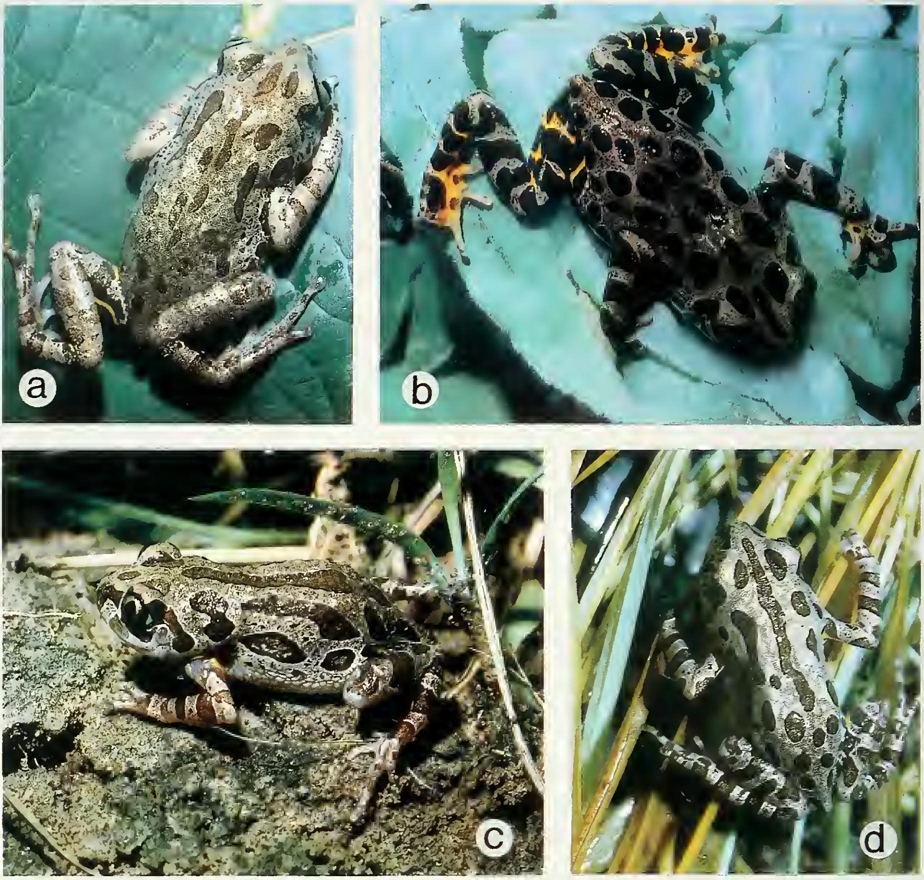


Planche I

Kassina decorata et *K. maculosa*. (a) *K. decorata* Ouest, Santchou, 24.V.71. (b) *K. maculosa* Mt Cameroun, Bonianango, 11.VII.81. (c) *K. decorata* Adamaoua, Sadolkoulaye, 28.IV.73. (d) *K. decorata* Adamaoua, Ngaoundéré Vina, 02.VII.71. En a, c et d, livrée claire (diurne), en b, livrée de transition. Remarquer comment les orteils V et IV de l'individu figuré en d se replient ensemble et indépendamment des autres orteils sur une encoche d'une penne de fougère.

Fig. 1 et carte Fig. 14), en prenant le rebord septentrional du Plateau de l'Adamaoua comme limite, mais il s'agit là d'un choix surtout pratique.

Populations méridionales: la maculation dorsale est très développée, avec une large bande médio-dorsale continue, deux bandes latéro-dorsales plus ou moins discontinues et de grosses macules sub-circulaires dans la région postérieure; il peut y avoir un alignement de macules entre la bande médiane et les latéro-dorsales, esquissant deux bandes supplémentaires; ce type de maculation est illustré par la rangée supérieure de la Fig. 11. La taille moyenne est relativement grande, en particulier chez les individus du Plateau de l'Adamaoua, auxquels correspondent, sur la Fig. 1, cinq des six valeurs de L les plus élevées (Pl. II, Fig. b).

Planche II

Kassina senegalensis, *K. wazae* et *K. cassinoides*. (a) *K. senegalensis* Nord, Salak, 03.VII.73. (b) *K. senegalensis* Sud, Sadolkoulaye, 28.IV.73. (c) *K. wazae*, holotype, Mora / Waza, 14.VII.75. (d) *K. senegalensis* Sud, sac vocal gonflé, Minkama, 07.X.77. (e) de gauche à droite, face ventrale de *K. wazae*, *K. senegalensis* et *K. cassinoides*, Mora / Waza, 14.VII.75. Remarquer les macules sous-oculaires fusionnées en b, les denticulations irrégulières du pourtour des macules et l'absence de sous-oculaires en c. En e, sac vocal de type 1 chez *K. senegalensis* (au centre), et de type 2 chez *K. wazae* (à gauche) et *K. cassinoides* (à droite).

Populations septentrionales: à partir du piedmont de l'Adamaoua, la taille et la maculation ont tendance à se réduire en allant vers le nord. Au sud de la Bénoué, on trouve encore des individus bien maculés (comme le spécimen de gauche, ligne du milieu, de la Fig. 11) mêlés à des individus à bandes rétrécies. Dans la région de Garoua et de Mora-Waza, ils sont nettement plus petits et chez tous les bandes sont encore plus minces; les bandes latéro-dorsales sont les premières affectées par la réduction de la maculation; dans les cas extrêmes, seule subsiste la bande médiane, plus ou moins discontinue (Pl. II, Fig. a). De plus, les membres postérieurs sont proportionnellement plus courts dans les populations septentrionales (Tab. 2).

Une comparaison portant seulement sur les populations les plus méridionales et les plus septentrionales pourrait suggérer une distinction subspécifique. Mais celle-ci rendrait mal compte du fait qu'il n'y a pas de gradient régulier, pas plus qu'une discontinuité franche, dans le passage d'un type à l'autre. D'autre part, il faudrait savoir si une situation semblable se retrouve dans d'autres territoires, ce que la littérature ne dit pas. Il vaut mieux donc en rester au seul statut spécifique, en admettant une assez forte variation géographique des populations.

ECOLOGIE

Au Cameroun, plusieurs espèces d'Anoures, savanicoles à l'origine, ont pénétré plus ou moins profondément dans la zone forestière, en profitant des milieux herbacés de substitution dus à l'extension des surfaces cultivées et déboisées (voir plus haut, *K. maculosa*). Au contraire, *K. senegalensis* fait partie d'un groupe d'espèces qui sont restées cantonnées aux formations de savane, fussent-elles au contact immédiat de la forêt (*Ptychadena stenocephala* et *bibroni*, *Phrynobatrachus natalensis*, *Hyperolius igbettensis*, *Hemisus guineensis*). Cette incapacité paraît assez paradoxale en regard de l'immense répartition de l'espèce au Cameroun et, plus généralement, en Afrique subsaharienne.

Du sud au nord de son aire camerounaise, *K. senegalensis* peuple en effet toute une succession de zones bioclimatiques allant des savanes humides de type guinéen, à vocation forestière dans les conditions climatiques actuelles, aux steppes sahélo-soudaniennes, et il est même probable que, encore plus au nord, elle atteigne le secteur sahélo-saharien aux abords du Lac Tchad. Elle est ainsi soumise à des régimes de précipitations très différents : deux saisons pluvieuses et environ 1500 mm de pluie par an au sud, puis une saison des pluies unique de 7 mois, avec un surcroît de précipitations dû à l'altitude sur le Plateau de l'Adamaoua (environ 1700 mm / an), et ensuite un gradient climatique régulier marqué par l'allongement de la saison sèche (8 à 9 mois dans la région de Mora) et la diminution des précipitations (environ 750 mm dans le même secteur). L'adaptabilité de cette espèce se manifeste aussi au niveau des températures: de 28°C de moyenne annuelle dans la plaine du Logone, à environ 20° dans la plus haute station relevée (1540 m, près de Bélel).

Dans toute son aire de répartition, *K. senegalensis* est très souvent associée à d'autres *Kassina*: *K. maculosa* jusqu'à la bordure nord de l'Adamaoua, puis, successivement, les deux espèces suivantes. On trouvera, dans les parties relatives à ces espèces, des indications sur les diverses phonocénoses auxquelles participe *K. senegalensis*.

Kassina wazae sp. n.

TYPES

Holotype: mâle capturé entre Mora et Waza, Cameroun, le 14.VII.75; numéro de collection Amiet: 75.378; déposé au Musée d'histoire naturelle de Genève sous le numéro MHNG 2680.50.

Paratypes: cinq autres mâles, même localité et même date; deux sont déposés au Musée d'histoire naturelle de Genève sous les numéros MHNG 2680.51 et 2680.52; autres paratypes actuellement dans la collection de l'auteur (numéros 75.361, 75.362 et 75.363).

DIAGNOSE

Kassina ressemblant beaucoup par sa taille et son aspect à *K. senegalensis* de la « forme sud », mais s'en distinguant par: – son sac vocal de type 2, à glande gulaire petite et à bords convergents vers l'arrière (forme sub-triangulaire ou trapézoïdale), – la présence d'un petit tubercule tarsien, – l'absence de macules sous-oculaires, – l'aspect finement déchiqueté sur les bords de toutes les macules, – les vocalisations.

ETYMOLOGIE

De la localité de Waza, sur la limite ouest du Parc national de Waza, proche de l'endroit où l'espèce a été trouvée.

DESCRIPTION

Principaux caractères de l'holotype: mensurations en mm: L: 35,5; T: 11,9; AB: 7,1; C: 11,6; J: 11; P: 17. Proportions, en %: T/L: 33,5; AB/L: 20; C+J/L: 63,6; P/L: 47,9. Glande gulaire avec un sillon longitudinal dans sa partie postérieure (artefact probable). Maculation de la face dorsale: voir Fig. 11; maculation céphalique latérale: voir Fig. 12; livrée in vivo (livrée claire): voir Pl. II, Fig. c.

Habitus, tégument, membres: espèce de taille moyenne (les 6 spécimens collectés mesurent entre 32,3 et 35,5 mm) à habitus allongé, semblable à celui des plus grandes *K. senegalensis*. Vu en plan, le museau paraît tronqué à son extrémité, alors que son contour est plutôt arqué chez *K. senegalensis*. Tympan un peu plus haut que large, presque vertical (à peine visible de dessus), situé juste derrière l'œil. Pas de dents vomériennes.

Tégument dorsal d'apparence lisse sur toute sa surface; tégument ventral fortement et régulièrement granuleux (au moins chez les mâles), y compris sous les cuisses.

Membres antérieurs relativement courts pour un représentant du genre *Kassina* (moyenne AB/L = 21 %). Main (Fig. 2) à doigts courts et épais, se rétrécissant progressivement vers l'extrémité, leurs pelotes non dilatées, plus étroites que les phalanges qui les portent; tubercules sous-articulaires larges et saillants; des excroissances supplémentaires modérément marquées sous certaines phalanges; aucune trace de palmure.

Membres postérieurs épais et relativement plus courts que chez toutes les autres espèces camerounaises de *Kassina*, sauf la forme septentrionale de *K. senegalensis* (moyenne C+J/L = 64,5 %, P/L = 49 %). Pied (Fig. 2) large et épais; orteils se rétrécissant assez régulièrement depuis leur base, leur pelote terminale plus étroite que les

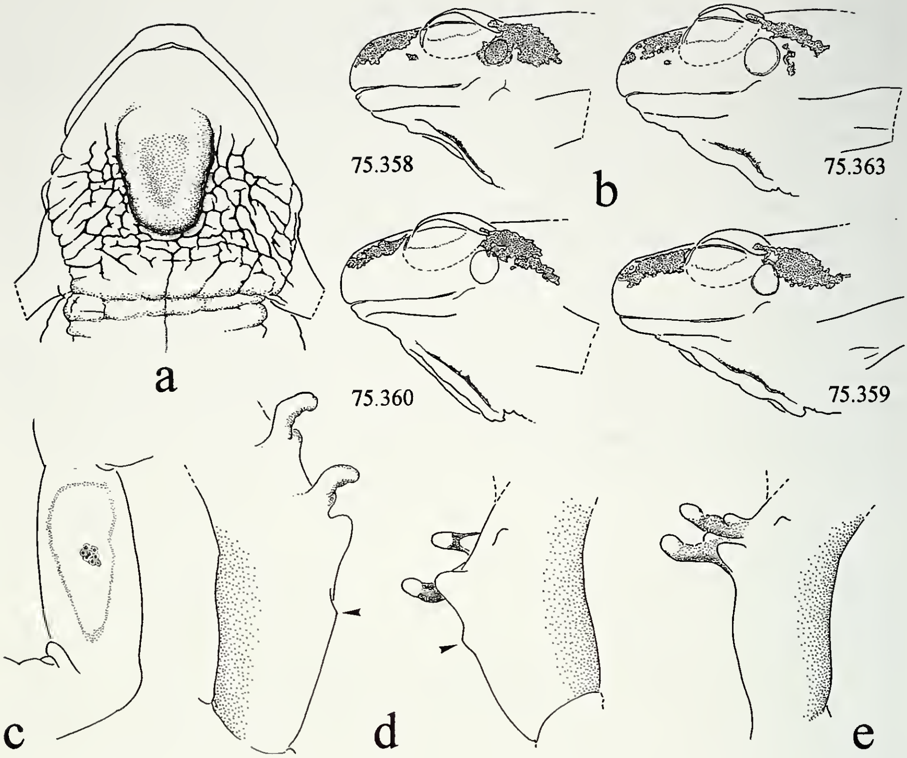


FIG. 13

Caractères diagnostiques de *Kassina wazae* n. sp. (a) Région gulaire (sac vocal de type 2). (b) Maculation céphalique latérale (disparition des sous-oculaires). (c) Empâtement glandulaire de l'avant-bras. (d) Tubercule tarsien sous deux angles d'observation différents. (e) Pour comparaison, tarse chez *K. senegalensis* (pas de tubercule tarsien). Voir aussi Fig. 11 (maculation dorsale).

phalanges qui les précèdent (différence avec *K. senegalensis* et *K. cassinoides*); tubercules sous-articulaires tous présents, larges, bien saillants; un gros tubercule métatarsien interne, large, et un net tubercule métatarsien interne, petit et conique; une petite excroissance souple sur le tarse, en retrait du métatarsien interne (Fig. 13 d), assimilable à un tubercule tarsien (caractère propre à cette seule espèce au Cameroun, existant aussi chez *K. fusca*); un rudiment de palmure, épaissi, à peine différencié entre les orteils I et II et II et III.

Caractères sexuels secondaires: région gulaire des mâles caractéristique (Fig. 13 a et Pl. II, Fig. e): – partie médiane épaissie du sac vocal (= glande gulaire) relativement petite, ses bords épais et tendant à converger vers l'arrière, d'où un contour en triangle à sommet tronqué (trapézoïdal chez un des six individus), sa surface plutôt concave; – pas de fossettes de rétraction apparentes mais, sur le pourtour de la partie médiane, de forts plis circonvolués délimités par de profonds sillons. Cette structure de la région gulaire, assez proche de celle de *K. cassinoides*, correspond au type 2 défini plus haut. Un bourrelet interbrachial.

Sur la face interne des bras, une zone glandulaire plus ou moins saillante, non pigmentée, s'élargissant vers le poignet (Fig. 13 c).

Livrée: livrée dorsale (Fig. 11 et Pl. II, Fig. c) de même type que chez *K. senegalensis*, et plus précisément les populations méridionales de celle-ci, car la maculation est large et très apparente: une bande médio-dorsale continue débute entre les yeux et se poursuit jusqu'à la région sacrée en s'élargissant d'avant en arrière (chez un individu, elle montre un début de dédoublement postérieur); de part et d'autre, de grandes macules beaucoup plus longues que larges forment deux alignement latéro-dorsaux débutant par les macules supra-oculaires; dans la région tout à fait postérieure, il peut y avoir de grosses macules sub-circulaires; contrairement à ce qui s'observe chez les *K. senegalensis* les plus maculées, il n'y a pas de rangées intermédiaires paravertébrales.

Latéralement, un caractère important de la maculation réside dans l'*absence des macules sous-oculaires* (Fig. 12 b), aussi bien antérieure que postérieure (ces macules sont présentes, séparées ou fusionnées, chez *K. senegalensis*).

Membres peu ornés: 0 ou 1 macule sur le bras, 1 ou 2 sur l'avant-bras, 1 ou 2 sur la cuisse, 2 sur la jambe, 2 ou 3, très petites, sur la tranche externe du pied. Comme chez *K. senegalensis* et *K. cassinoides*, il n'y a pas de coloration jaune à la base des membres.

Une particularité notable, bien qu'elle ne soit pas apparente au premier coup d'œil, est que toutes les macules sont très finement et irrégulièrement dentelées sur leur pourtour, qui a de ce fait un aspect déchiqueté. Sur le vif, en livrée diurne contrastée, les macules ont une teinte cuivreuse contrastant élégamment avec le blanc argenté de la teinte de fond.

La face ventrale est incolore, sauf la région gulaire qui est assombrie, d'un gris plus ou moins foncé (caractère probablement propre aux mâles).

DISTRIBUTION ET ÉCOLOGIE

L'unique localité où *K. wazae* a été repérée, à environ 40 km au NE de Mora, se situe à la limite des steppes à épineux et des prairies inondables sahélo-soudaniennes (ou « yaérés »). Dans une grande plaine sans arbres, en contrebas de la route surélevée, plusieurs mares étaient, le 14 juillet 1975, déjà bien remplies: il avait plu au début du mois puis, assez abondamment, le 11 et le 12. La phonocénose accompagnant *K. wazae* ne comprenait plus guère d'espèces précoces, mais des espèces relativement tardives, appelant de préférence à proximité de collections d'eau assez profondes: *Bufo steindachneri*, *Hydrophylax galamensis* et *Hyperolius viridiflavus pallidus*. La forme septentrionale de *K. senegalensis* était représentée par des mâles beaucoup plus nombreux que ceux de *K. wazae*.

Dès l'arrivée sur le site, la présence de cette dernière a été détectée par ses appels, des « hou » brefs, assez étouffés, bien distincts des « oui » modulés de *K. senegalensis*. Au moment de ma visite, les mâles de *K. wazae* se tenaient plus loin de l'eau que ceux de *K. senegalensis*.

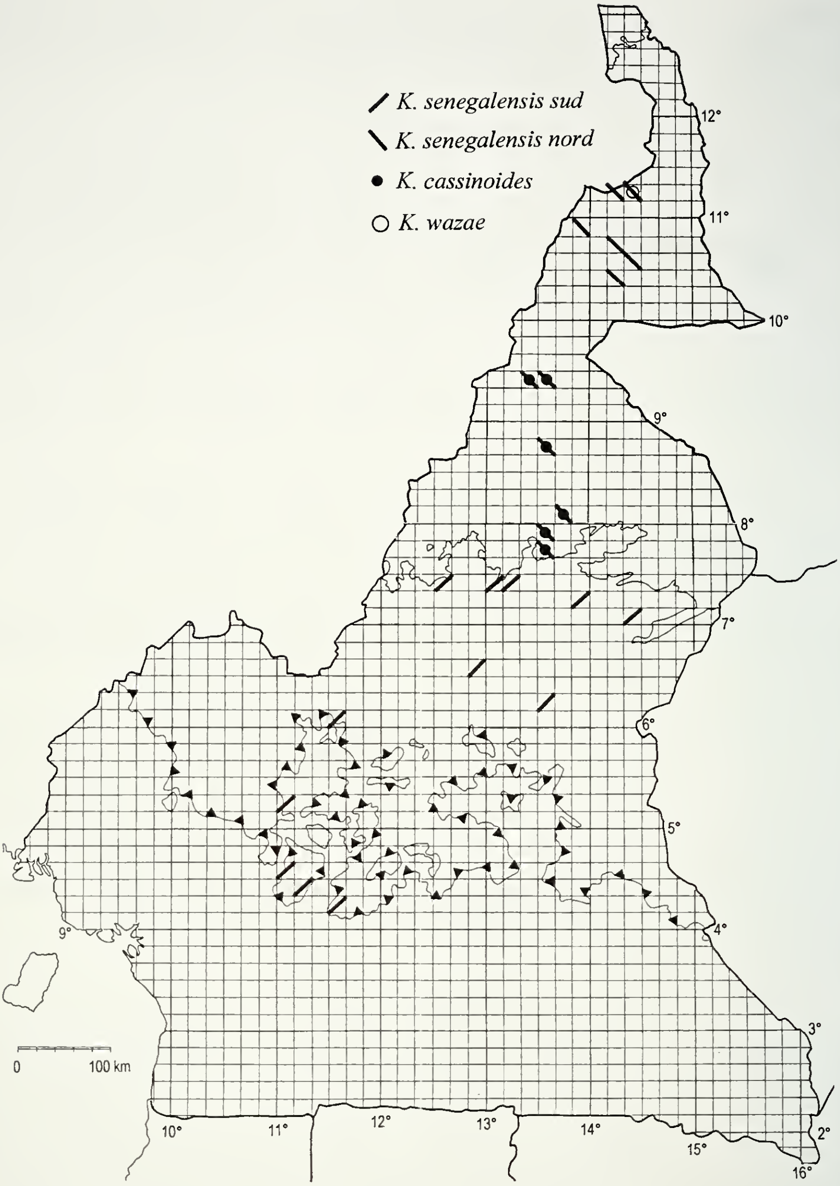


FIG. 14

Carte du Cameroun montrant la répartition des mailles où ont été repérées *K. senegalensis* (populations « sud » et « nord »). *K. cassinoides* et *K. wazae*. La limite forêt – savane est symbolisée par la ligne avec triangles (pointés vers la savane) et le rebord septentrional du Plateau de l'Adamaoua par la courbe de niveau de 900 m.

DISCUSSION

Comme le relève Schiøtz (1999), de nombreuses « formes » de statut taxonomique incertain sont rattachées à *K. senegalensis*. L'espèce décrite ci-dessus en est apparemment proche mais plusieurs bons caractères permettent de l'en séparer et le fait que les deux soient localement syntopiques confirmerait, si besoin était, qu'elles sont spécifiquement distinctes. *K. wazae* est peut-être une espèce adaptée à la zone sahélo-soudanienne, et donc à de longues saisons sèches, de l'ordre de neuf mois là où elle a été trouvée. Bien que ses appels soient aisément repérables, elle n'a pas été notée plus au sud, où elle paraît être remplacée par *K. cassinoides*.

La batrachofaune de l'extrême nord du Cameroun, en gros entre les 11ème et 13ème parallèles, reste quasiment inconnue. On peut supposer que la découverte de *K. wazae* ne représente pas un cas exceptionnel et que la prospection de la zone des yaérés et des confins du Lac Tchad permettrait de trouver d'autres espèces nouvelles pour la science ou, au moins, pour le territoire camerounais.

Kassina cassinoides (Boulenger, 1903)

COMPLÉMENTS DE DESCRIPTION

Cette *Kassina* est la plus grande du Cameroun (cf. Tab. 2 et Fig. 1). Il n'y a aucune différence entre les spécimens camerounais et ceux d'Afrique de l'Ouest, tels qu'ils ont été décrits et figurés par les auteurs qui ont pu les observer sur le terrain (Schiøtz, 1967, 1999; Rödel, 2000; Böhme, 2005). Il est donc superflu d'en donner une description et seules seront relevées ici les particularités suivantes.

Dents vomériennes: chez 9 des 11 spécimens étudiés, elles sont bien développées; chez les deux autres, elles sont petites et plus ou moins masquées par la muqueuse buccale, mais décelables en passant un objet dur à leur emplacement.

Maculation céphalique latérale: elle est caractérisée par la fusion des sous-oculaires en une macule linéaire unique, aux bords plus ou moins nets, reliant la loréale et la nasale, fusionnées, à la macule supra-tympanique très étendue et recouvrant le tympan (Fig. 12); cet ensemble, qui réunit toutes les macules latérales de la tête, est au point de départ des bandes latérales et latéro-dorsales.

Disques digitaux: Schiøtz (1967) et Rödel (2000) relèvent la présence de disques de la largeur des tubercules sous-articulaires à l'extrémité des doigts et des orteils. Ce caractère se retrouve chez les spécimens camerounais (Fig. 2). Il peut paraître surprenant chez une espèce savanicole et apparemment terrestre mais Rödel (op. cit.) indique qu'il a observé des mâles appelant depuis des arbres à des hauteurs de plusieurs mètres. Même si ce comportement n'est pas général (il pourrait dépendre du type de formation végétale localement fréquenté par l'espèce), il permet de mieux comprendre, du point de vue fonctionnel, l'existence de ces disques.

Région gulaire des mâles: *K. cassinoides* partage avec l'espèce précédente la particularité d'avoir un sac vocal de type 2. D'après Schiøtz (1967), « The "protective flap", characteristic of the other members of the genus, is missing or very poorly developed ». Chez les individus du Cameroun la partie médiane du sac vocal (glande gulaire) est effectivement plus petite que chez les autres espèces et, surtout, son pourtour forme des bourrelets recoupés par des sillons: l'aspect qui en résulte est très semblable à celui du reste du tégument gulaire, très fortement plissé, ce qui peut donner l'impression que la partie médiane manque. De plus, il n'y a pas d'aires noirâtres à la surface du sac vocal, donc pas de fossettes de part et d'autre de la glande gulaire. Une autre particularité est que, chez les 10 mâles examinés, il n'y a pas de repli interbrachial, bien que le sac vocal s'étende loin vers l'arrière (Pl. II, Fig. e).

Tégument ventral de la femelle: il est lisse sur presque toute sa surface. Seule la partie postérieure de l'abdomen montre des granulations, ou plutôt des ridules transverses.

DISTRIBUTION, ÉCOLOGIE, PHONOCÉNOSES

Ses appels caractéristiques et audibles de loin facilitent le repérage de *K. cassinoides*. L'espèce n'a été rencontrée que dans la partie nord du Cameroun, où elle a été relevée dans 6 mailles de 10 minutes de côté (Fig. 14). Vers le sud, son aire de distribution s'arrête juste au pied du versant septentrional de l'Adamaoua (Amiet, 1972). D'autres espèces savanicoles butent aussi sur cet obstacle, qui paraît jouer le rôle de « filtre thermique »: *Phrynomantis microps*, *Hydrophylax galamensis*, *Ptychadena schubotzi*. Vers le nord, *K. cassinoides* paraît absente dans les régions de Maroua et de Mora-Waza, où de nombreuses espèces d'Anoures ont pourtant été notées dans les diverses stations prospectées. Si elle était confirmée, cette différence pourrait être d'origine climatique. La région où *K. cassinoides* a été trouvée est en effet soumise à un climat soudanien de basse altitude, avec 900 à 1500 mm de précipitations annuelles et une saison sèche de moins de 7 mois; sa végétation est constituée de savanes boisées de type méso-soudanien ou soudano-sahélien. Celle où elle paraît absente connaît des conditions climatiques plus rigoureuses, avec moins de 900 mm de précipitations et plus de 7 mois de saison sèche, ce qui se traduit par un appauvrissement de la végétation: steppes à épineux, ou prairies inondables dans la vallée du Logone.

Sur les sites de reproduction, les mâles de *K. cassinoides* ne sont jamais très nombreux, contrairement à ceux de *K. senegalensis*, les effectifs pouvant s'estimer en unités pour la première et en dizaines pour la seconde. En 1981, près de Mbé, au pied de l'Adamaoua, l'espèce était déjà bien active le 21 mai, probablement à la suite de pluies précoces, mais la période optimale d'activité se situe plutôt entre la mi-juin et la mi-juillet. Les autres espèces vocalement actives en même temps que *K. cassinoides* ont été relevées dans les six stations où l'espèce a été entendue. Celles qui ont été notées dans au moins la moitié des relevés sont les suivantes: *K. senegalensis* et *Ptychadena bibroni* (6/6), *Hoplobatrachus occipitalis* (5/6), *Phrynomantis microps*, *Phrynobatrachus natalensis* et *Leptopelis viridis* (4/6), *Ptychadena schubotzi*, *Hydrophylax galamensis* et *Afrixalus weidholzi* (3/6).

D'autres espèces peuvent définir des variantes géographiques de cette phonocénose. Dans la partie sud, plus arrosée par suite de la proximité de l'Adamaoua, s'ajoutent: *Afrixalus fulvovittatus*, *Hyperolius balfouri viridistriatus*, *Hyperolius igbettensis* et *Ptychadena oxyrhynchus*, alors que dans la partie nord ces espèces sont remplacées par *Bufo xeros*, *Ptychadena trinodis*, *Ptychadena floweri* et *Hildebrandtia ornata* (*Afrixalus vittiger* existe aussi dans ce secteur mais n'a pas été relevé dans les mêmes biotopes que *K. cassinoides*).

CONCLUSION

Cinq espèces de *Kassina* peuvent être à présent reconnues au Cameroun. Une est nouvelle pour la science et connue d'une seule localité. Deux autres, morphologiquement très proches, avaient été confondues auparavant. Quant au genre *Phlyctimantis*, il n'est représenté que par une seule espèce. Ce bilan est relativement modeste en regard de la richesse spécifique globale de la batrachofaune camerounaise (environ 200 espèces)

Un fait surprenant est l'absence d'une espèce de *Kassina* sylvicole, comparable aux *K. lamottei* ou *K. arboricola* de l'Afrique de l'Ouest. Il semble improbable qu'une telle espèce ait pu échapper aux investigations des chercheurs qui ont prospecté la zone forestière du Cameroun. Je n'en ai pas non plus trouvé trace malgré environ 1000 sorties de nuit effectuées dans tout le sud du pays.

En revanche, il est très possible que *K. fusca*, ou un taxon proche, soit représentée au Nord-Cameroun, car la faune batrachologique de cette région est relativement plus mal connue que celle de la zone forestière ou de la Dorsale.

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Redescription of *Protaphorura octopunctata* (Tullberg, 1876) and *Protaphorura quadriocellata* (Gisin, 1947) with description of two new related species from Siberia and Europe (Collembola: Onychiuridae)

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Redescription of *Protaphorura octopunctata* (Tullberg, 1876) and *Protaphorura quadriocellata* (Gisin, 1947) with description of two new related species from Siberia and Europe (Collembola: Onychiuridae). - *Protaphorura octopunctata* (Tullberg, 1876) and *Protaphorura quadriocellata* (Gisin, 1947) are redescribed based on type specimens and new materials. *Protaphorura flavorufula* (Martynova, 1976) is a junior synonym of *P. octopunctata*. *Protaphorura tolae* sp. n. and *Protaphorura saltuaria* sp. n. two new, closely related species from Yakutia and East Carpathians are described. An identification key to all Palearctic *Protaphorura* species with 4 and more pseudocelli at base of antenna is provided.

Keywords: Collembola - Onychiuridae - *Protaphorura* - taxonomy - Europe - Siberia.

INTRODUCTION

Protaphorura octopunctata (Tullberg, 1876) was described on the basis of one specimen collected in the delta of the Yenisei river near "Dudino" (at present Dudinka near Norilsk [69°24'N 86°08'E]). According to the information of Dr Kronestedt (Stockholm) there is no such specimen in the collections of the Swedish Museum of Natural History in Stockholm and in the Museum of Evolution, Uppsala University (Tullberg worked at Uppsala University). Only specimens collected during the "Yenissey-Expedition, 1876" have survived until today, labelled "Tschulkowa, *Lipura octopunctata*, Sibirien" (Chulkovo [62°45'N 88°25'E], situated on the left bank of the Yenisei river, about 45 km to the north of the Sukhaya Bakhta river mouth and Bakhta settlement) and determined by H. Schött.

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A short Latin diagnosis and three drawings (Tullberg, 1876) point out the following characters of *P. octopunctata*:

- postantennal organ consists of 30 simple vesicles, arranged perpendicularly to the long axis of the organ;
- 4 pseudocelli at base of antenna;
- claw with denticle;
- small anal spines, a little arched;
- length – 2.5 mm.

During more than one hundred years this laconic description was a basis for many faunistic records from Europe, Asia and North America (Salmon, 1964; Yosii, 1977; Christiansen & Bellinger, 1989; Jordana *et al.,* 1997; Deharveng, 2005). Most of these records also contained a redescription of the species, but none of them was based on type or topotype material. Also Martynova's (1976) records were based on the materials from Chukotka and Magadan. At present, there is no convincing redescription of this species in the literature.

Thanks to the kindness of Dr Babenko (Moscow) we have received onychiurid material collected during ecological investigation of ecosystems of northern areas of Siberia. Some of these samples come from geographically and ecologically nearby areas (ca. 225 km eastern [69°08'N 91°49'E]) of the type locality of *P. octopunctata*. Within this material we have found two *Protaphorura* species with 4 pseudocelli at the base of antenna. Because of small size of reproductive adults (less than 1.5 mm in length) one could not be identified as *P. octopunctata* and represents a new species, belonging to an other *Protaphorura* group of species. The second one we have compared with the specimens from Chulkovo (determined by Schött) and with the type material of *Protaphorura flavorufula* (Martynova, 1976) and we have ascertained that they are conspecific. The absence of other similar *Protaphorura* species in the closest neighbourhood of the delta of the Yenisei river is suggesting that *P. flavorufula* is a junior synonym of *P. octopunctata*.

Among the other Siberian materials (Yakutia) received from Dr Babenko we have found one species without pseudocelli at subcoxa, closely related to *P. octopunctata*.

Because of the presence of 4+4 pseudocelli at the antenna base *Protaphorura quadriocellata* (Gisin, 1947) is similar to *P. octopunctata* and initially the two species were confused. *Protaphorura quadriocellata* was first recorded from Switzerland by Gisin (1943) as "*Onychiurus octopunctatus* (Tullbg.) Stach (f. *daviesi* Bagn.)". In the next two publications the author gave it a subspecies rank (*Onychiurus armatus quadriocellatus*) (Gisin 1947) and subsequently species rank (*Onychiurus quadriocellatus*), and he listed the most important characters in a table (Gisin, 1952). The presence of 3+3 pseudocelli only on abdominal tergum IV (versus – 4+4 pseudocelli) is the character which makes it possible to distinguish *P. quadriocellata* from *P. octopunctata* and was used in Gisin's (1960) and Palissa's (1964) keys. At present *P. quadriocellata* is commonly accepted as a valid species and has been recorded from many European countries, viz. Austria, Great Britain, Denmark, Germany, Norway, South Russia, Slovakia, Spain, Switzerland and Ukraine (Deharveng, 2005). Only one attempt at a redescription of this species is known, but it is based on specimens from Spain, far from the type locality (Jordana *et al.,* 1997).

Thanks to the kindness of Dr Lienhard (Geneva) we had a possibility to examine the holotype of *P. quadriocellata*. Its comparison with Ukrainian specimens from the East Carpathians (Kaprus', 1999) reveals that they represent different species.

In the light of the facts presented above we have decided to redescribe of *P. octopunctata* and *P. quadriocellata*. Besides, the present work contains descriptions of two new species.

The material is deposited in following institutions:

MC	Martynova's Collection in Moscow State Pedagogical University, Moscow;
MNHG	Museum of the Natural History, Genève;
MNHU	Museum of Natural History, Ukrainian National Academy of Sciences, L'viv;
SMNH	Swedish Museum of Natural History, Stockholm;
ZIW	Department of Biodiversity and Evolutionary Taxonomy, Zoological Institute, Wrocław University, Wrocław.

SPECIES DESCRIPTIONS

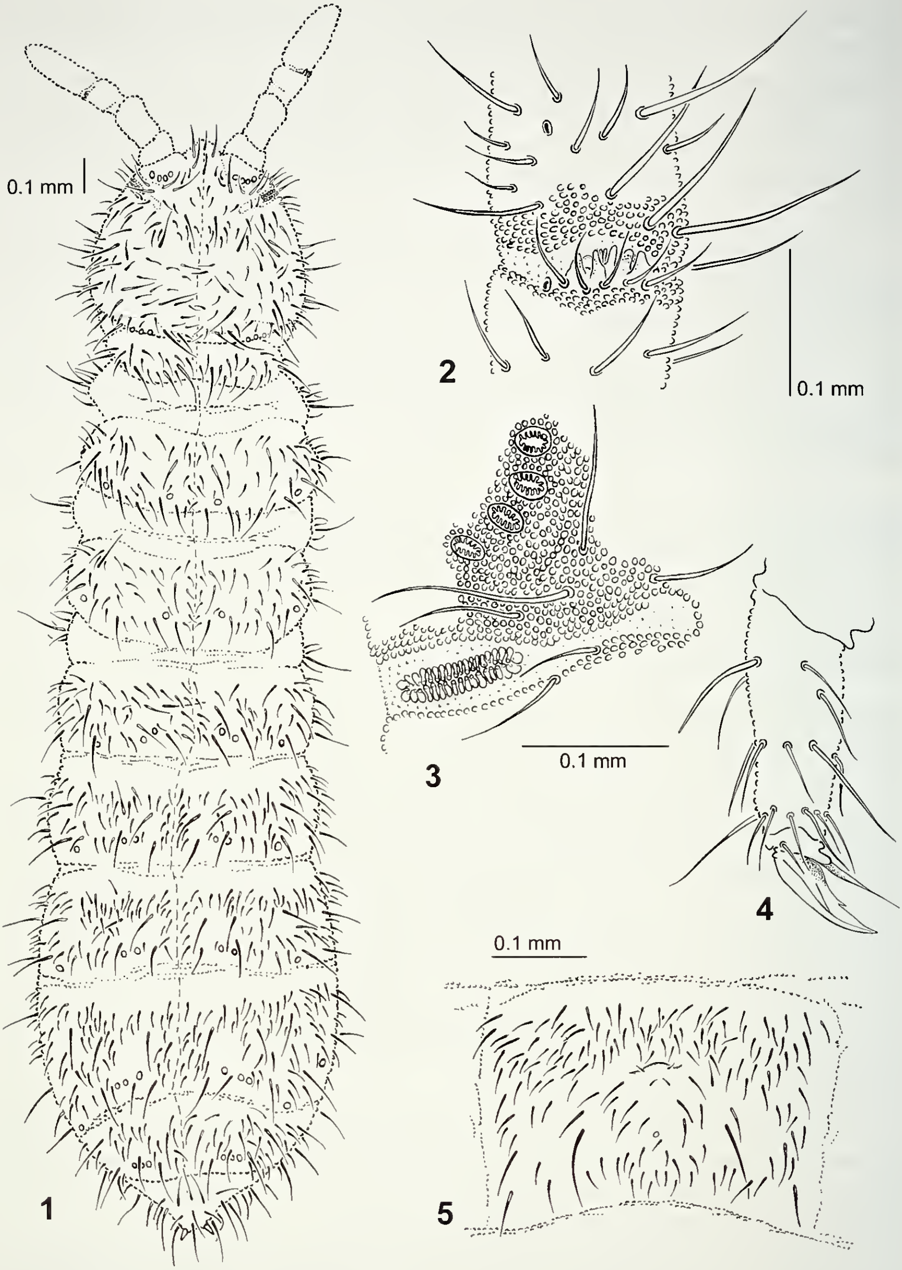
Protaphorura octopunctata (Tullberg, 1876) Figs 1-5

Bas. *Lipura octopunctata* Tullberg, 1876: 40.
Onychiurus (Protaphorura) flavorufulus Martynova, 1976 **syn. nov.**

Material: 2 unreproductive males, 6 females: Russia, Putorana Plateau, Dyngengda Mt., the *Alnetum* forest, near Sobachje Lake (Yt Kjuul') [69°08'N 91°49'E], litter, bush vegetation, 350 m alt., 27 VII 1997, leg. A. Babenko (MNHU, ZI). – 5 paratypes of *P. flavorufula* (2 unreproductive males, 3 females): Russia, Jakutia, harbor Ambartchik near Medvezhka river, 12 VIII 1972, leg. Shilov (MC). – 4 juvenile males, 2 juvenile females and 3 spp. fixed in alcohol: Russia, Krasnoyarskyi Krai, Chulkovo, the left bank of the Yenisei river (about 45 km north of the Sukhaya Bakhta river mouth and Bakhta settlement, 1876, leg. ? [62°45'N 88°25'E]) (originally labeled: *Lipura octopunctata* Tullb., Tchulkova, Jenisiejexp.76 determ. H. Schött) (SMNH). – 3 males, 5 females: Russia, Jakutia, delta of the Indigirka river, *Salix*, *Carex* and moss community on bog, 14-16 VII 1994, leg. A. Babenko. – 1 male, 1 female: Russia, Magadanskaya oblast, delta of the Kolyma river, Pokhotskaya jedoma, meadow, 18 VII 1994, leg. A. Babenko (ZIW).

Diagnosis: Within the group of *Protaphorura* with four and more pseudocelli at base of antenna *P. octopunctata* is characterized by lack of pseudocelli on subcoxa1 and yellowish orange body color. It is closely related with described below *P. tolae* sp. n. (differences – see diagnosis of *P. tolae*).

Redescription: Color in alcohol from yellowish to yellowish orange and reddish yellow. Length without antennae: males 2.5-3.1 mm, females 2.8-3.8 mm. Body shape cylindrical, with relatively small anal spines set on distinct papillae (Fig. 1). Antennae approximately as long as the head. Furca reduced to shallow cuticular pocket with 2+2 setulae – 1+1 setulae located on a cuticular fold, remaining



FIGS 1-5

Protaphorura octopunctata (Tullberg). (1) Habitus and dorsal chaetotaxy. (2) Antennal III sense organ. (3) Postantennal organ and anterior cephalic pseudocelli. (4) Tibiotarsal chaetotaxy and claw of legs III. (5) Chaetotaxy of abdominal sternum IV.

1+1 setulae located distinctly below of the fold (Fig. 5). Granulation is more or less uniform, distinct. Antennal area well marked.

Antennal segment IV with a subapical organite. Microsensillum on antennal segment IV in latero-external position, c.1/3 length from the base. Antennal segment III with microsensillum slightly below antennal III sense organ. Thoracic terga II and III with microsensilla laterally.

Antennal III sense organ built of 5 guard setae, 5 low papillae, 2 sensory rods and 2 similarly sized sensory clubs: one is morel-like distinctly granulated, the other is sponge-like (Fig. 2). Sensory rods are relatively high, reached papillae length.

Postantennal sense organ consists of 30-40 simple vesicles (Fig. 3).

Pseudocellar formula dorsally: 4(5-6)3(4)/022/3335(4)3(4-5); ventrally: 1/000/00000, all subcoxa1 without pseudocelli. Formula of parapseudocelli ventrally: 1/000/111(0)101^m, all subcoxa1 with 1 parapseudocellus ventrally.

Dorsal chaetotaxy variable with a tendency to plurichaetosis, well differentiated into macro- and microsetae as in Fig. 1. Sensilla invisible. Head without d_0, with p_2 at the same level as other p setae. Abdominal tergum V without or with seta p_0, abdominal tergum VI usually with two, sometimes with three medial setae. Straight lines, passing through bases of short setae situated above anal spines, parallel. Between legs on pro-, meso- and metathorax 1+1, 2+2 and 2+2 setae respectively. Tubus ventralis with ca. 13-19+13-19 setae and 2-3+2-3 setae at base.

Claws always with large teeth. Empodial appendage without basal lamella, appendage longer than inner edge of the claw. Tibiotarsi with 11 distal setae (Fig. 4). Male ventral organ is absent.

BIOLOGY: *P. octopunctatata* lives in humid habitats in mountains and lowlands. It has been collected in forest soil and litter and mosses, which covered the river bank and bog.

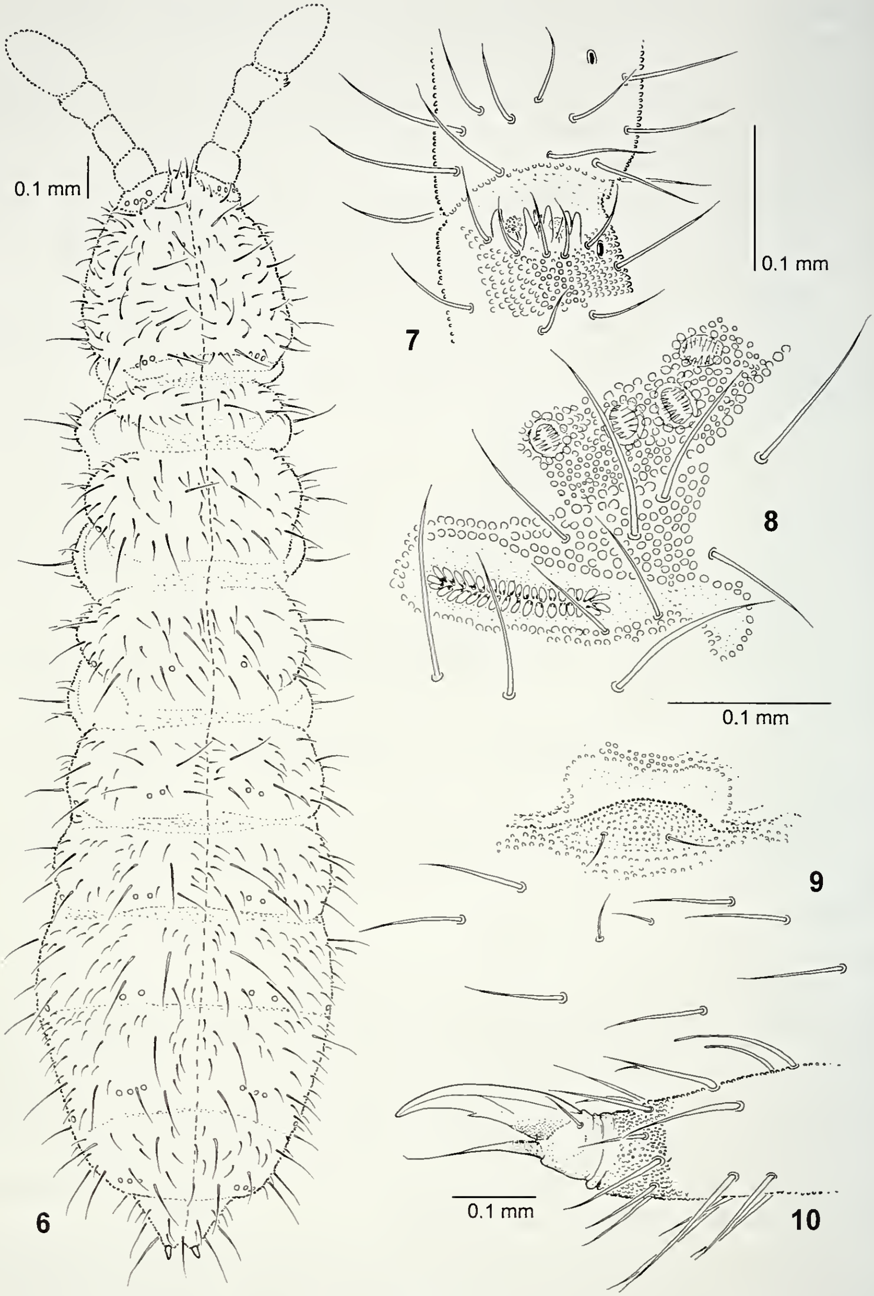
DISTRIBUTION: The species recorded from many countries, but probably most records are misidentifications. Univocal data come only from North and Middle Siberia.

Protaphorura tolae sp. n. Figs 6-10

TYPE MATERIAL: Holotype female and 14 paratypes (7 adult females, 7 unreproductive males): Russia, Yakutia, Suntar Khayata Mt. Range, upper currents of Kyubyume river (63°13'N; 139°36'E, about 250 km to the east [along the only road] of Khangyga on Aldan River), 1430 m alt., southern slope, forest edge, droppings of mouse-hare or rock rabbit (= Ochotona), 7 VII 2002, leg. O. Makarova. The type material is preserved in following collections: ZIW – holotype and 5 paratypes (3 males and 2 females), MC – 2 females and 2 males, MNHG – 1 female and 1 male, MNHU – 3 males and 2 females).

ETYMOLOGY: The species is dedicated to our friend Dr Anatolyi Babenko (Moscow), for his material and valuable help.

DIAGNOSIS: Yellowish orange body color, relatively low papillae in antennal III sense organ, a shallow cuticular pocket as a remnant of furca and particularly the absence of pseudocelli on subcoxae are suggesting a close relationship of *P. tolae* sp. n. with *P. octopunctata*. The new species distinctly differs from *P. octopunctata* in pseudocellar formula and in more symmetrical chaetotaxy, without plurichaetosis.



Figs 6-10

Protaphorura tolae sp. nov. (6) Habitus and dorsal chaetotaxy. (7) Antennal III sense organ. (8) Postantennal organ and anterior cephalic pseudocelli. (9) Remnant of furca. (10) Tibiotarsal chaetotaxy and claw of legs III.

DESCRIPTION: Color in alcohol from yellowish to yellowish orange and reddish yellow. Length without antennae: males 1.8-2.0 mm, females 2.5-2.75 mm. Body shape cylindrical, with relatively small anal spines set on distinct papillae (Fig. 6). Antennae approximately as long as the head. Furca reduced to shallow cuticular pocket with 2+2 setulae – 1+1 setulae located on a cuticular fold, remaining 1+1 setulae located distinctly below of the fold (Fig. 9). Granulation more or less uniform and distinct. Antennal area well marked.

Antennal segment IV with subapical organite. Microsensillum on antennal segment IV in latero-external position, c. 1/3 length from the base. Antennal segment III with microsensillum slightly below antennal III sense organ. Thoracic terga II and III with microsensilla laterally.

Antennal III sense organ built of 5 guard setae, 5 low papillae, 2 sensory rods and 2 similarly sized sensory clubs: one is morel-like distinctly granulated, the other sponge-like. (Fig. 7). Sensory rods relatively high, reached papillae length.

Postantennal sense organ consists of 36-40 simple vesicles (Fig. 8).

Pseudocellar formula dorsally: 43/012/332-343 (on thoracic tergum IV lack of anterolateral pseudocelli); ventrally: 1/000/00000, all subcoxal without pseudocelli. Formula of parapseudocelli ventrally: 1/000/100000, all subcoxal with 1 parapseudocellus ventrally.

Dorsal chaetotaxy rather regular, well differentiated into macro- and microsetae as in Fig. 6. Sensilla invisible. Abdominal tergum V with seta p_0, abdominal tergum VI with one medial setae. Straight lines, passing through bases of short setae which are situated above anal spines are parallel. There are 1+1, 2+2 and 2+2 setae respectively. Tubus ventralis with ca. 10-11+10-11 setae and 2+2 setae between legs on pro-, meso- and metathorax at the base.

Claws always with large teeth. Empodial appendage without basal lamella, appendage longer than inner edge of the claw (Fig. 10). Tibiotarsi with 11 distal setae. Male ventral organ is absent.

Protaphorura quadriocellata (Gisin, 1947) Figs 11-15

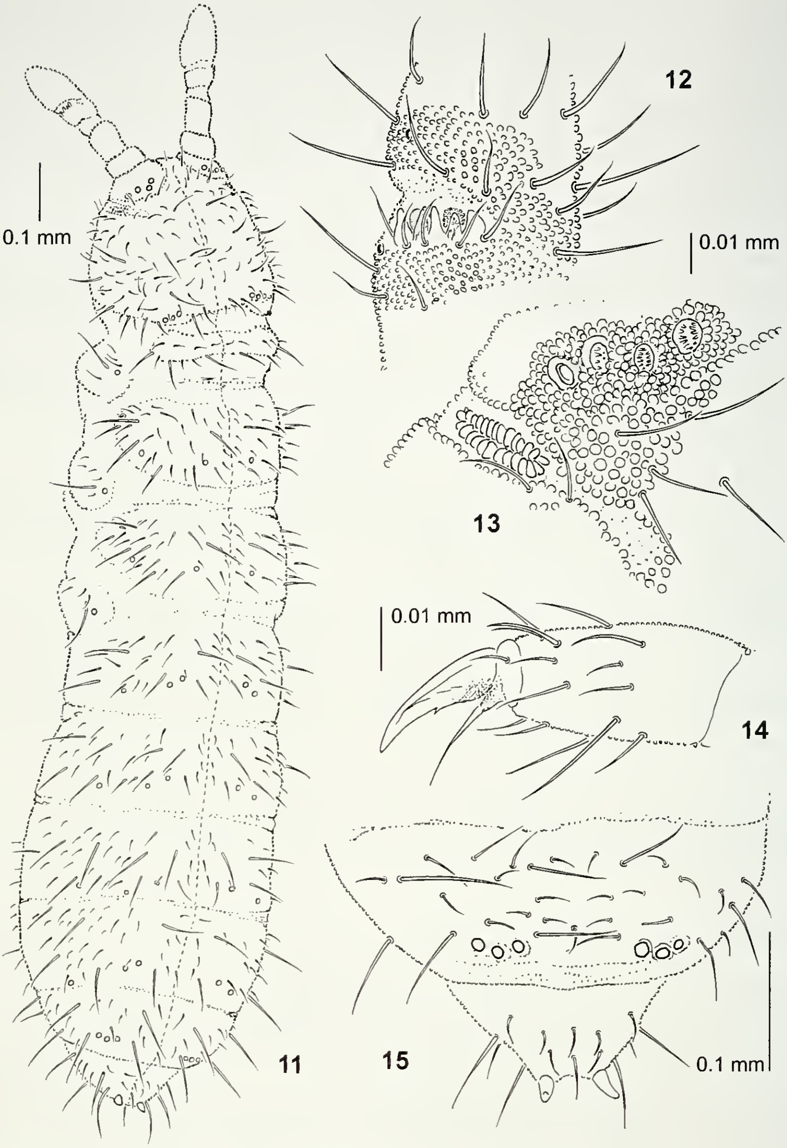
Bas. *Onychiurus armatus quadriocellatus* Gisin, 1947:

TYPE MATERIAL: Holotype – unreproductive/reproductive, moulting male, (G930) Switzerland, Langenthal (BE), *Sphagnum* in *Fagus* forest, 24 VIII 1941 (MNHG).

OTHER MATERIAL EXAMINED: 1 male, 2 females, 7 juveniles Germany, Hessen, Hochtaunus near Frankfurt am Main, litter of cultivated, mixed forest; 21 VII 2001. leg. A. Smolis (ZIW). – 5 males, 4 females, Germany, Augsburg, near Munich, litter +soil , *Fagus-Abies* forest; 15 IV 2003. leg. T. Zieche (MNHU).

DIAGNOSIS: *P. quadriocellata* belongs to the group of *Protaphorura* species with 4+4 pseudocelli at base of antenna, 2+2 pseudocelli on thoracic terga II and III and without anterolateral pseudocelli on abdominal tergum IV. It is closely related with described below *P. saltuaria* sp. n. (differences – see diagnosis of *P. saltuaria*).

REDESCRIPTION: Color white. Length without antennae: males 1.8-2.0 mm, females 2.1-2.4 mm. Body shape is cylindrical, with relatively small anal spines set on distinct papillae (Fig. 11). Antennae approximately as long as the head. Furca



FIGS 11-15

Protaphorura quadriocellata (Gisin). (11) Habitus and dorsal chaetotaxy. (12) Antennal III sense organ. (13) Postantennal organ and anterior cephalic pseudocelli. (14) Tibiotarsal chaetotaxy and claw of legs III. (15) Chaetotaxy of abdominal tergum V and VI (11 specimen from Germany; 12-15, holotype).

reduced to cuticular pocket with 2+2 setulae. Granulation more or less uniform, distinct. Antennal area well marked.

Antennal segment IV with a subapical organite. Microsensillum on antennal segment IV in latero-external position, usually at 1/3 height of antennal IV, somewhat above the second row of setae. Antennal segment III with microsensillum slightly below antennal III sense organ (Fig. 12). Thoracic terga II and III with microsensilla laterally.

Antennal III sense organ built of 5 guard setae, 5 low papillae, 2 sensory rods and 2 similarly sized sensory clubs: one is morel-like finely granulated, the other is sponge-like (Fig. 12).

Postantennal sense organ consists of 28-36 simple vesicles (Fig. 13).

Pseudocellar formula dorsally: 43(4)/022/33333; ventrally: 1/000/00000, each subcoxa1 with 1 pseudocellus. Formula of parapseudocelli ventrally: $1/000/111101^{m}$, all subcoxa1 with 1 parapseudocellus ventrally.

Dorsal chaetotaxy symmetrical, well differentiated into macro- and microsetae as in fig. 11. Sensilla invisible. Head without d_0, with p_2 shifted forward in relation to other p setae. Abdominal tergum V with seta p_0, abdominal tergum VI usually with two medial setae (Figs 11, 15). Straight lines, passing through bases of short setae situated above anal spines, parallel. Between legs on pro-, meso- and metathorax 1+1, 2+2 and 2+2 setae respectively. Tubus ventralis with ca. 13-19+13-19 setae and 2+2 setae at base.

Claws with large teeth (claw III of holotype is without teeth). Empodial appendage without basal lamella, appendage longer than inner edge of the claw. Tibiotarsi with 11 distal setae (Fig. 14). Male ventral organ absent.

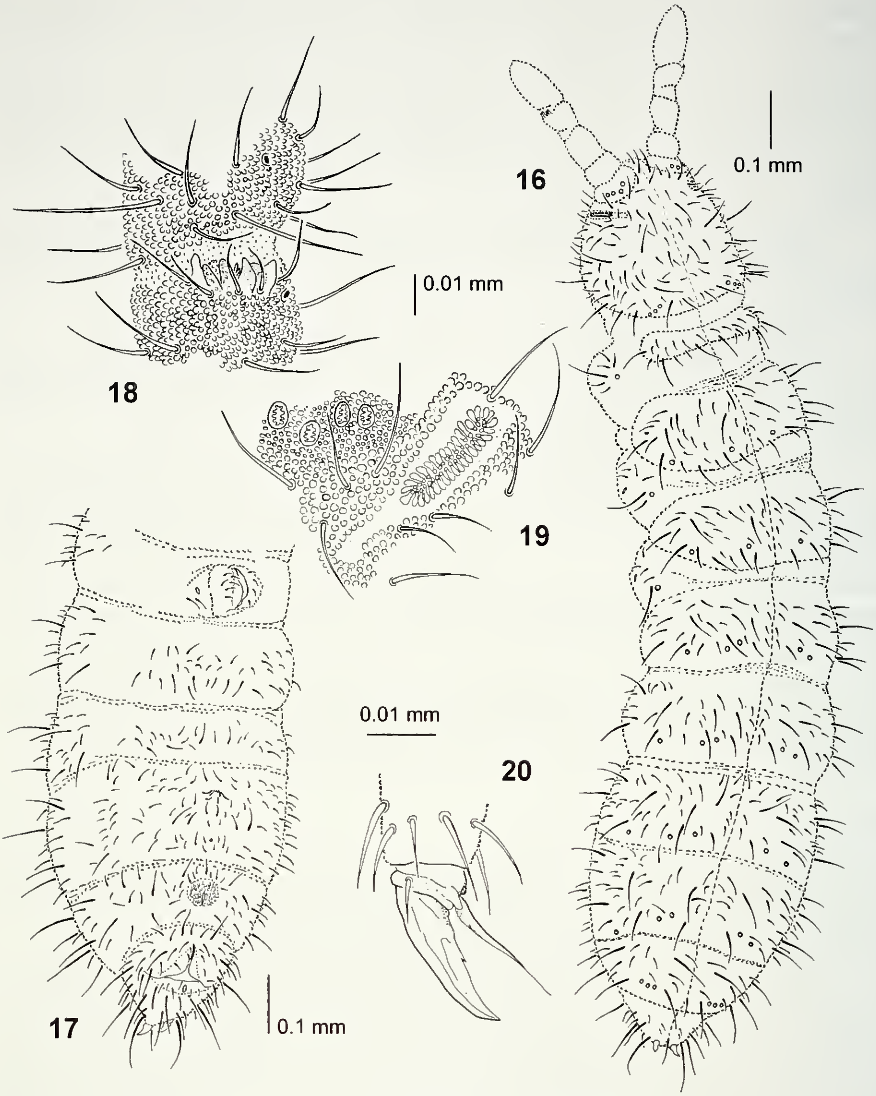
Protaphorura saltuaria sp. nov. Figs 16-20

TYPE MATERIAL: Holotype – 1 male and 14 paratypes (4 males, 10 females) Ukraine, East Carpathians, Chornoghora Mt., Vorochta, soil and litter in Piceetum forest, 1450 m alt., 24 VIII 1993, leg. I. Kaprus'. The type material is preserved in following collections: MNHU –holotype and 11 paratypes (4 males and 7 females), MNHG – 3 females.

OTHER MATERIAL EXAMINED: 3 males, 4 females, Ukraine, East Carpathians, Skolivs'ki Beskydy Mt., Kamianka, soil and litter in Fagaetum forest, 900 m alt., 25 X 1989, leg. I. Kaprus' (MNHU). – 1 male, Ukraine, East Carpathians, Chyvchyny Mt., Burkut, soil and litter of Piceetum forest, 1100 m alt., 4 VIII 1991, leg. I. Kaprus' (MNHU). – 2 males, Ukraine, East Carpathians, Chorna Mt., Vynoghradove, soil and litter in Fagaetum forest, 450 m alt., 5 IV 1989, leg. I. Kaprus' (MNHU). – 1 female, Poland, East Carpathians, Bieszczady Mt., Muczne, soil and litter in Abieto-Fagaetum forest, 650 m alt., 1 X 1996, leg. I. Kaprus' (MNHU). – 1 female, Poland, East Carpathians, Bieszczady Mt., Sękowiec, soil and litter in Abieto-Fagaetum forest, 550 m alt., 1 X 1996, leg. I. Kaprus' (ZIW).

ETYMOLOGY: The species name is derived from the Latin word "saltus" – mountain forest.

DIAGNOSIS: Because of the presence of pseudocelli on all subcoxa and the same dorsal pseudocellar formula *P. saltuaria* sp. n. is closely related with *P. quadriocellata*. This new species distinctly differs from *P. quadriocellata* in the lack of parapseudocelli on abdominal sterna II-IV, in the presence of only one medial seta in



FIGS 16-20

Protaphorura saltuaria sp. nov. (16) Habitus and dorsal chaetotaxy. (17) Chaetotaxy of abdominal sterna I-VI. (18) Antennal III sense organ. (19) Postantennal organ and anterior cephalic pseudocelli. (20) Distal part of leg III.

abdominal tergum VI and in location of p_2 seta on the head. *P. quadriocellata* has parapseudocelli on all abdominal sterna, p_2 seta in anterior position and usually has two medial setae on abdominal tergum VI.

DESCRIPTION: Color in alcohol yellowish white. Length without antennae: males 1.8-2.0 mm, females 1.7-2.2 mm. Body shape cylindrical, with strong anal spines set on distinct papillae (Fig. 16). Antennae approximately as long as the head. Furca reduced to cuticular pocket with 2+2 setulae. Granulation more or less uniforms and distinct. Area antennalis well marked.

Antennal segment IV with a subapical organite. Microsensillum on antennal segment IV in latero-external position, c. 1/3 length from the base. Antennal segment III with microsensillum slightly below of antennal III sense organ. Thoracic terga II and III with microsensilla laterally.

Antennal III sense organ consists of 5 guard setae, 2 sensory rods, 2 straight and granulated sensory clubs and 5 papillae (Fig. 18).

Postantennal sense organ consists of 35-42 simple vesicles (Fig. 19).

Pseudocellar formula dorsally: 4(3)3/022/33333; ventrally: 1/000/00000, all subcoxa1 with pseudocellus. Formula of parapseudocelli ventrally: $1/000/100001^{m}$, all subcoxa1 with 1 parapseudocellus. Position of pseudocelli and parapseudocelli is presented in Figs 16 and 17.

Dorsal chaetotaxy, usually symmetrical, well differentiated into macrochaetae and microchaetae as in fig. 16. Sensilla weakly marked. Head without seta d_0, with p_2 at the same level as other p-setae. Abdominal tergum V with seta p_0, abdominal tergum VI with one medial seta. Straight lines, passing through bases of short setae with are situated above anal spines, parallel. There are 1+1, 2+2 and 2+2 setae between legs on pro-, meso- and metathorax, respectively. Tubus ventralis with ca. 9+9 setae and 2+2 setae at the base. Ventral abdominal chaetotaxy as in Fig. 17.

Claws are with small teeth. Empodial appendage without basal lamella, slightly longer than inner edge of the claw. Tibiotarsi with 11 distal setae (Fig. 20). Male ventral organ absent.

BIOLOGY: *P. saltuaria* lives in humid litter and soil of beech and spruce forests of the Eastern Carpathians.

A KEY TO THE PALEARCTIC *PROTAPHORURA* SPECIES WITH 4 AND MORE PSEUDOCELLI AT BASE OF ANTENNA

1 Subcoxae1 of I, II and III pair of legs without pseudocelli 2
- Subcoxae1 of I, II, and III pair of legs with 1, 0, 0 pseudocelli respectively . . 3
- Subcoxae1 of I, II, and III pair of legs with 1, 1, 1 pseudocelli respectively . . 4

2 Pseudocellar formula dorsally: 4-63-4/022/3334-53-5 dorsomedial pseudocelli on thoracic tergum I and anterolateral pseudocelli on abdominal tergum IV present . . . . *P. octopuntata* (Tullberg, 1876) North Asiatic part of Russia
- Pseudocellar formula dorsally: 43/012/332-343, on thoracic tergum I lack of dorsomedial pseudocelli, on thoracic tergum IV lack of anterolateral pseudocelli . . . . *P. tolae* sp. n. Russia: Jacutia

3 Pseudocellar formula dorsally: 43/022/33342, claw with strong denticle . . . . *P. mongolica* (Martynova, 1970) Mongolia
- Pseudocellar formula dorsally: 43/022/33343, claw without or rarely with very small denticle . . . . *P. serbica* (Loksa & Bogojevic, 1976)

Central and South East Europe, Caucasus Mts., Crimea Mts., Kazakhstan, Tadzhykistan, South Siberia

4 Thoracic terga II-III with 3+3 and 3+3 pseudocelli respectively
. . . . *P. pseudocellata* (Naglitsch, 1962)
Great Britain, Czech Republic, Germany, Poland, Ukraine

- Thoracic terga II-III with 2+2 and 3+3 pseudocelli respectively 5
- Thoracic terga II-III with 2+2 and 2+2 pseudocelli respectively 6

5 Pseudocellar formula dorsally: 54/023/454-75-65
. . . . *P. decempunctata* (Kos, 1939) Slovenia

- Pseudocellar formula dorsally: 44/023/34353
. . . . *P. caledonica* (Bagnall, 1937) Great Britain
- Pseudocellar formula dorsally: 43/023/44453 . . . . *P. macfadyeni* (Gisin, 1953)
Denmark, Finland, Germany, Iceland, Norway, Jan Mayen & Svalbard, Sweden

6 Abdominal tergum IV without anterolateral pseudocelli 7

- Abdominal tergum IV with anterolateral pseudocelli 9

7 Head with 4+4 posterior pseudocelli; pseudocellar formula dorsally: 44/022/33333 . . . . *P. suboctopuntata* (Khanislamova, 1986) Russia: Bashkiria

- Head with 3+3 posterior pseudocelli; pseudocellar formula dorsally: 43/022/33333 8

8 Abdominal sterna II-IV with 1+1 parapseudocelli
. . . . *P. quadriocellata* (Gisin, 1947)
Austria, Great Britain, Denmark, Germany, Norway, Slovakia, South Russia, Spain, Switzerland

- Abdominal sterna II-IV without parapseudocelli
. . . . *P. saltuaria* sp. n. Ukraine, Poland

9 Sensory rods of antennal III sense organ higher than accompanying papillae, the first one is located at external surface of base of first internal papilla, the second one located between of third and fourth papillae; pseudocellar formula dorsally: 43/022/33353(4)
. . . . *P. nutak* (Yosii, 1972) Japan, Far East of Russia

- Sensory rods of antennal III sense organ shorter than accompanying papillae and arranged typical, closely together, behind of papillae in the middle part of the organ 10

10 Males with ventral organ 11

- Males without ventral organ 12

11 Males ventral organ located between abdominal sterna II and III; pseudocellar formula dorsally:43/022/3334-33
. . . . *P. janstachi* (Yosii, 1972) Russia: Caucasus

- Males ventral organ located between abdominal sterna III and IV; pseudocellar formula dorsally: 44-3/022/3335(4,6)3
. . . . *P. eichhorni* (Gisin, 1954) Luxemburg

12 Pseudocellar formula dorsally: 43/022/46655
. . . . *P. asensitiva* (Stach, 1954) Slovenia

- Pseudocellar formula dorsally: 43/022/33353
. . . . *P. valsainensis* (Acón, 1981) Spain

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Cestodes of the genus *Biuterina* Fuhrmann, 1902 (Cyclophyllidea: Paruterinidae) from passeriform and piciform birds in the Ivory Coast, with a key to the species of the genus

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Cestodes of the genus *Biuterina* Fuhrmann, 1902 (Cyclophyllidea: Paruterinidae) from passeriform and piciform birds in the Ivory Coast, with a key to the species of the genus.- On the basis of recently collected material from the Ivory Coast (République de Côte d'Ivoire) and other specimens from the collections of Geneva Natural History Museum, we review the species of *Biuterina* (Paruterinidae) known from that country. Five species are recorded, among which two are new: *B. pogoniuli* sp. n. from *Pogoniulus scolopaceus* (Piciformes: Capitonidae) and *B. petroniae* sp. n. from *Petronia dentata* (Paseriformes: Ploceidae). *B. africana* Joyeux & Baer, 1928, from *Tchagra* spp. (Passeriformes: Laniidae), is redescribed on the basis of the type material from Benin, as well as of specimens from Angola, Guinea and the Ivory Coast. The species is reported for the first time from the latter two countries. *B. pentamyzos* (Mettrick, 1960) from *Prionops plumata* in Zimbabwe is recognised as a synonym of *B. africana* (new synonymy). *B. cordifera* Murai & Sulgostowska, 1983 and *B. triangula* (Krabbe, 1869) are reported from new hosts (*Acrocephalus arundinaceus* and *Anthus leucophrys gouldii*, respectively) and for the first time in Africa. An identification key to the 34 species of *Biuterina* presently recognized worldwide is given.

Keywords: Parasite - helminths - Paruterinidae - Biuterina - Africa - Ivory Coast - systematics - morphology - Laniidae - Ploceidae - Capitonidae - Sylviidae - Motacillidae.

INTRODUCTION

Biuterina Fuhrmann, 1902 comprises cestode parasites from passeriform and coraciiform birds; the number of the included species is considered to be between 30 and 40 depending on the generic definition adopted or on the views on the species validity (Matevosyan, 1969; Bona & Maffi, 1984; Schmidt, 1986; Kornyushin, 1989;

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Mariaux & Vaucher, 1989; Georgiev & Kornyushin, 1994; Georgiev *et al.*, 2002, 2004). The species diversity of this genus is relatively well studied in temperate latitudes (e.g., Matevosyan, 1969; Kornyushin, 1989; Georgiev *et al.*, 2004). However, most of the tropical *Biuterina* spp. are known from single records only. Five of the six species originally described from Afrotropical birds were recently redescribed (Mariaux & Vaucher, 1989; Georgiev *et al.*, 2002), but data on their geographical distribution and host ranges remained scarce. The only extensive faunistic survey on avian cestode in Africa during the last 20 years was carried out in the Ivory Coast (for summarised data, see Mariaux, 1994); however, some of the paruterinid species remained identified only at the generic level and their detailed taxonomic description required additional studies.

The aim of the present article is to report new data on the morphology and taxonomy of *Biuterina* spp. collected from birds in the Ivory Coast, West Africa. In addition, we provide an identification key to the species of the genus.

MATERIAL AND METHODS

In total, 1,252 birds belonging to 174 species, 104 genera and 39 families were studied in the Ivory Coast by one of the present authors (JM) during 1985-1988 (for more detailed data, see Mariaux, 1994). Birds were captured with mist nets or shot. They were dissected immediately after death. Cestodes were removed from guts and fixed in 5% hot formalin. They were stored in 70% ethanol, stained in alcoholic hydrochloric carmine, dehydrated in ethanol series, cleared in clove oil and mounted in Canada balsam. Some scoleces were mounted in Berlese's medium to facilitate the examination of the rostellar hooks. The specimens were deposited in the Invertebrate Collection of the Natural History Museum, Geneva (MHNG). Details on their collection data and number of specimens are given in the text for each species.

The metrical and meristic data are presented as the range, with the mean in parentheses and the number of measurements or counts taken (n). The measurements are given in micrometres unless otherwise stated. The developmental stages of the proglottides are designated as previously described (Georgiev & Vaucher, 2001). The nomenclature for the birds follows Howard & Moore (1980).

TAXONOMIC PART

Biuterina africana Joyeux & Baer, 1928

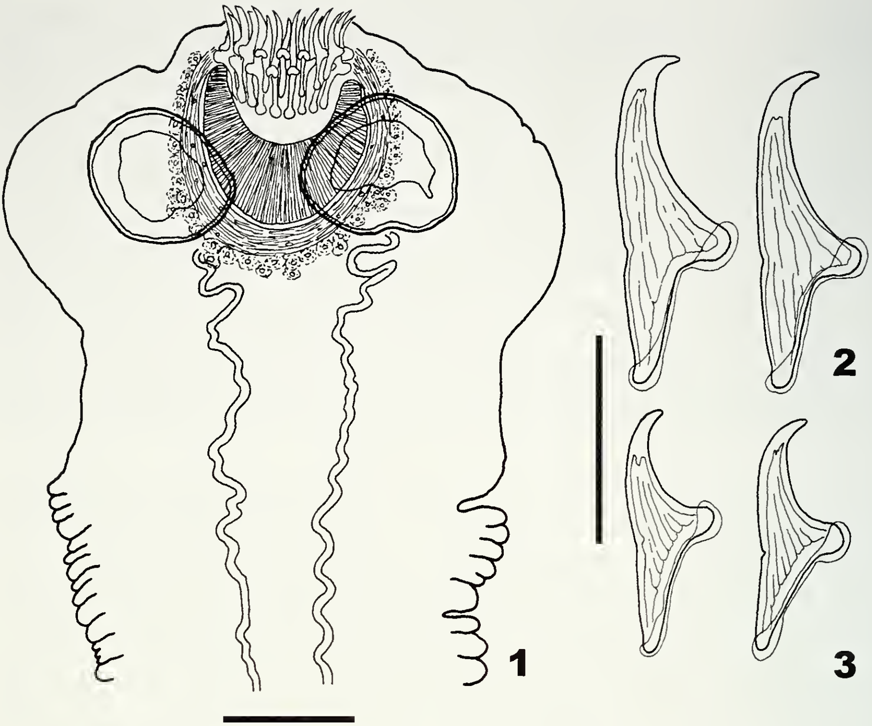
Paruterina pentamyzos Mettrick, 1960, new synonymy
Biuterina pentamyzos (Mettrick, 1960) Matevosyan, 1964

MATERIAL EXAMINED: MHNG INVE 44454-44455 (Collection Joyeux, nos CJ 28/73a and CJ 28/74a), 2 slides, labelled "*Biuterina africana*, *Telephonus senegalus*, Gendre", one of them containing a stained scolex squashed in Canada balsam, and the other containing three stained pregravid specimens in Canada balsam; recognised here as syntypes of *B. africana* (see Remarks); from *Tchagra senegala* (synonyms *Pomatorhynchus senegalus*, *Telephonus senegalus*) (Passeriformes: Laniidae) collected at Bohicon, Benin by E. Gendre (see Joyeux & Baer, 1928); substantial parts of strobila contracted. – MHNG INVE 44456 (Collection Joyeux, nos CJ 28/75a and CJ 28/78), 2 slides, labelled "*Biuterina africana*, *Telephonus senegalus*, Gendre, Labé", containing longitudinal sections of strobilar fragments of mature and postmature proglottides; from *Tchagra senegala* collected at Labé, Guinea by E. Gendre; these specimens were not mentioned in the publications of Joyeux. – MHNG INVE 40301 (Collection Fuhrmann - Baer nos 20/60-63), 4 slides, labelled "*Biuterina africana*, pie grièche, Angola" (two slides) or "*Biuterina africana*, *Pomatorhynchus*, Angola" (2 slides); mentioned by Fuhrmann (1943). Exact host names are not given in the labels; according to Fuhrmann (1943), *B. africana* was recorded in Angola from *Pomatorhynchus australis* (Smith) [now *Tchagra australis* (Smith)], *Pomatorhynchus senegalus* (L.) [now *Tchagra senegala* (L.)] and *Pomatorhynchus anchietae* (Bogage) [now *Tchagra minuta anchietae* (Bocage)] (Passeriformes, Laniidae). – MHNG INVE 16117 (former no 988.414, see Mariaux, 1994), 4 slides (2 fragmented specimens stained in hydrochloric carmine and mounted in Canada balsam and 2 scoleces mounted in Berlese's medium), from *Tchagra senegala pallida* (Neumann) (Passeriformes: Laniidae), collected at Tortyia, Ivory Coast, on 10 February 1987, by J. Mariaux; mentioned by Mariaux (1994). The host specimen has been deposited in the Ornithological Collection of the MHNG, no. 1768.047.

RE-DESCRIPTION OF THE SYNTYPES: Pregravid specimens with band-like body, 11.2-14.2 mm (12.4 mm, n =3) long, consisting of 106-114 (109, n=3) proglottides; contracted, single specimen with relaxed portions of strobila; maximum width at pregravid proglottides, 612-734 (654, n = 3). Scolex wider than neck, laterally rounded, with maximum width at middle of suckers, 385-450 (420, n = 3) (Fig. 1). Suckers oval, 115-130 (121, n = 7) in diameter, with well-developed musculature; in single specimen, inner surface of suckers with punctiform spines (not distinct in remaining specimens). Rostellum sucker-like, retracted in all available specimens, with diameter 125-145 (133, n = 3); vertical muscular fibres inside distinct. Thick layer of radial muscular fibres surround rostellum (Fig. 1); glandular cells surround radial musculature. Rostellar hooks arranged in 2 regular rows; 2 of 4 available scoleces had missing rostellar hooks and others had densely packed hooks, for which exact number is difficult to determine but there are at least 38. Each hook with epiphyseal thickening on both handle and guard. Anterior hooks 75-80 (78, n = 12) long; blade longer than handle (Fig. 2). Posterior hooks 55-60 (58, n = 12) long; blade shorter than handle (Fig. 3). Rostellar hooks with blades directed anteriorly when rostellum is retracted. Genital pores irregularly alternating in short series, e.g. ... 2, 1, 3, 1, 2, 1, 2, 5, 1, 2, 2, 2; pores open about middle of lateral proglottis margin. Genital atrium represented by infundibular distal part with thick walls and tubular proximal part surrounded by aggregation of glandular cells (Fig. 5). Dorsal osmoregulatory canals 5-8 (n = 10) in diameter; ventral osmoregulatory canals with diameter 13-38 (n = 10), with transverse anastomoses along posterior proglottis margin. Genital ducts pass between osmoregulatory canals.

Testes 10-14 (11, n = 15) in number, oval, form compact group in posterior most part of median field, posterior, dorsal and lateral to vitellarium and posterior and lateral to ovary, may overlap posterior margins of ovary dorsally (Fig. 4). External vas deferens coiled, with diameter 5-8 (7, n = 10), forms dense body in anterior poral part of median field together with surrounding glandular cells. Cirrus-sac highly elongate, 193-225 x 27-41 (215 x 33, n = 10), mostly cylindrical, tapered porally and rounded antiporally, thick-walled, usually crosses poral osmoregulatory canals. Internal vas deferens coiled. Evaginated cirrus not observed; minute (>1 μm long) triangular spines present in canal of withdrawn cirrus.

Ovary 110-145 (122, n = 10) wide, symmetrical, consisting of 2 compact rounded wings. Vitellarium compact, oval, 42-60 (52, n = 10) in diameter, at some distance from posterior proglottis margin (Fig. 4). Mehlis' gland indistinct. Seminal receptacle elongate, situated dorsally, mostly between wings of ovary, extends from



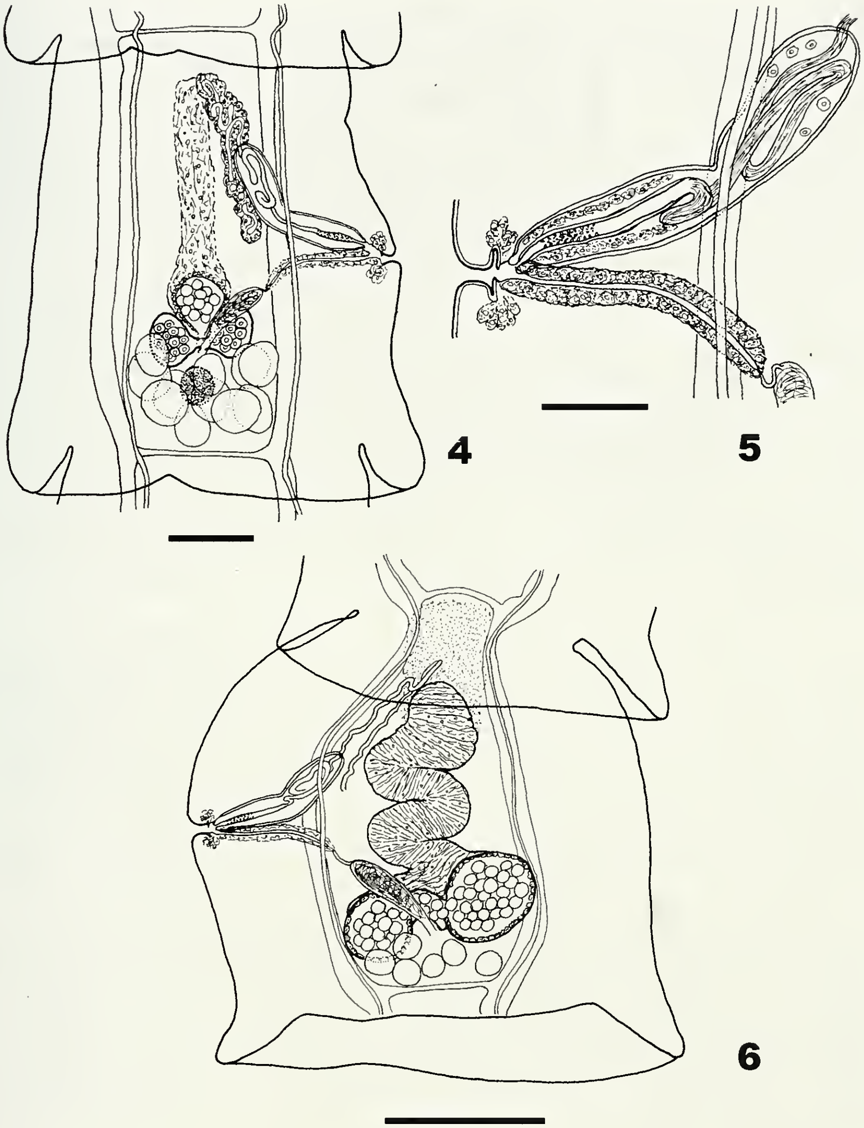
Figs 1-3

Biuterina africana Joyeux & Baer, 1928, syntypes from *Tchagra senegala* in Benin. (1) Scolex. (2) Anterior rostellar hooks. (3) Posterior rostellar hooks. Scale bars: 1, 100 μm; 2, 3, 50 μm.

poral part of median field at level anterior to ovary to level of vitellarium, 105-118 x 28-33 (112 x 30, n = 7). Vagina opens postero-laterally to male pore, with copulatory part 138-180 (169, n = 7) long and 18-23 (20, n = 10) in diameter, consisting of thick-walled vaginal canal and cellular sleeve along entire length, with diameter of lumen 4-7 (6, n = 7), wider at poral end; conductive part of vagina short, narrow.

Uterus in mature proglottides sac-like, spherical or with slightly irregular shape, thick-walled (Fig. 4). Primordium of paruterine organ appears as consolidation of central part of medullary parenchyma anterior to uterus. In pregravid proglottides, uterus consists of 2 sacs connected by transverse isthmus; paruterine organ elongate, may be slightly convoluted, with tapering anterior end surrounded by granular tissue (Fig. 6). No fully-developed eggs in specimens available.

Description of the material from the Ivory Coast: Strobila band-like, gradually widening in posterior direction, with maximum width 751-848 (n = 2) at level of pregravid proglottides. Scolex rounded, wider than neck, with conical anterior protrusion (Fig. 7); maximum width 372-437, at middle of suckers. Suckers oval, 130-161 (144, n = 8) in diameter, with developed musculature; their inner surface provided punctiform spine-like structures in transverse rows (Fig. 7, 12). Rostellum sucker-like,



Figs 4-6

Biuterina africana Joyeux & Baer, 1928, syntypes from *Tchagra senegala* in Benin. (4) Mature proglottis, dorsal view. (5) Genital ducts in a mature proglottis, dorsal view. (6) Gravid proglottis. Scale bars: 4, 6, 200 μm; 5, 50 μm.

with diameter 148 (n = 1) when retracted and 186 (n = 1) when protruded. Rostellum surrounded by thick layer of radial muscular fibres and intensely staining glandular cells (Fig. 7). Rostellum armed with 38 (n = 3) or 42 (n = 1) rostellar hooks arranged in 2 regular rows. Each hook provided with epiphyseal thickening on both handle and guard. Anterior hooks 82-85 (83, n = 6) long, with length of refractive particle 81-82;

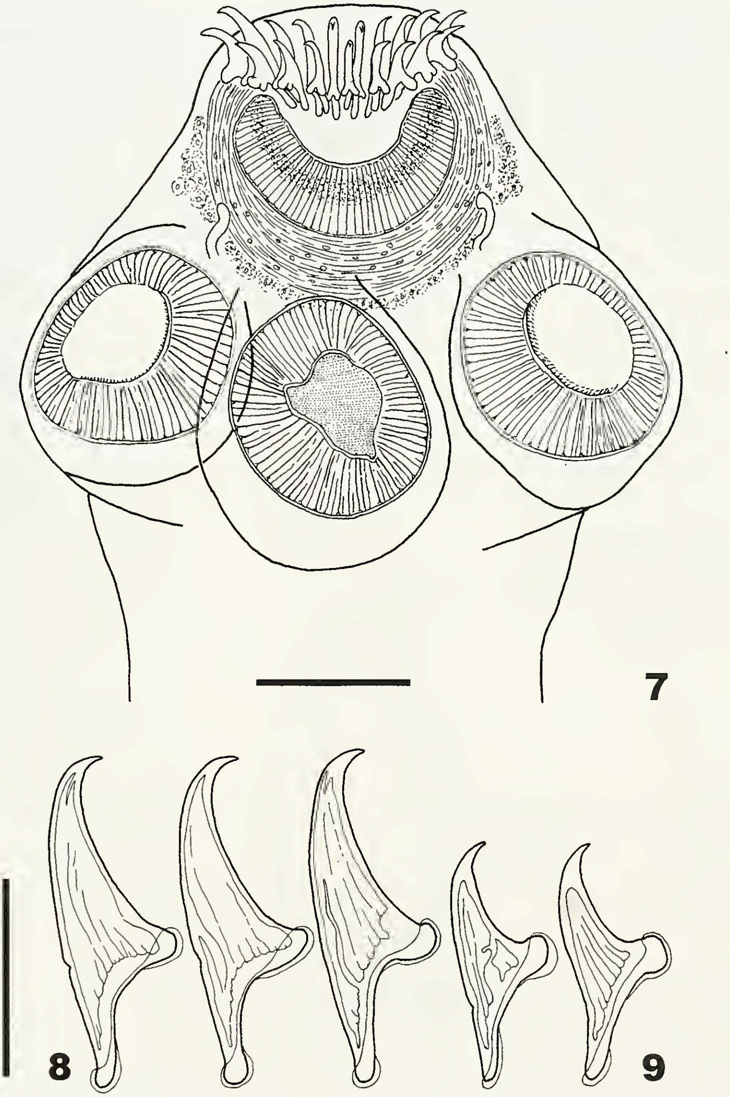
blade longer than handle (Fig. 8). Posterior hooks 61-63 (62, n = 6) long, with length of refractive particle 58-60; blade shorter than handle (Fig. 9). Proglottides craspedote; mature proglottides wider than long (Fig. 10); gravid proglottides slightly longer than wide (Fig. 11). Genital pores irregularly alternating in short series, open about middle of lateral proglottis margin. Genital atrium consists of infundibular thick-walled orifice and tubular hermaphroditic canal surrounded by intensely staining cells. Dorsal osmoregulatory canals 4-8 (n = 10) in diameter. Ventral osmoregulatory canals with diameter 22-47 (n = 10), with transverse anastomoses along posterior margin of each proglottis. Genital ducts between poral osmoregulatory canals.

Testes 10-15 (12, n = 11) in number, oval, situated in compact group posterior, dorsal and lateral to vitellarium and posterior and lateral to ovary, may overlap posterior margins of ovary (Fig. 10). External vas deferens coiled, with diameter 5-12 (7, n = 10), together with surrounding intensely stained cells forming dense body in anterior poral part of median field. Cirrus-sac highly elongate, 171-232 x 30-37 (201 x 34, n = 10), mostly cylindrical, with tapering poral end and rounded antiporal end, thick-walled; in mature proglottides, usually cross poral osmoregulatory canals; in gravid proglottides, often entirely situated in lateral field or slightly crossing poral osmoregulatory canals. Internal vas deferens coiled. Evaginated cirrus not observed; minute (length < 1 μm) triangular spines with pointed tips seen in canal of withdrawn cirrus.

Ovary consisting of 2 compact symmetrical wings. Vitellarium compact, oval, 51-69 (62, n = 10) in diameter, at some distance from posterior proglottis margin (Fig. 10). Mehlis' gland not observed as glandular structure. Seminal receptacle elongate, situated mostly dorsally between wings of ovary, extends from poral part of median field at level anterior to ovary to level of vitellarium. Vagina opens posterolaterally to male orifice, with copulatory part 174-223 (193, n = 7) long, 14-23 (18, n = 10) in diameter, consisting of thick-walled vaginal canal and thick cellular sleeve along entire length; poral part of vaginal canal wider, covered with distinct microtriches; conductive part of vagina short and thin.

Uterus in mature proglottides sac-like, spherical or with irregular shape, thick-walled (Fig. 10). Primordium of paruterine organ appears as consolidation of central part of medullary parenchyma anterior to uterus. In pregravid and gravid proglottides, uterus consists of 2 sacs connected by thin transverse isthmus; paruterine organ elongate, with tapering anterior end surrounded by granular tissue (Fig. 11). Eggs oval; outer envelopes thin, often not distinct. Embryophore oval, thick, with diameter 40-45 (43, n = 10). Oncosphere oval, with diameter 28-34 (31, n = 10). Embryonic hooks: central pairs 19-21 (20, n = 7) long; lateral pairs 16-18 (17, n = 10) long.

REMARKS: *Biuterina africana* Joyeux & Baer, 1928 was described from *Tchagra senegala* (L.) (Passerifomes, Laniidae) at Bohicon, Benin (Joyeux & Baer, 1928). Subsequently, it was recorded from the type host in Angola (Fuhrmann, 1943) and the Ivory Coast (Mariaux, 1994), and also from two other species of *Tchagra* Lesson, *T. minuta* (Hartlaub) and *T. australis*, in Angola (Fuhrmann, 1943). The only information on its morphology is the brief original description (Joyeux & Baer, 1928). We found substantial differences between the material from the Ivory Coast and the original description in relation to the size of the rostellar hooks. Other characters were

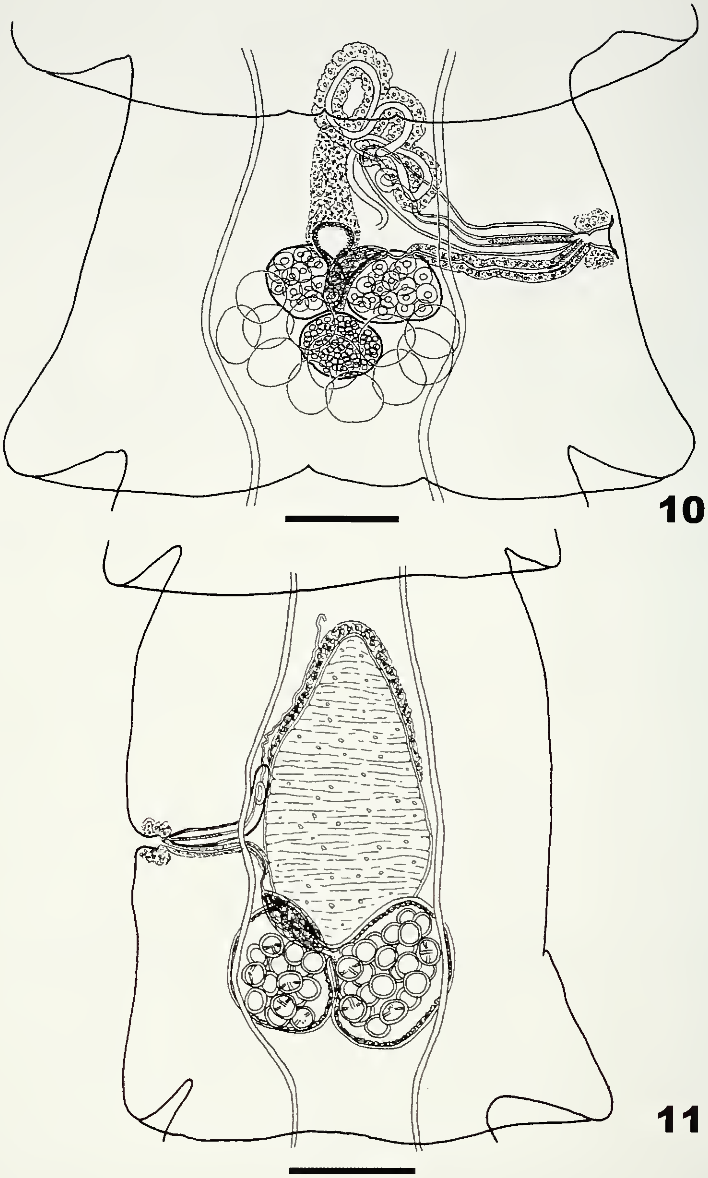


Figs 7-9

Biuterina africana Joyeux & Baer, 1928, material from the Ivory Coast. (7) Scolex. (8) Anterior rostellar hooks. (9) Posterior rostellar hooks. Scale bars: 7, 100 μm; 8, 9, 50 μm.

difficult to compare because the original description is illustrated with drawings of the scolex and rostellar hooks only; few strobilar characters are described and none of them illustrated. This provoked the present redescription of the type material.

None of the specimens of *B. africana* in the Collection of C. Joyeux (currently deposited in the MHNG) is indicated as type material. We examined 4 slides from the type host «*Telephonus senegalus*» and recognised as syntypes two slides, MHNG



Figs 10-11

Biuterina africana Joyeux & Baer, 1928, material from the Ivory Coast. (10). Mature proglottis, dorsal view. (11) Gravid proglottis. Scale bars: 10, 100 μm; 11, 200 μm.

44454 and MHNG 44455 (Collection Joyeux nos CJ 28/73a and CJ 28/74a), since their labels are concordant with the information included in the paper containing the original description (Joyeux & Baer, 1928). The other two slides of *B. africana* in Joyeux' collection, MHNG 44456 (Collection Joyeux nos CJ 28/75a and CJ 28/78), contain sectioned strobilar fragments of the same species; however, according to the labels, they were collected at Labé (Guinea) and therefore do not belong to the type series.

Our study revealed discrepancies in the original description in relation to the length of the posterior rostellar hooks and the number of the testes (Table 1). In addition, we found that the most developed specimens of the type series were pregravid; therefore, the original measurements of the body length and the diameter of the eggs are not reliable. The material from the Ivory Coast corresponds well with the morphology of the type series; some differences in the measurements of the rostellum and suckers are probably due to the different state of the material (rather contracted type specimens versus relaxed specimens from the Ivory Coast).

We confirm the identification of Fuhrmann's (1943) material from Angola, although we are not sure of the identity of the host species of the available specimens. Their morphology corresponds well with that of the type series, including to the respective metrical and meristic data (Table 1).

The new morphological data on *B. africana* enables a re-evaluation of the validity of another Afrotropical species of *Biuterina*, *B. pentamyzos* (Mettrick, 1960), a parasite of *Prionops plumata poliocephala* Shaw (Passeriformes, Laniidae) in Zimbabwe (Mettrick, 1960). Its type material was recently redescribed (Georgiev *et al.*, 2002). The morphology of the scolex and both mature and uterine proglottides of *B. pentamyzos* entirely corresponds to the present redescription of *B. africana*, including the metrical data (Table 1). The difference in the body dimensions is due to taking measurements from a fully-developed (gravid) and well-relaxed specimen from the type series of *B. pentamyzos* (see Georgiev *et al.*, 2002) compared with the rather contracted and not fully-developed syntypes of *B. africana*. Therefore, we recognise *B. pentamyzos* as a junior synonym of *B. africana*.

Georgiev *et al.* (2002) reported the presence of an armature on the inner surface of the suckers of *B. pentamyzos* consisting of "fine, punctiform, spine-like structures in transverse rows". This is distinct in the material from the Ivory Coast (Fig. 12). However, it is hardly seen in one of the syntypes of *B. africana* and not distinct in the remaining specimens, probably because of the contracted condition of the scoleces resulting in a highly folded internal surface of suckers.

Matevosyan (1969) mentioned Tunisia as the only locality for *B. africana*. However, we did not find any published record of the species from that country. Summarising the above data, the geographical range of *B. africana* includes Guinea, the Ivory Coast, Benin (type locality), Angola and Zimbabwe; its hosts are restricted to birds of the family Laniidae: *Tchagra senegala* (type host), *T. australis*, *T. minuta* and *Prionops plumata*.

Biuterina cordifera Murai & Sulgostowska, 1983

MATERIAL EXAMINED: MHNG INVE 15927 (formerly no. 987.273, see Mariaux, 1994), 1 slide (fragments of 2 specimens), 14 January 1987, host collection number CI 440 and MHNG INVE 15928 (formerly no. 987.274, see Mariaux, 1994), 1 slide (fragments of 2 specimens), 15 January 1987, host collection number CI 447, from *Acrocephalus arundinaceus* (L.) (Passeriformes, Sylviidae), collected at Adiopodoumé. One of the host specimens (CI 447) has been deposited in the Ornithological Collection of the MHNG, no. 1769.041.

DESCRIPTION: Strobila gradually widening posteriorly; maximum width at level of gravid proglottides 559-578 (n = 2). Scolex (Fig. 13) rounded, with maximum width

TABLE 1. Comparison of some metrical and meristic data for *Biuterina africana* Joyeux & Baer, 1928 and its synonym *B. pentamyzos* (Mettrick, 1960).

Species Host Locality Source	*B. africana* *Tchagra senegala* Benin Joyeux & Baer (1928)	*B. africana* *Tchagra senegala* Benin Present study	*B. africana* *Tchagra* spp. Angola Present study	*B. africana* *Tchagra senegala* Ivory Coast Present study	*B. pentamyzos* *Prionops plumata* Zimbabwe Mettrick (1960)	*B. pentamyzos* *Prionops plumata* Zimbabwe Georgiev *et al.* (2002)
Body: length (mm)	15	11.2-14.2[1]	> 31	-	58[5]	55[5]
Body: maximum width	750	612-734[1]	1,120-1,140	751-848	1,300	1,273
Scolex: diameter	500 x 300	385-450	460	372-437	447	465
Suckers: diameter	190 x 140	115-130	133-145	130-161	133-142	134-157
Rostellum: diameter	200	125-145	145	148-186	182	160
Rostellar hooks: number	44	> 38	40	38-42	42	42
Rostellar hooks, length:						
anterior	84	75-80	80-82	82-85	80-82[3]	84-85
posterior	40	55-60	59-61	61-63	80-82[3]	60-61
Testes: number	5-8	10-14	10-13	10-15	8-10	11-14
Cirrus-sac:						
length	190-250	193-225	163-190	171-232	196	180-227
width	50	27-41	32-40	30-37	26	28-36
Vagina, copulatory part:						
length	-	138-180	162-180	174-223	-	198-247
width	-	18-23	13-22	14-23	-	13-21
Eggs: diameter	25[2]	-		-	35-39	-
Embryophore: diameter	-	-	36-42	40-45	-	41-49
Oncosphere: diameter	-	-	26-32	28-34	-	26-34
Embryonic hooks, length:						
central pair	-	-	20-21	19-21	10-11[4]	19-21
lateral pairs	-	-	17-19	16-18	10-11[4]	16-18

[1] Pregravid specimens; entire strobila or substantial parts of them contracted.

[2] Data on the diameter of eggs do not seem reliable because the type material lacks proglottides with fully-developed eggs.

[3] Lengths of anterior and posterior hooks not given separately.

[4] Lengths of central and lateral embryonic hooks not given separately.

[5] Well-relaxed specimen.

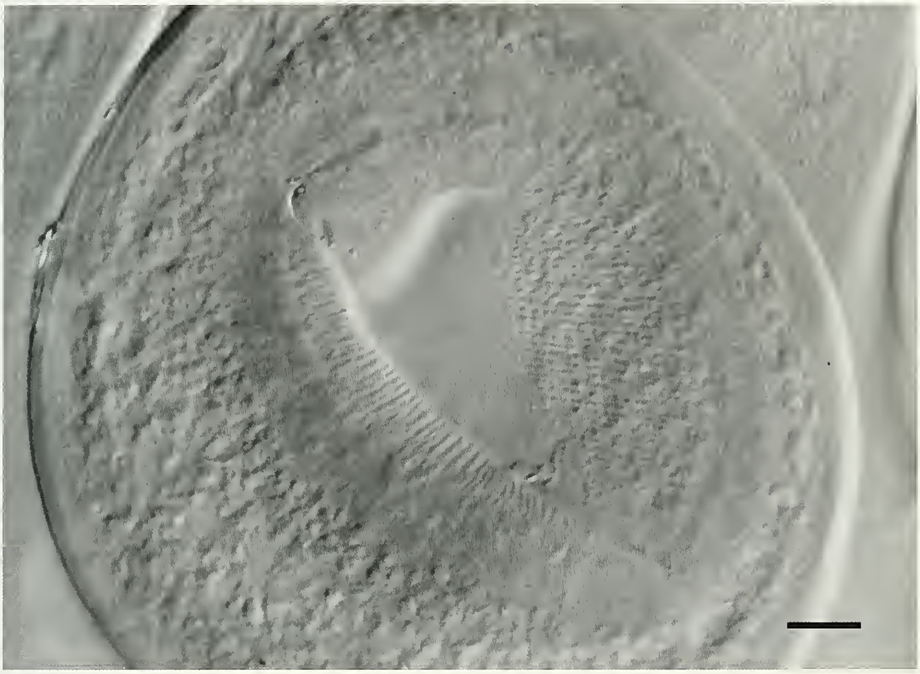
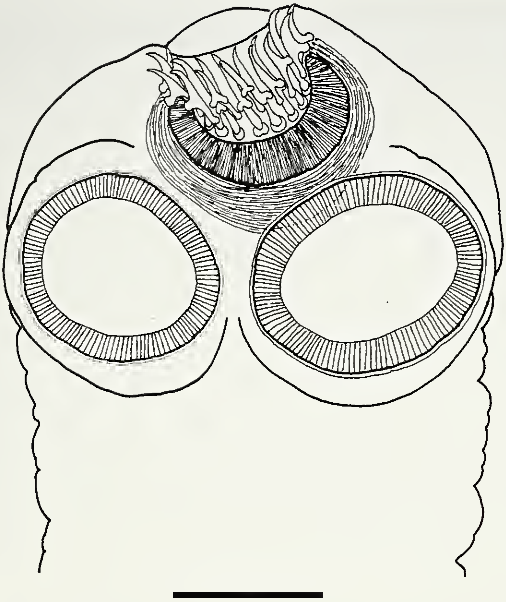


FIG. 12

Biuterina africana Joyeux & Baer, 1928, material from the Ivory Coast. Sucker. Note armament consisting of punctiform spine-like structures arranged in transverse rows on the internal surface of the sucker. Scale bar: 10 μm.

at level of middle of suckers 321 (n = 1). Suckers slightly oval, with well-developed musculature, with diameter 129-150 (142, n = 4). Rostellum of only available scolex retracted (Fig. 13), with diameter 123, sucker-like, highly muscular; no glandular cells visible within or around rostellum. Rostellar hooks 30 in number, arranged in 2 regular rows; their blades directed anteriorly when rostellum retracted; each hook provided with 2 epiphyseal thickenings, 1 on handle and 1 on guard. Anterior hooks 58-62 (61, n = 5) long, with blade considerably longer than handle (Fig. 14). Posterior rostellar hooks 42-45 (44, n = 4), with blade almost as long as handle (Fig. 15). Neck contracted, 207 wide; first proglottides appear at 339 from posterior margin of suckers. Proglottides craspedote (Figs 16-18); mature, postmature and pregravid proglottides wider than long; gravid proglottides as long as wide or slightly longer than wide (Fig. 18). Genital pores irregularly alternating in short series. Genital atrium infundibular, thin-walled; no surrounding intensely stained cells. Genital ducts pass between osmoregulatory canals. Dorsal osmoregulatory canals 4-7 (n = 10) in diameter. Ventral osmoregulatory canals 24-34 (n = 10) in diameter, with transverse anastomoses along posterior margin of each proglottis.

Testes oval, 8-11 (9, n = 10) in number, form compact group situated laterally, dorsally and posteriorly to vitellarium, often overlap posterior margin of ovary and



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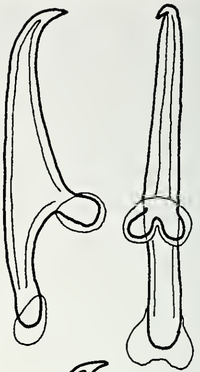

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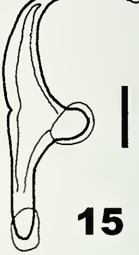

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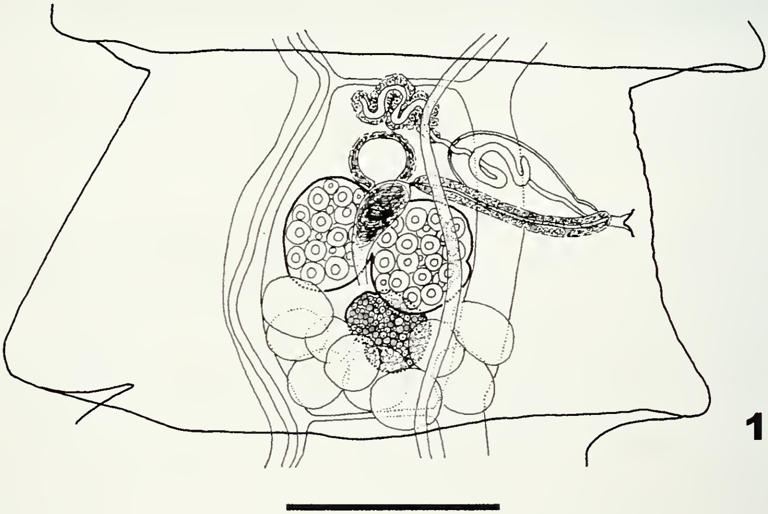

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FIGS 13-16
Biuterina cordifera Murai & Sulgostowska, 1983. (13) Scolex. (14) Anterior rostellar hooks. (15) Posterior rostellar hook. (16) Mature proglottis, dorsal view. Scale bars: 13, 16, 100 μm; 14, 15, 10 μm.

ventral osmoregulatory canals (Fig. 16). External vas deferens convoluted, surrounded by intensely stained cells but not forming dense body. Cirrus-sac oval (Fig. 16), 57-84 x 27-33 (70 x 30, n = 10), tapered porally and rounded antiporally, thin-walled, may reach or just cross poral osmoregulatory canals. Internal vas deferens forms several coils in antiporal part of cirrus sac. Evaginated cirrus not observed; no armament within duct of withdrawn cirrus.

Ovary bi-winged, medial, symmetrical, occupies entire width of median field (Fig. 16); wings round, compact. Vitellarium compact or slightly lobed, oval or irregular in shape, with diameter 39-72 (48, n = 10). Seminal receptacle ovoid to elliptical, dorsal to ovary. Vagina opens dorsally to male pore; not clearly separated into copulatory and conductive parts.

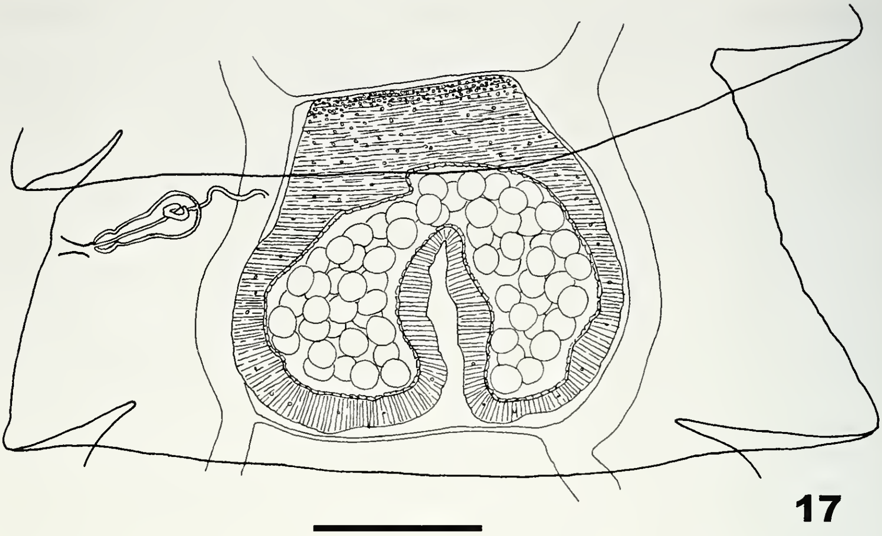
Uterus in mature proglottides antero-dorsal to ovary, sac-like, thick-walled, almost spherical or with irregular shape (Fig. 16). In postmature proglottides, uterus horseshoe-shaped, with lateral ends directed posteriorly; primordium of paruterine organ as consolidation of medullary parenchyma, entirely enveloping uterus. In pregravid (Fig. 17) and gravid (Fig. 18) proglottides, uterus with elongate lateral branches; paruterine organ occupies entire median field; anterior part of paruterine organ granular. In slightly contracted gravid proglottides, uterine branches convoluted, suggesting presence of uterine capsules each containing several eggs (Fig. 18). Eggs oval; outer shell thin, often not distinct, closely envelops embryophore. Embryophore oval, 30-38 (34, n = 10) in diameter, thick-walled. Oncosphere oval, 20-25 (23, n = 10) in diameter. Embryonic hooks: central pair thin, 16-17 (n = 7) long; intra-lateral hooks thin, 14-15 (n = 7) long; extra-lateral hooks stout, 14-15 (n=7) long.

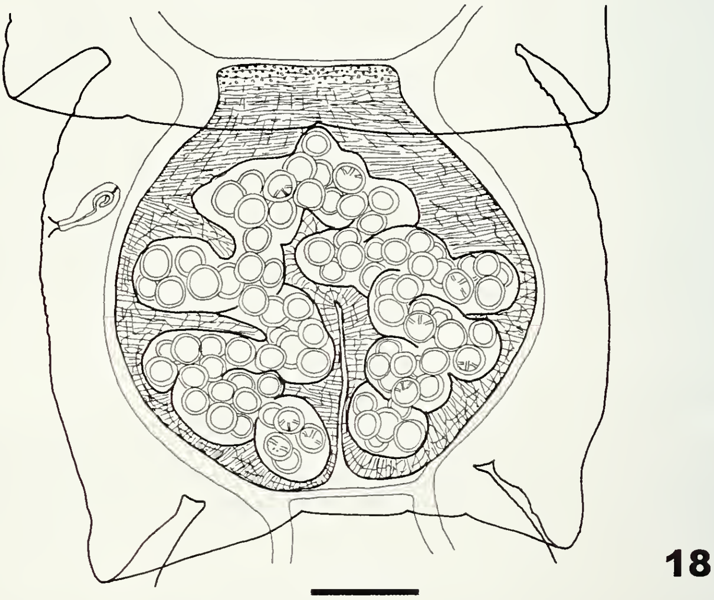
REMARKS: The present material was reported as *Paruterina* sp. from two of nine examined specimens of the host species (Mariaux, 1994). Its morphology fits well with the previous descriptions of *B. cordifera* (see Murai & Sulgostowska, 1983; Georgiev *et al.*, 2004). This species was originally described from *Lusciniola melanopogon* (Temmink) (type host), *Acrocephalus scirpaceus* Hermann and *A. shoenobaenus* (L.) in Hungary (Murai & Sulgostowska, 1983) and later reported from *A. scirpaceus* in the Czech Republic and from *Erithacus megarhynchos* (L.) in Bulgaria (Georgiev *et al.*, 2004). The present study reports the first record of this species in *A. arundinaceus* and the first record for Africa.

Biuterina triangula (Krabbe, 1869) Fuhrmann, 1908

MATERIAL EXAMINED: MHNG INVE 15961 (formerly no. 988.401, see Mariaux, 1994), 5 slides: 1 stained entire pregravid specimen, 5 stained juvenile specimens and 4 stained strobilar fragments without scoleces, and 3 scoleces in Berlese's medium; 11 February 1988, host collection number CI 1051, ex *Anthus leucophrys gouldii* Fraser (Passeriformes, Motacillidae), collected at Tortyia. The host specimen has been deposited in the Ornithological Collection of the MHNG, no. 1765.070.

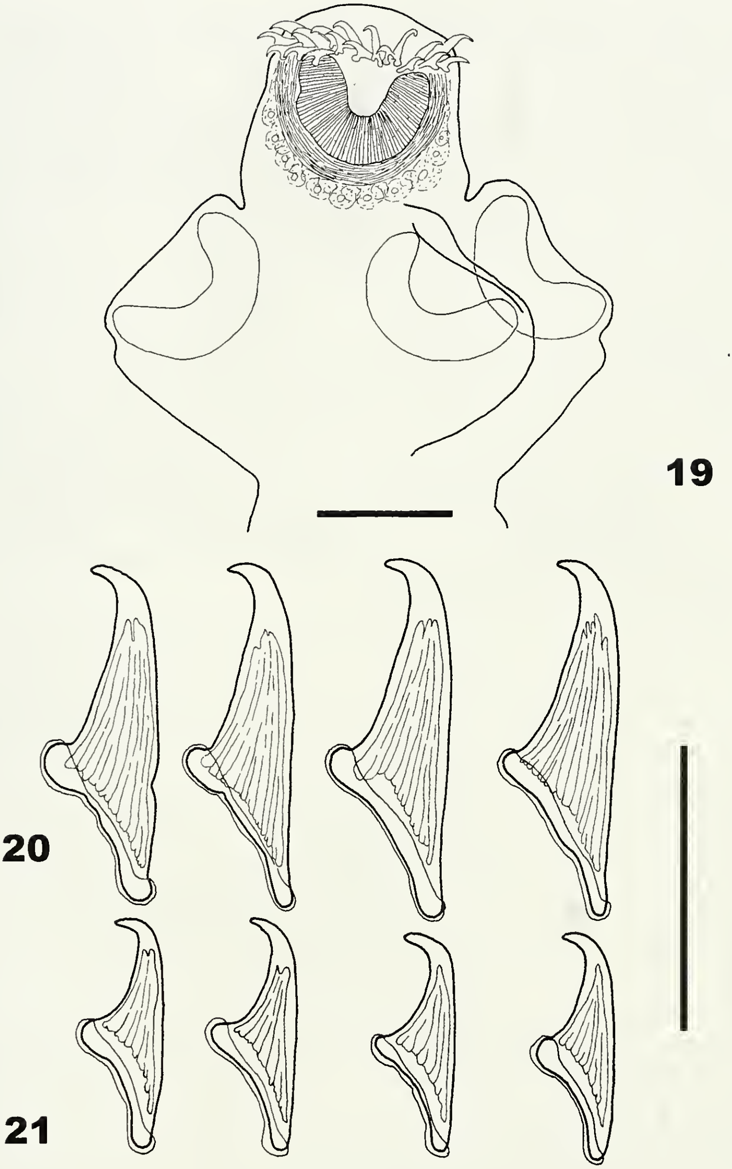
DESCRIPTION: Pregravid specimen 18.5 mm long, with strobila gradually widening posteriorly and reaching maximum width of 770 (n = 1) at level of pregravid proglottides, consists of 107 proglottides: 24 juvenile, 33 premature, 21 mature, 18 postmature and 11 pregravid. Scolex with protruded apical part (Fig. 19), clearly outlined from neck by its greater diameter, with maximum width 350-405 (381, n = 6) at level of suckers. Suckers somewhat oval, with well-developed musculature, 100-140 (121, n = 24) in diameter, with their apertures directed antero-laterally. Rostellum sucker-like (Fig. 19), 102-110 (106, n = 6) in diameter, highly muscular; numerous intensely-staining cells present in anterior half of rostellum. Rostellum separated from





FIGS 17-18
Biuterina cordifera Murai & Sulgostowska, 1983. (17) Pregravid proglottis. (18) Gravid proglottis. Scale bars: 100 µm.

surrounding parenchyma by thick layer of radial musculature, outside of which is aggregation of intensely-staining (glandular) cells. Rostellar hooks 40-44 (n = 9) in number (40, n = 3; 42, n = 2; 44, n = 4), arranged in 2 regular rows; blades directed anteriorly when rostellum retracted. Each hook provided with slightly expressed



FIGS 19-21
Biuterina triangula (Krabbe, 1869). (19) Scolex. (20) Anterior rostellar hooks. (21) Posterior rostellar hooks. Scale bars: 19, 100 mm; 20, 21, 50 mm.

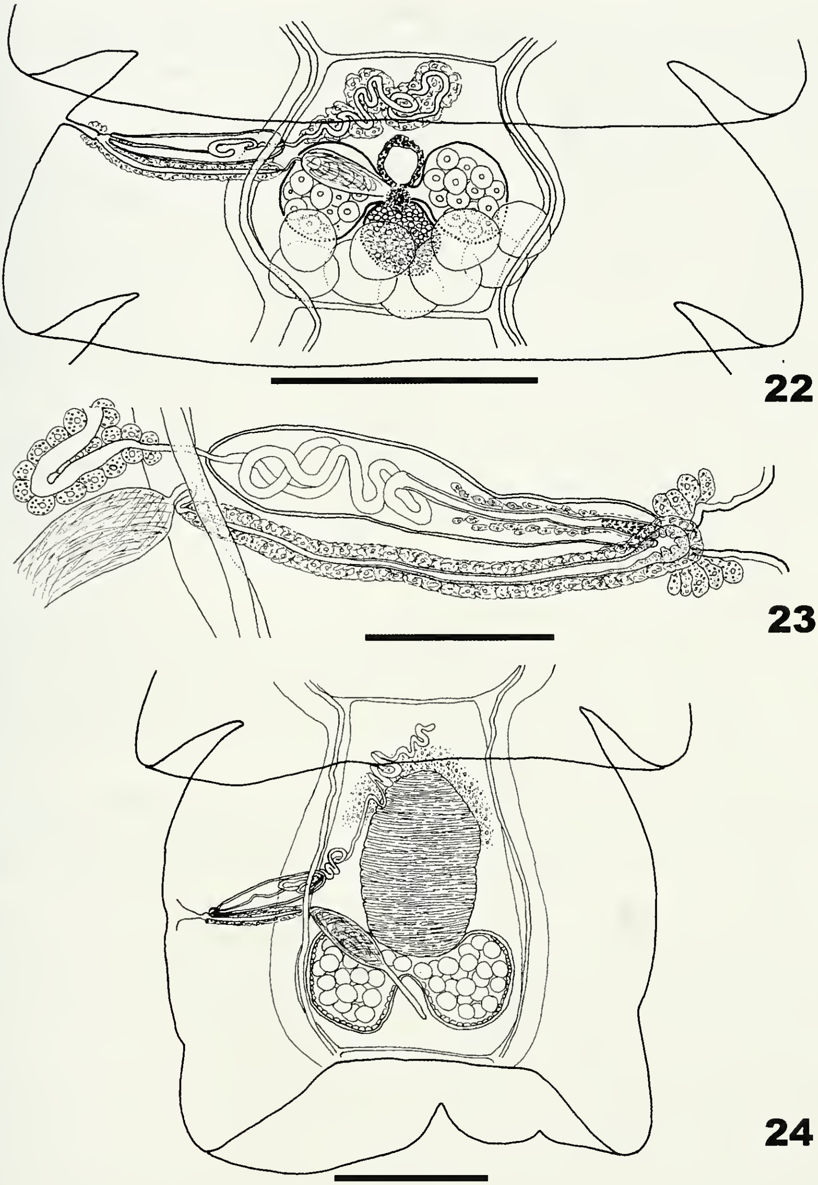
epiphyseal thickening on both handle and guard. Anterior hooks 58-65 (62, n =24) long, with blade considerably longer than handle (Fig. 20). Posterior rostellar hooks 37-43 (41, n =23), with blade almost as long as handle (Fig. 21). Neck 160-202 (180, n = 6) wide in its narrowest part; first proglottides appear at 540-800 (620, n = 6) from posterior margin of suckers. Proglottides craspedote (Figs 22, 24); mature and postmature wider than long; pregravid as long as wide. Genital pores irregularly alternating in short series, e.g. ... 3, 3, 2, 1, 1, 1, 1, 2,1, 2, 1, 3, 1, 1... No genital papilla. Genital atrium thick-walled, 22-27 (24, n = 10) deep, with infundibular aperture, 10-19 (14, n = 10) in diameter, and cylindrical proximal part; intensely staining cells surround genital atrium. Genital ducts pass between osmoregulatory canals. Dorsal osmoregulatory canals 5-12 (n = 10) in diameter. Ventral osmoregulatory canals 18-52 (n = 10) in diameter, with transverse anastomoses along posterior margin of each proglottis.

Testes oval, 6-9 (8, n = 14) in number, form compact group situated laterally, dorsally and posteriorly to vitellarium, overlapping osmoregulatory canals and posterior margin of ovary (Fig. 22); maximum diameter of fully-developed testes 48-58 (54, n = 10). External vas deferens convoluted, surrounded by intensely stained cells, which form dense body at anterior proglottis margin. Cirrus-sac elongate-oval (Fig. 23), with almost cylindrical poral part, thick-walled, reaches or just crosses poral osmoregulatory canals, 135-155 x 24-33 (145 x 29, n = 9) in mature proglottides, 133-155 x 30-33 (142 x 32, n = 4) in postmature and pregravid proglottides. Internal vas deferens forms several coils in antiporal part of cirrus sac. Evaginated cirrus not observed; armament within ductus cirri consisting of small triangular spines (< 1 mm long) which occupy only its distal part (Fig. 23).

Ovary bi-winged, medial, symmetrical, occupies almost entire width of median field, when fully developed 147-162 (155, n = 6) wide, with round or slightly oval, compact wings (Fig. 22). Vitellarium compact, oval or with irregular shape close to oval, with diameter 45-68 (43, n = 7). Seminal receptacle elongate, almost tubular, with slightly expanded and rounded poral end 22-30 (26, n = 8) in diameter, tapers antiporally and gradually forms straight canal passing towards Mehlis' gland. Mehlis' gland situated anterior to vitellarium, globular, with diameter 23-35 (31, n = 8), not distinct in some proglottides. Vagina opens dorsally to male pore; its copulatory part 113-128 (125, n = 8) long, slightly shorter than cirrus sac or of same length, consisting of thin-walled canal with diameter of lumen 4-6 (n = 8), surrounded by cellular sleeve (Fig. 23); diameter of copulatory vagina 13-18 (15, n = 8). Conductive part of vagina thin, short.

Uterus in mature proglottides antero-dorsal to ovary, sac-like, thick-walled, almost spherical or with irregular shape (Fig. 22). In postmature proglottides, uterus gradually divides into 2 lateral expanded sacs connected by narrow anterior isthmus; primordium of paruterine organ forms as consolidation of medullary parenchyma anterior to developing uterus. In pregravid proglottides (Fig. 24), uterus situated in posterior third of median field, consisting of 2 lateral round sacs; paruterine organ cylindrical, with rounded anterior end surrounded by granular tissue. No developed eggs in material studied.

REMARKS: The original description of *Biuterina triangula* (= *Taenia triangulus* Krabbe, 1869) was based on specimens from '*Turdus* sp.' and did not mention the type locality (Krabbe, 1869). The subsequent revisers considered that the material originated from 'West Europe' (Matevosyan, 1969) or 'Central Europe' (Kornyushin, 1989), probably because the collector was Bremser (the naturalist J. G. Bremser of Vienna,



Figs 22-24

Biuterina triangula (Krabbe, 1869). (22) Mature proglottis, dorsal view. (23) Genital ducts in postmature proglottis, dorsal view. (24) Pregravid proglottis, dorsal view. Scale bars: 22, 24, 200 mm; 23, 50 mm.

see Sattman, 2000). As demonstrated by previous studies (Kornyushin, 1989; Georgiev *et al.*, 2004), two other species with anterior rostellar hook of a similar length but with different strobilar morphology, *B. cordifera* and *Spasskyterina trianguloides*

Kornyushin, 1989, were sometimes misidentified as *B. triangula*. Therefore, the data for the host range and the geographical distribution of *B. triangula* need to be re-evaluated, which is difficult for the moment because of the lack of morphological information accompanying most of previous records.

The original description of *B. triangula* is very brief, giving information on the number and the length of rostellar hooks (Table 2) and the irregular alternation of the genital pores (Krabbe, 1869). Fuhrmann (1908) re-examined the type material and additional material from *Turdus pilaris* L. and reported the length of the rostellar hooks of the type as 57 and 39 μm. He mentioned that the types are in bad condition and only added the length of the cirrus sac (0.1 mm) to the original description. Kornyushin (1989) published a detailed redescription on the basis of specimens from *Anthus campestris* (L.) from the Crimea, Ukraine, very much resembling the present material. Some differences in the metrical data (Table 2) are of minor importance and are probably due to the different methods of fixing and processing the specimens.

All the previous records of *B. triangula* are from the Palaearctic Region (Matevosyan, 1969; Kornyushin, 1989). The present finding is the first record of this species in Africa and a new host record.

Biuterina pogoniuli sp. n.

MATERIAL EXAMINED: MHNG INVE 16064, 49753 (formerly no 988.174, see Mariaux, 1994), 3 slides, 1 entire specimen, 1 specimen with scolex mounted separately in Berlese's medium and strobilar fragments of 2 further specimens, from *Pogoniulus scolopaceus* (Bonaparte) (Piciformes: Capitonidae), collected on 20 April 1988 at Dabou. The host specimen has been deposited in the Ornithological Collection of the MHNG, no. 1765.018.

Holotype: MHNG INVE 16064, an entire specimen in Canada balsam, mounted in the same slide with another strobilar fragment.

Paratypes: MHNG INVE 49753, 1 specimen with scolex mounted separately in Berlese's medium and 2 strobilar fragments, 1 of them on the same slide as the holotype.

ETYMOLOGY: The species name *pogoniuli* is a derivate of the generic name of the host.

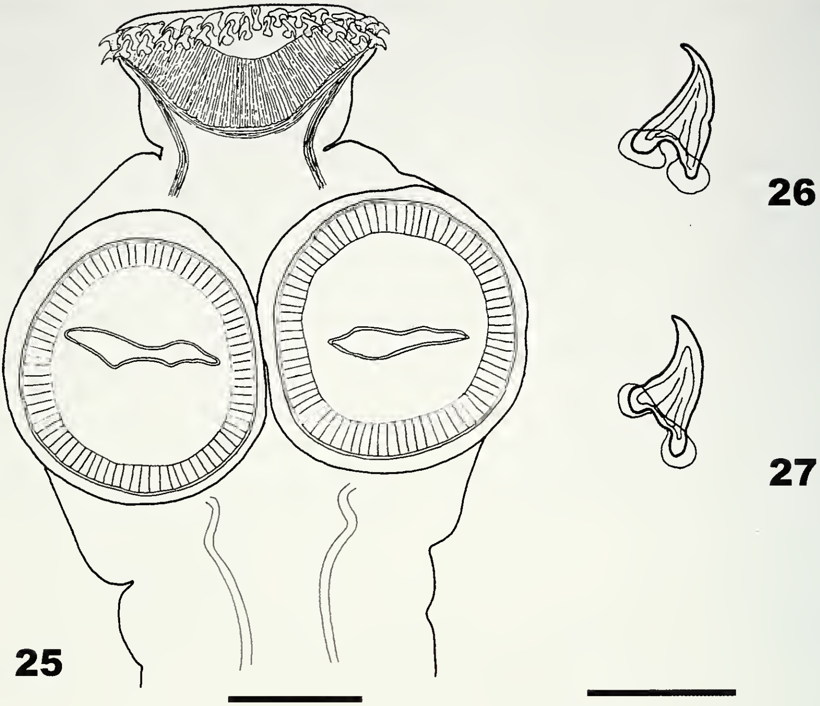
DESCRIPTION: Body band-like. Entire gravid specimen with scolex 37 mm long, consisting of 145 proglottides (44 juvenile, 24 premature, 23 mature, 19 postmature, 26 pregravid and 9 gravid). Specimen without scolex and initial part of strobila, 38 mm long, consisting of 107 proglottides (7 juvenile, 27 premature, 19 mature, 12 postmature, 33 pregravid and 9 gravid). Maximum width 0.95-1.20 mm (1.05 mm, n = 4), at level of gravid proglottides. Scolex (Fig. 25) almost globular, with maximum diameter 420 (n = 1) at level of middle of suckers; anterior part of scolex protrusible. Suckers round, 179-192 x 179-183 (188 x 180, n = 4) in diameter, with moderately developed musculature, open via transverse slit-like aperture. Rostellum sucker-like, with concave anterior surface, 192 (n = 1) in diameter; numerous vertical muscular fibres and few glandular cells present within rostellum. Layer of radial musculature separates rostellum from surrounding parenchyma. No glandular tissue observed around rostellum. Retractor muscular bundles attached at periphery of rostellum. Rostellar armament consists of 56-62 (n = 2) rostellar hooks arranged in 2 regular rows. Each hook triangular, with epiphyseal thickening on both handle and guard; blades curved. Anterior and posterior hooks of different shape, also differ slightly in

TABLE 2. Comparison of some metrical and meristic data for *Biuterina triangula* (Krabbe, 1869).

Host	*Turdus* sp.	"*Turdus* sp." *Turdus pilaris*	*Anthus campestris*	*Anthus leucophrys*
Locality	Unknown	Unknown	Crimea, Ukraine	Ivory Coast
Source	Krabbe (1869)	Fuhrmann (1908)	Kornyushin (1989)	Present study
Body: length (mm)	-	~30	15-20	18.5[2]
Body: maximum width	-	~1000	450-470	770
Scolex: diameter	-	-	320-450	350-405
Suckers: diameter	-	-	120-170	100-140
Rostellum: diameter	-	-	110-160	102-110
Rostellar hooks: number	32	-	40	40-44
Rostellar hooks, length:				
anterior	55	57	60	58-65
posterior	38-41	39	40	37-43
Testes: number	-	-	8-10	6-9
Cirrus-sac:				
length	-	100	120	135-155
width	-	-	30-40	30-33
Vagina, copulatory part:				
length	-	-	-	113-128
width	-	-	-	13-18
Embryophore: diameter	-	-	27-35	-
Oncosphere: diameter	-	-	20-25	-
Embryonic hooks, length:				
central pair	-	-	17[1]	-
lateral pairs	-	-	17[1]	-

[1] Lengths of the central and lateral embryonic hooks not given separately.
[2] Pregravid specimen.

size. Anterior hooks 24-25 (24.5, n = 6) long; blade considerably longer than handle (Fig. 26). Posterior hooks 22-25 (23, n = 4) long; blade slightly longer than handle (Fig. 27). Neck 224 (n=1) wide, long; first proglottides appear at 860 from posterior end of suckers. Proglottides craspedote; juvenile, premature, mature (Fig. 28) and postmature (Fig. 30) and early pregravid proglottides (Fig. 31) wider than long; pregravid proglottides with more advanced development and gravid proglottides (Fig. 33) almost as long as wide or slightly longer than wide. Genital pores alternating irregularly, predominantly in short series but long unilateral series may also occur, e.g., ... 3, 1, 3, 1, 1, 2, 1, 1, 1, 1, 1, 3, 2, 2, 1, 1, 3, 1, 1, 2 or ...9, 1, 1, 1, 1, 1, 10, 2 ... 7, 1, 1, 1, 1, 1, 1, 1, 2, 1, 2, 2, 1, 2, 7...; pores open at junction of anterior and second thirds of lateral proglottis margin in mature and postmature proglottides and slightly anterior to middle of lateral proglottis margin in gravid proglottides. Genital atrium 41-70 (54, n = 10) deep, thick-walled, cylindrical, slightly expanded at its base (Fig. 29), with infundibular aperture 36-66 (52, n = 10) in diameter, provided with aggregation of intensely staining cells. Atrial region might be surrounded by muscular bundles (sometimes not distinct), thus assuming spherical appearance; contraction of these bundles results in formation of short but well-expressed genital papilla. Dorsal osmoregulatory canals 5-9 (n = 10) in diameter, without transverse anastomoses. Ventral osmoregulatory canals 17-40 (n = 10) in diameter, with transverse anastomoses along posterior margin of each proglottis. Genital ducts pass between poral osmoregulatory canals.

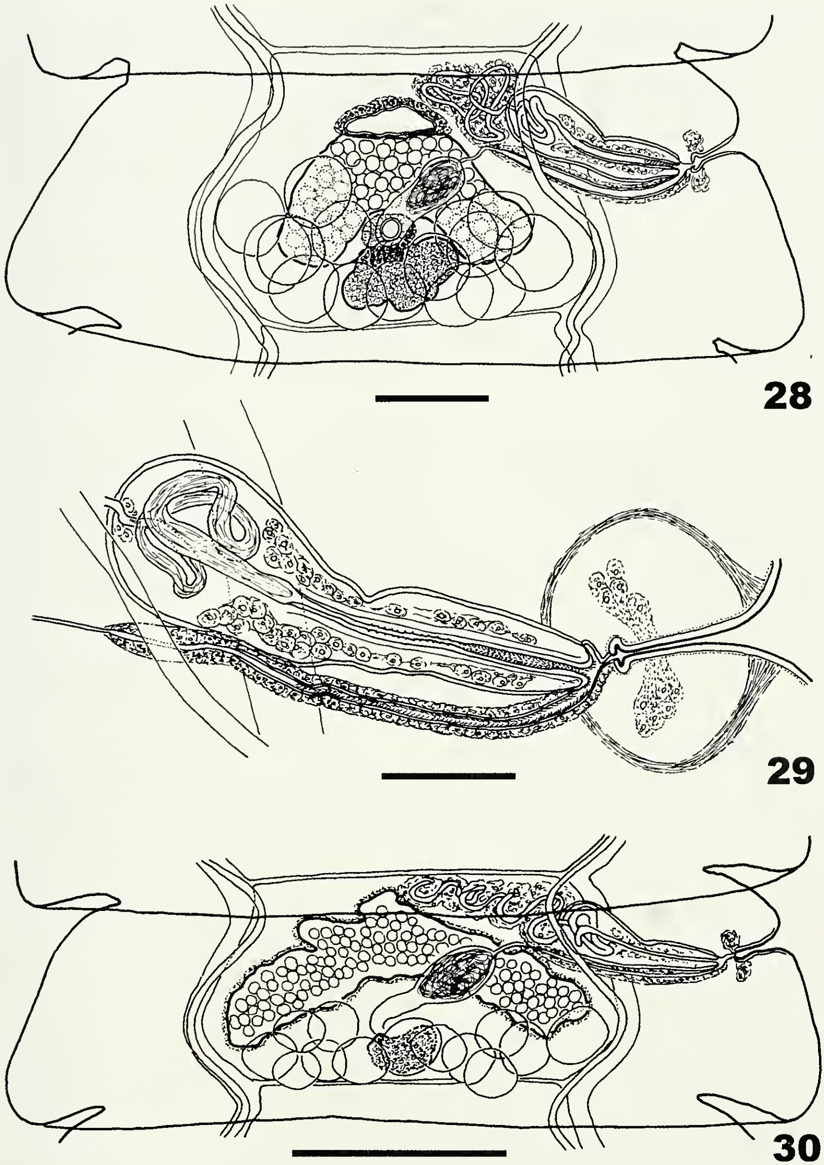


Figs 25-27

Biuterina pogoniuli sp. n. (25) Scolex. (26) Anterior rostellar hooks. (27) Posterior rostellar hook. Scale bars: 25, 100 μm; 26, 27, 25 μm.

Testes 12-17 (14, n = 15) in number, round or slightly oval, form compact group occupying whole width of posterior half of median field, laterally and postero-dorsally to ovary and dorsally and laterally to vitellarium, reach posterior proglottis margin; when fully developed, testes with diameter 68-84 (76, n = 10). External vas deferens convoluted in anterior poral part of median field, surrounded by prostate cells and forming together with them compact transversely-elongate body just adjacent to anterior proglottis margin; diameter of external vas deference 4-7 (5, n = 10). Cirrus-sac oblique, elongate, thick-walled, 165-192 x 49-63 (179 x 55, n = 15), with tapered poral end and widely rounded antiporal end, overlapping or just crossing poral osmoregulatory canals (Figs 28-30). Internal vas deferens convoluted in antiporal part of cirrus-sac, with diameter 8-13 (11, n = 10); intensely staining cells surround withdrawn cirrus. Partly evaginated cirrus cylindrical, 44-66 (n = 2) long, 14-15 (n = 2) in diameter; cirral armament (distinct in both evaginated cirrus and in canal of withdrawn organ) consisting of triangular spines 2-3 μm in length.

Ovary arcuate, with ends directed postero-laterally (Fig. 28), compact or slightly lobate, 179-268 (230, n = 10) wide. Vitellarium with irregular shape, compact, width 98-150 (119, n = 10). Seminal receptacle oval, situated dorsally to ovary and uterus; with rounded poral end; antiporal end gradually forms wide seminal duct.



FIGS 28-30

Biuterina pogoniuli sp. n. (28) Mature proglottis, dorsal view. (29) Genital ducts in postmature proglottis, dorsal view. (30) Early postmature proglottis, dorsal view. Scale bars: 28, 100 μm; 29, 50 μm; 30, 250 μm.

Vagina opens postero-dorsally to male pore; copulatory part almost as long as cirrus-sac, covered with thick cellular sleeve; vaginal canal thick-walled, with its distal part lined with long microtriches and conductive part long, thin (Fig. 29).

In mature proglottides, uterus thick-walled sac, transversely elongate, situated just anterior to ovary; around it, modification of medullary parenchyma forms primordium of paruterine organ (Fig. 28). With further development, uterus expands in lateral direction, becoming arcuate (Fig. 30). In late post-mature proglottides, uterus assuming shape of horseshoe; paruterine organ surrounds entire uterus, its anterior part being thicker (Fig. 31). In gravid proglottides, uterus in general appearance horseshoe-shaped, lobate, entirely embedded by paruterine organ. Anterior part of paruterine organ fills entire median field (Fig. 33). Eggs with thin, irregular outer shell, situated closely to embryophore (Fig. 32). Embryophores thick-walled, spherical or slightly oval, with diameter 41-48 (44, n = 10). Oncospheres spherical, 28-32 (30, n = 10) in diameter. Embryonic hooks of central pair 20-22 long, with collar about their middle. Embryonic hooks of lateral pairs 17-19 long, with collar at about one third of their length.

REMARKS: This species was previously reported as *Paruterina* sp. collected from 1 of 17 specimens of the host species studied (Mariaux, 1994). The identification was based on its correspondence with the generic concept of *Paruterina* Fuhrmann, 1906 as presented by Matevosyan (1969) and Schmidt (1986). The current concept of *Paruterina* is restricted to a small group of species parasitising Strigiformes, while *Biuterina* includes species with two symmetrical uterine sacs connected by an anterior isthmus, no matter whether the entire uterus is embedded by the paruterine organ or only its anterior part (Bona & Maffi, 1984; Kornyushin, 1989; Georgiev & Kornyushin, 1994). Therefore, the morphology of the specimens studied corresponds to the diagnosis of *Biuterina* (see Georgiev & Kornyushin, 1994).

According to the structure of its uterus and paruterine organ, *B. pogoniuli* sp. n. corresponds to a group of species having a horseshoe-shaped uterus entirely embedded in the paruterine organ. This includes *B. cordifera*, a parasite of European and African insectivorous birds of the families Sylviidae and Turdidae (see above), and *B. chlorurae* (Rausch & Schiller, 1949), a parasite of North-American emberizid birds (Rausch & Schiller, 1949). The new species differs from *B. cordifera* by its considerably smaller rostellar hooks, greater number of testes and larger cirrus sac (Table 3). The ovary of *B. pogoniuli* is arcuate, while that of *B. cordifera* is more or less bi-winged (Georgiev *et al.*, 2004; present study). Other differences are related to the cirral armament (present in the new species and lacking in *B. cordifera*), the shape of the cirrus sac (elongate and oval, respectively) and the number of rostellar hooks (Table 3).

From *B. chlorurae*, the new species differs in its larger rostellar hooks, greater number of testes and larger cirrus sac (Table 3).

Other species possessing rostellar hooks of a similar size are *B. fuhrmanni* Schmelz, 1941 and *B. cylindrica* Fuhrmann, 1908. However, these two species possess a paruterine organ situated anterior to the uterus (Fuhrmann, 1908; Schmelz, 1941; Georgiev *et al.*, 2004).

Biuterina petroniae sp. n.

MATERIAL EXAMINED: MHNG INVE 16114, 49754 (formerly no 988.186, see Mariaux, 1994), 3 entire gravid specimens and 2 strobilar fragments stained and mounted in Canada balsam (2 slides) plus 2 scoleces mounted in Berlese's medium (2 slides); from *Petronia dentata*

(Sundevall) (Passeriformes: Ploceidae, Passerinae), collected on 19 February 1987 at Ouango-Fitini (9°37'N, 4°03'W). The host specimen has been deposited in the Ornithological Collection of the MHNG, no. 1773.018.

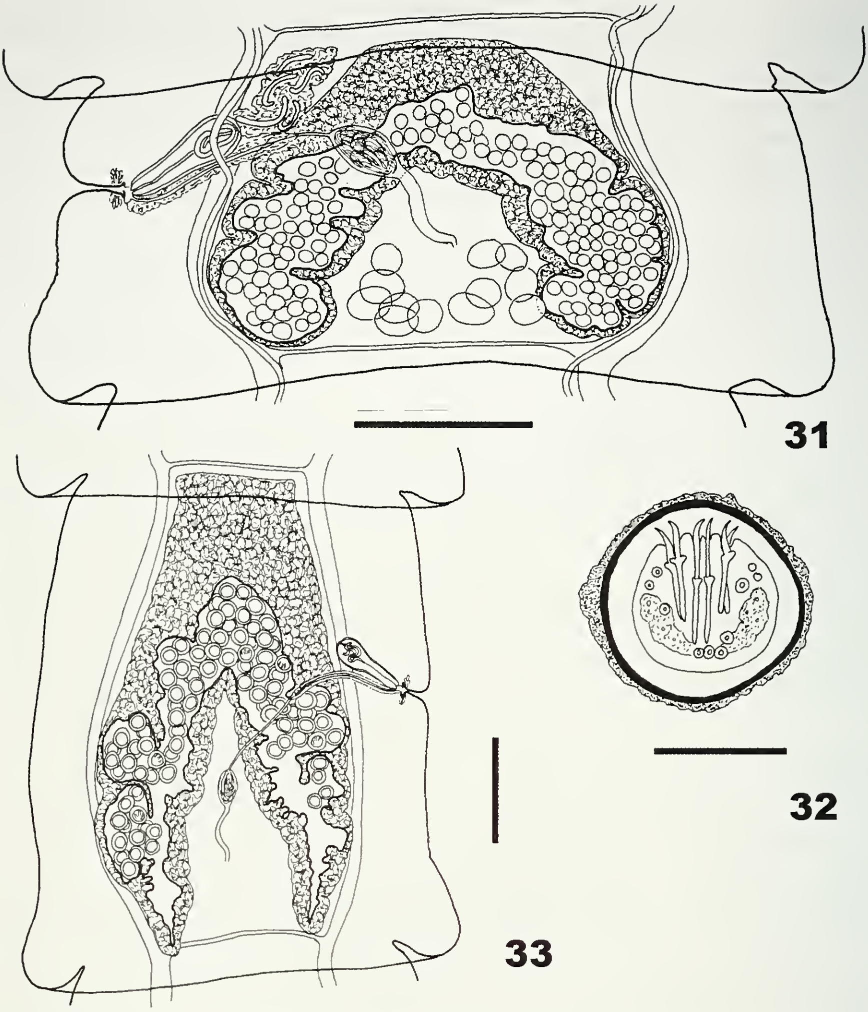
Holotype: MHNG INVE 16114, an entire specimen in Canada balsam, mounted on the same slide with 2 strobilar fragments.

Paratypes: MHNG INVE 49754, 2 entire specimens in Canada balsam; 2 scoleces in Berlese's medium; 2 fragments mounted on the same slide with the holotype.

ETYMOLOGY: The species name *petroniae* is a derivate of the generic name of the host.

DESCRIPTION: Body gradually expands in posterior direction to level of pregravid proglottides and then with almost parallel lateral sides; gravid specimens 10.6-13.1 mm (11.7 mm, n = 3) in length, consisting of 51-56 (54, n = 3) proglottides (10-12 juvenile, 10-16 premature, 8-9 mature, 4-5 postmature, 13-15 pregravid and 2-3 gravid). Maximum width 0.63-0.70 mm (0.67 mm, n = 3) at pregravid proglottides. Scolex (Fig. 34) clearly outlined from neck by constriction, with maximum diameter 365-405 (680, n = 3) at level of posterior margin of sucker apertures; anterior part of scolex protruded, almost dome-shaped. Suckers situated on small but well-expressed pedicles (Fig. 34), cup-shaped, oval, 120-147 (131, n = 12) in diameter, with well-developed musculature. Rostellum sucker-like, cup-shaped, with diameter 90-112 (103, n = 3); numerous vertical muscular fibres and few glandular cells present within rostellum. Thick layer of radial musculature separate rostellum from surrounding tissue. Aggregations of glandular tissue present around rostellum. Rostellar armament consisting of 42-48, i.e. 42 (n = 2) or 48 (n = 2), rostellar hooks arranged in 2 regular rows. Each hook triangular, with epiphyseal thickening on both handle and guard; blades curved. Anterior and posterior hooks of different shape and size. Anterior hooks 38-40 (39, n = 12) long; blade slightly longer than handle (Fig. 35). Posterior hooks 28-30 (29, n = 11) long; blade and handle of almost equal length (Fig. 36). Neck 175 (n = l) wide in narrowest part (at constriction between it and scolex); first proglottides appear at 220-340 (n = 3) from posterior end of suckers. Proglottides craspedote; juvenile, premature, mature (Fig. 37), postmature and early pregravid (Fig. 39) proglottides wider than long; pregravid proglottides with more advanced development and gravid proglottides (Fig. 40, 41) almost as long as wide or slightly longer than wide. Genital pores alternating irregularly, predominantly in short series, e.g. ... 1, 2, 3, 2, 5, 1, 6, 1, 1, 1, 1, 1, 1, 5, 1; pores open slightly posterior to middle of lateral proglottis margin in mature proglottides (at border of anterior 38-45% of length of lateral proglottis margin) and at middle (48-55%) in gravid proglottides. Genital atrium 22-27 (24, n = 10) deep, thick-walled, with infundibular orifice and diameter of 10-14 (12, n = 10), provided with surrounding aggregation of intensely staining cells. No genital papilla. Dorsal osmoregulatory canals 4-6 (n = 10) in diameter, without transverse anastomoses. Ventral osmoregulatory canals 10-45 (n = 10) in diameter, with transverse anastomoses along posterior margin of each proglottis. Genital ducts pass between poral osmoregulatory canals.

Testes 7-10 (8, n = 11) in number, round or slightly oval, form compact group situated entirely in median field, laterally and postero-dorsally to ovary and dorsally and laterally to vitellarium; diameter when fully developed 43-53 (49, n = 10). External vas deferens convoluted in anterior poral corner of median field, surrounded by pro-

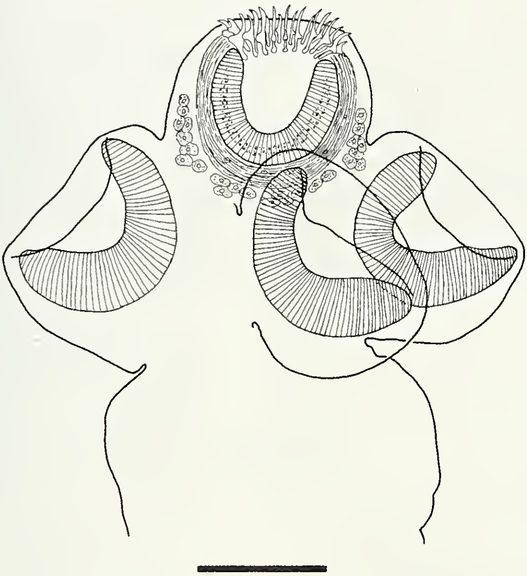


FIGS 31-33

Biuterina pogoniuli sp. n. (31) Late postmature proglottis, dorsal view. (32) Egg. (33) Gravid proglottis. Scale bars: 31, 33, 250 μm; 32, 50 μm.

static cells and together with them forming compact body; diameter of external vas deference 5-10 (8, n = 10). Cirrus-sac usually not reaching or only slightly overlapping poral osmoregulatory canals, 82-98 x 28-33 (92 x 31, n = 10), with rounded antiporal end and gradually tapering poral end; antiporal portion thick-walled; cirrus sac contains glandular cells surrounding canal of withdrawn cirrus and ejaculatory duct (Fig. 38). Internal vas deferens convoluted in antiporal part of cirrus-sac. No evaginated cirrus in material studied; no cirral armament observed in canal of withdrawn cirrus.

Ovary compact, bi-winged, occupies most of width of median field; wings rounded, connected by narrow isthmus (Fig. 37). Vitellarium median, oval or irregu-



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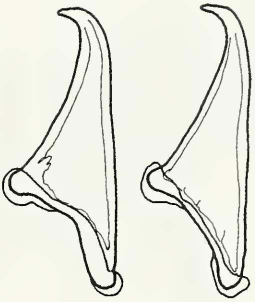

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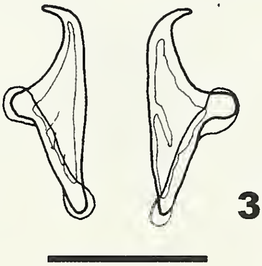

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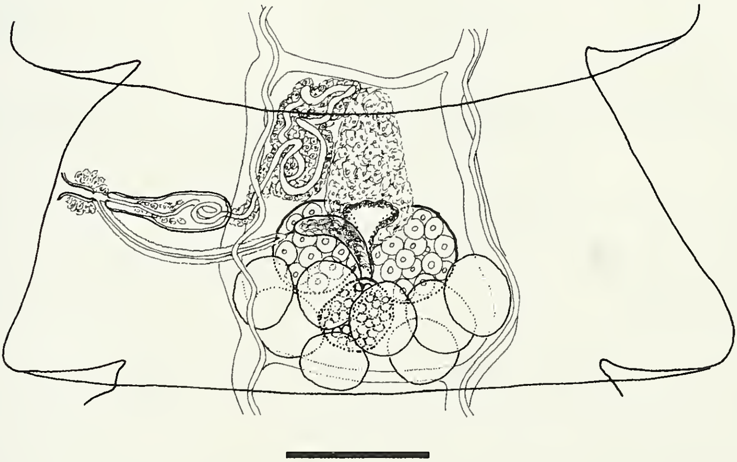

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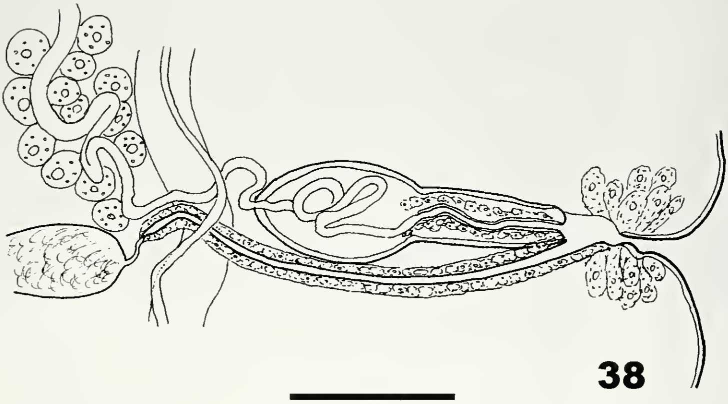
Figs 34-37

Biuterina petroniae sp. n. (34) Scolex. (35) Anterior rostellar hooks. (36) Posterior rostellar hooks. (37) Mature proglottis, dorsal view. Scale-bars: 34, 37, 100 Ìm; 35, 36, 20 μm.

larly suboval, slightly lobed or compact, 45-70 (57, n = 10) wide. Mehlis' gland globular, 18-24 (20, n = 10). Seminal receptacle dorsal to ovary and uterus, with rounded poral end with diameter 25-35 (31, n = 8) and antiporal end gradually forms wide seminal duct. Vagina opens posteriorly to male pore; copulatory part 137-162 (148, n = 8) long, consists of thin-walled vaginal canal with luminal diameter 6-10 (8,



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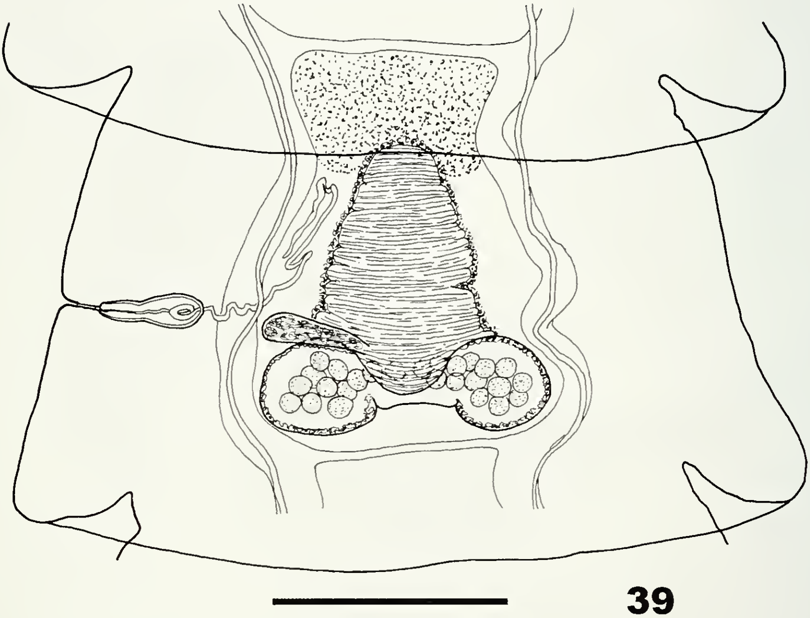

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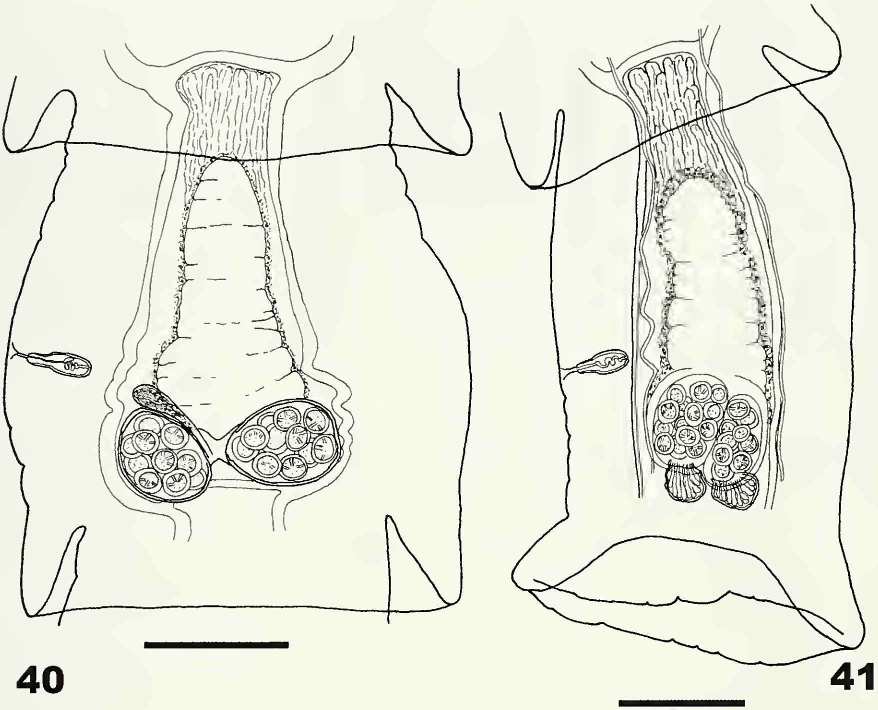
FIGS 38-39

Biuterina petroniae sp. n. (38) Genital ducts, dorsal view. (39) Pregravid proglottis, dorsal view. Scale bars: 38, 50 μm; 39, 200 μm.

n = 8) and thin, slightly expressed cellular sleeve; diameter of cellular sleeve 18-24 (21, n = 8); conductive part short, thin (Fig. 38).

In mature proglottides, uterus a thick-walled sac with irregular shape situated antero-dorsal to ovary; around and anteriorly to it, modification of medullary parenchyma forms primordium of paruterine organ (Fig. 37). With further development, uterus expands in lateral direction. In early pregravid proglottides (Fig. 39), uterus in form of single, transversely-elongate sac in most posterior part of median field; its



FIGS 40-41
Biuterina petroniae sp. n. (40, 41) Gravid proglottides showing the final stages of the development of the uterus and paruterine organ. Scale bars: 40-41, 200 μm.

lateral ends gradually differentiate as 2 distinct sacs divided by median constriction (Fig. 40). Paruterine organ consists of 2 parts; conical formation consisting predominantly of fibrilar tissue just anterior to uterine sac and modification of medullar parenchyma situated near anterior proglottis margin (Figs 39, 40); in addition, all medullary parenchyma are compacted. In most developed gravid proglottides available, eggs pass from uterine sacs into paruterine organ (Fig. 41). Eggs with thin, often indistinct, outer shell closely covering embryophore. Embryophore thick-walled, oval, with diameter 38-45 (42, n = 10). Oncosphere spherical, with diameter 27-34 (31, n = 10). Embryonic hooks of central pair 17-18 long, of lateral pairs 12-13 long; intralateral and extralateral embryonic hooks of the same shape.

REMARKS: The present material was reported as *Biuterina* sp. by Mariaux (1994). Judging by the size of the rostellar hooks, it is close to *B. macrancistrota* (Fuhrmann, 1908), *B. trapezoides* Fuhrmann, 1908, *B. campanulata* (Rudolphi, 1819) and *B. landsdowni* Malhotra & Capoor, 1987 (Table 3). The latter species, a parasite of *Upupa epops* L. in India (Malhotra & Capoor, 1987), is the only member of the genus for which the posterior hooks are reported to be longer than anterior hooks. The structure of its uterus and paruterine organ and the shape of the rostellar hooks, as illustrated by Malhotra & Capoor (1987), very much resemble those of *Neyraia* Joyeux

TABLE 3. Some characteristics of the species currently placed in *Biuterina* Fuhrmann, 1902 (ordered by decreasing length of the anterior rostellar hooks).

Species	Hosts	Distribution (faunal realms)	Rostellar hooks			Testes: number	Cirrus sac: measurements	Source
			Number	Length				
				Anterior	Posterior			
B. africana Joyeux & Baer, 1928, syn. *B. pentamyzos* (Mettrick, 1960) Matevosyan, 1964,	Laniidae	Afrotropical	38-44	75-85	55-63	10-15	163-232x27-40	Georgiev *et al.* (2002), present study
B. cordifera Murai & Sulgostowska, 1983	Sylviidae, Turdidae	Palaearctic, Afrotropical.	26-30	56-71	43-51	7-11	52-105x21-42	Georgiev *et al.* (2004), present study
B. morgani (Rausch & Schiller, 1949) Matevosyan, 1965	Troglodytidae	Nearctic	34-36	66	40	15-18	86-105x16-20	Matevosyan (1969)
B. triangula (Krabbe, 1869) Fuhrmann, 1908	Turdidae, Motacillidae	Palaearctic, Afrotropical	40-44	58-65	37-43	6-9	120-155x30-40	Kornyushin (1989), present study
B. erithaci Ryšavý & Sixl, 1977	Turdidae	Palaearctic	14	56-60	48	12-16	~140x-[6]	Ryšavy (1977)
B. planirostris (Krabbe, 1882) Fuhrmann, 1908	Alaudidae	Palaearctic	40	49	27	-	-	Fuhrmann (1908)
B. sobolevi Sudarikov, 1950	Turdidae	Palaearctic	42	48	33	8-10	111-114x-	Sudarikov (1950)
B. fallax Meggitt, 1928	Meropidae	Palaearctic	18-20	44-48[1]	44-48[1]	12	90x26	Meggitt (1928)
B. diversihamata Sawada, Hassan & Saleen, 1994	Coraciidae	Palaearctic	36-38	46	39	9-10	98-105x28-35	Sawada *et al.* (1994)
B. campanulata (Rudolphi, 1819) Fuhrmann, 1908	Tyrannidae, Formicariidae	Neotropical	26	43-46	32-36	8-10	-	Fuhrmann (1908)
B. macrancistrota (Fuhrmann, 1908) Mariaux & Vaucher, 1989, Syn. *B. meropina* var. *macrancistrota* Fuhrmann, 1908	Meropidae	Afrotropical	43-49	38-44	28-34	8-11	89-113x34-40	Mariaux & Vaucher (1989)
B. trapezoides Fuhrmann, 1908	Icteridae, Emberizidae (?), Caprimulgidae (?)	Neotropical	~30	41	34	-	-	Fuhrmann (1908)
B. lansdowni Malhotra & Capoor, 1987	Upupidae	Oriental	34-50	39-40	43-45	17-37	104-143x24-46	Malhotra & Capoor (1987)
B. petroniae sp. n.	Ploceidae	Afrotropical	42-48	38-40	28-30	7-10	82-98x28-33	Present study
B. reynoldsi (Daly, 1958) Matevosyan, 1964	Corvidae	Nearctic	44-48	33	21	12-14	-	Daly (1958)
B. passerina Fuhrmann, 1908	Alaudidae	Palaearctic	-	25-28[1]	25-28[1]	11-14	75-86x25-30	Fuhrmann (1908), Georgiev *et al.* (2004)
B. meropina (Krabbe, 1869) Fuhrmann, 1908	Meropidae	Palaearctic	40	27	22	-	-	Krabbe (1869)

B. distincta Fuhrmann, 1908	Icteridae (?)[2]	Neotropical	~20	25[1]	25[1]	12	140x-	Fuhrmann (1908)
B. pogoniuli sp. n.	Capitonidae	Afrotropical	56-62	24-25	22-25	12-17	165-192x49-63	Present study
B. cylindrica Fuhrmann, 1908	Thraupidae	Neotropical	52	23-25[1]	23-25[1]	~8	80?-	Fuhrmann (1908)
B. fuhrmanni Schmelz, 1941, syn. *B. clerci* Spasskii, 1946[4]	Emberizidae	Palaearctic	(42?) 48-52	20-25	17-21	12-17	89-120x39-54	Georgiev *et al.* (2004)
B. zambiensis (Mettrick, 1960) Matevosyan, 1964	Campephagidae	Afrotropical	48	19-22	16-18	7-10	70-77x23-31	Georgiev *et al.* (2002)
B. trigonacantha Fuhrmann, 1908	Furnariidae	Neotropical	~60	20-22[1]	20-22[1]	10	-	Fuhrmann (1908)
B. quelea (Mettrick, 1963) Spasskii, 1977	Ploceidae	Afrotropical	56-58	19-21	16-18	9-13	93-143x36-49	Georgiev *et al.* (2002)
B. ugandae Baylis, 1919	Nectariniidae	Afrotropical	58	20-21	17-19	12-14	82-90x34-41	Georgiev *et al.* (2002)
B. singhi Matevosyan, 1965, syn *B. meggitti* Singh, 1959, pre-occupied	Dicruridae	Oriental	56	17-21	13-16	9-12	80-120x27-38	Singh (1959)
B. chlorurae (Rausch & Schiller, 1949) Spasskaya & Spasskii, 1971	Emberizidae	Nearctic	40-42	20	16	10-12	105-119x23-29	Matevosyan (1969)
B. collurionis Matevosyan, 1950	Laniidae	Palaearctic	58-64	18-20	15-17	10-12	80-110x30-38	Matevosyan (1969), Kornyushin (1989)
B. dicruri Singh, 1964	Dicruridae	Oriental	40	18	14-16	7-11	80-110x26-40	Matevosyan (1969)
B. motacillabrasiliensis (Rudolphi, 1819) Fuhrmann, 1932	Motacillidae (?)[3]	Neotropical	30	15[1]	15[1]	-	-	Krabbe (1869)
B. globosa Fuhrmann, 1908	Cotingidae	Neotropical	24	14-16[1]	14-16[1]	-	-	Fuhrmann (1908)
B. motacillacayanae (Rudolphi, 1819) Matevosyan, 1969, syn. *B. motacilla* Fuhrmann, 1908	Thraupidae	Neotropical	32	14[1]	14[1]	-	-	Fuhrmann (1908)
B. clavula (von Linstow, 1888) Fuhrmann, 1908, syn. *B. paradisea* Fuhrmann, 1902[5]	Paradisaeidae	Australian	56-60	11-12[1]	11-12[1]	32	-	Fuhrmann (1908)
B. mertoni Fuhrmann, 1911	Paradisaeidae	Australian	-	-	-	~15	-	Fuhrmann (1911)

[1] Lengths of the anterior and posterior hooks not given separately.

[2] Originally described from '*Gracula* sp.' (Fuhrmann, 1908). The genus *Gracula* L. belongs to the family Sturnidae, which does not occur in South America (Howard & Moore,1980). The material originated from Vienna Museum and several icterid genera occurring in Brazil have as part of their German vernacular name 'Grackel'. In English, 'grackle' is used as a part of the vernacular name of both *Gracula* spp. and several icterid genera.

[3] Originally described from '*Motacilla* sp.' from Brazil (Krabbe, 1869). The genus *Motacilla* L. does not occur in South America (Howard & Moore, 1980).

[4] Synonymy after Georgiev *et al.* (2004).

[5] Synonymy after Fuhrmann (1908).

[6] Rysavy & Sixl (1977) did not report the length of the cirrus sac; the length given in the table is estimated on the basis of their drawing of mature proglottis.

& Timon-David, 1934 (see Georgiev & Kornyushin, 1994), a genus which includes specific parasites of hoopoes (Upupidae and Phoeniculidae); therefore, we believe that the affiliation of this species to *Biuterina* requires further confirmation. Nevertheless, *B. petroniae* differs from *B. landsdowni* by the considerably smaller number of testes and a substantial difference in the length of the posterior rostellar hooks (Table 3).

B. campanulata and *B. trapezoides* are poorly known Neotropical species; the only sources concerning their morphology are their original descriptions (Fuhrmann, 1908). They are both characterised by a considerably smaller number of rostellar hooks (26 and about 30, respectively) than in the present material (42-48).

Our worms are most similar to *B. macrancistrota* (for a redescription, see Mariaux & Vaucher, 1989). This species has a body about twice the length of our material (22 versus 10-13 mm) and consists of many more proglottides (180 versus 51-56). A substantial part of its cirrus sac is situated in the median field in mature proglottides, while in the new species this organ occurs in the lateral field. Another difference is the shape of ovary, which is clearly bi-winged in the new species and a massive, rather transversely elongate oval structure in *B. macrancistrota*.

On the basis of these differences, we consider that the present material is a new species.

DISCUSSION

In addition to the material described above, Mariaux (1994) reported a species of *Biuterina* from *Sylvietta virens* Cassin (Sylviidae). This material does indeed belong to this genus and might represent a new species. However, the specimens available are fragmented and do not permit the preparation of a complete description.

The concept of *Biuterina* adopted in the present article corresponds to those presented in previous studies (Bona & Maffi, 1984; Kornyushin, 1989; Georgiev & Kornyushin, 1994). It is defined by the presence of two symmetrical uterine sacs connected by an anterior isthmus, no matter whether the entire uterus is embedded by the paruterine organ or only its anterior part. However, whether this is a synapomorphy of a monophyletic *Biuterina* or not will be a subject for further studies. Furthermore, other paruterinid genera (*Triaenorhina* Spasskii & Shumilo, 1965, *Neyraia* Joyeux & Timon-David, 1934 and *Spasskyterina* Kornyushin, 1989) are characterised by two symmetrical uterine sacs, although of various shape.

Currently, we recognise 34 species as belonging to this genus (Table 3). The position of two of them in *Biuterina* is doubtful. *B. lansdowni* Malhotra & Capoor, 1987, from *Upupa epops* L. in India (Malhotra & Capoor, 1987), has hooks and gravid proglottides strongly resembling *Neyraia intricata* (Krabbe, 1878) from the same host species. Whereas *B. diversihamata* Sawada, Hassan & Saleen, 1994, from *Coracias garrulus* L. in Iraq (Sawada *et al.*, 1994), we suspect to be a synonym of *Triaenorhina rectangula* (Fuhrmann, 1908). It is our opinion that these two taxa represent *species inquirendae*, but they are retained in the key below, pending a re-examination of the type material.

Six species have previously been considered members of *Biuterina* (see Matevosyan, 1969; Schmidt, 1986) and are currently placed in other genera. *B. rectangula* Fuhrmann, 1908 from *Coracias garrulus* L. (Europe?) was selected as the type species of *Triaenorhina* (see Spasskii & Shumilo, 1965). Three cestode species from the same host were recognised as synonyms of *T. rectangula*; these are *B. coracii* Chiriac, 1963 from Romania, *B. garrulae* (Matevosyan, 1950) from Smolenskaya Oblast', Russia, and *B. uzbekiensis* Matevosyan, 1964 from Uzbekistan (synonymy after Spasskaya & Spasskii, 1971; Kornyushin, 1989; Georgiev & Gibson, 2006). In addition, *B. dunganica* Skrjabin, 1914 from *Oriolus oriolus* L. in Kazakhstan was transferred to *Spasskyterina* Kornyushin, 1989 (see Kornyushin, 1989) and *B. meggitti* (Johri, 1931) from bucerotid birds in India and Somalia is currently recognised as a species of *Triaenorhina* (see Kornyushin, 1989; Georgiev & Gibson, 2006).

Recent studies have provided new morphological data for most of the Old-World species and re-evaluated their validity (Kornyushin, 1989; Mariaux & Vaucher, 1989; Georgiev *et al.*, 2002, 2004). However, most of the New-World species are known from their original descriptions only and are in need of taxonomic revision. Nevertheless, we propose the following key based on our current knowledge of *Biuterina* spp. (*B. motacillabrasiliensis* and *B. motacillacayanae* are poorly described parasites of Neotropical passerines and lack reliable distinguishing features.

KEY TO THE SPECIES OF *BIUTERINA*
(See Table 3 for authorities for species names)

1a. Parasites of Paradisaeidae in the Australian Region 2
1b. Parasites of other birds 3
2a. Testes ~30 in number. Genital atrium without distinct dilatory muscles . . . . *B. clavula*
2b. Testes ~15 in number. Genital atrium with distinct dilatory muscles . . . . *B. mertoni*
3a. Anterior rostellar hooks ≤ 17 long; if anterior rostellar hooks 17 long then total number of rostellar hooks ≤ 32 4
3b. Anterior rostellar hooks □17 long; if anterior rostellar hooks 17 long or slightly longer then total number of rostellar hooks □40 5
4a. Rostellar hooks 24 in number . . . . *B. globosa*
4b. Rostellar hooks 30-32 in number . . . . *B. motacillabrasiliensis* and *B. motacillacayanae*
5a. Uterus entirely embedded in paruterine organ in pregravid proglottides 6
5b. Paruterine organ situated anterior to uterus in pregravid proglottides, not entirely embedding it 8
6a. Developing uterus horseshoe-shaped, with posteriorly directed lateral extremities 7
6b. Developing uterus consisting of two rounded lateral chambers connected anteriorly by narrow, branched isthmus . . . . *B. passerina*
7a. Rostellar hooks 26-30 in number; anterior hooks □56 long . . . . . . *B. cordifera*
7b. Rostellar hooks 56-62 in number; anterior hooks 24-25 long . . . . *B. pogoniuli*
7c. Rostellar hooks 40-42 in number; anterior hooks 20 long . . . . *B. chlorurae*
8a. Anterior rostellar hooks > 35 long 9
8b. Anterior rostellar hooks < 35 long 21

9a. Number of rostellar hooks ≤ 20 10
9b. Number of rostellar hooks □26 11
10a. Number of rostellar hooks 14; anterior rostellar hooks 56-60 long; cirrus sac ~140 long .... *B. erithaci*
10b. Number of rostellar hooks 18-20; anterior rostellar hooks 44-48 long; cirrus sac ~90 long .... *B. fallax*
11a. Anterior rostellar hooks 75-85 long .... *B. africana*
11b. Anterior rostellar hooks ≤ 70 long 12
12a. Anterior rostellar hooks 58-66 long 13
12b. Anterior rostellar hooks 38-49 long 14
13a. Rostellar hooks 34-36 in number; testes 15-18 in number; cirrus sac 86-105 long .... *B. morgani*
13b. Rostellar hooks 40-44 in number; testes 6-9 in number; cirrus sac > 120 long .... *B. triangula*
14a. Rostellar hooks spine-like .... *B. lansdowni*
14b. Rostellar hooks triangular, of typical shape for *Biuterina* 15
15a. Rostellar hooks ≤ 30 in number 16
15b. Rostellar hooks > 35 in number 17
16a. Rostellar hooks 26 in number, anterior rostellar hooks 43-46 long; paruterine organ wide, occupying almost entire width of median field .... *B. campanulata*
16b. Rostellar hooks ~30 in number; anterior rostellar hooks 41 long; paruterine organ in middle of median field .... *B. trapezoides*
17a. Anterior rostellar hooks < 45 long 18
17b. Anterior rostellar hooks > 45 long 19
18a. Gravid strobila consisting of ~180 proglottides; cirrus sac crosses poral osmoregulatory canals and substantial part of it situated in median field .... *B. macrancistrota*
18b. Gravid strobila consisting of ~50-60 proglottides; cirrus sac in lateral field .... *B. petroniae*
19a. Posterior rostellar hooks not longer than 55% of length of anterior rostellar hooks .... *B. planirostris*
19b. Posterior rostellar hooks longer than 60% of length of anterior rostellar hooks 20
20a. Blade of rostellar hooks 4-5 times shorter than handle .... *B. diversihamata*
20b. Blade of rostellar hooks slightly longer than handle or of same length .... *B. sobolevi*
21a. Rostellar hooks ~20 in number .... *B. distincta*
21b. Rostellar hooks > 30 in number 22
22a. Anterior rostellar hooks > 30 long .... *B. reynoldsi*
22b. Anterior rostellar hooks < 30 long 23
23a. Rostellar hooks > 56 in number 24
23b. Rostellar hooks ≤ 52 in number 27
24a. Rostellum consists of weak musculature and strongly developed glandular tissue .... *B. quelea*

24b. Rostellum consists of strongly developed musculature, with no glandular tissue or glandular tissue weakly developed 25
25a. Paruterine organ in pregravid proglottides occupies entire width of median field . . . . *B. ugandae*
25b. Paruterine organ distinctly narrower than width of median field 26
26a. Parasite of Furnariidae in the Neotropics (Brazil) . . . . *B. trigonacantha*
26b. Parasite of Dicruridae in India . . . . *B. singhi*
26c. Parasite of Laniidae in the Palaearctic . . . . *B. collurionis*
27a. Rostellar hooks 40 in number 28
27b. Rostellar hooks □48 (possibly, as exception, 42 in *B. fuhrmanni*) 29
28a. Anterior rostellar hooks 27 long . . . . *B. meropina*
28b. Anterior rostellar hooks < 20 long . . . . *B. dicruri*
29a. Testes number □12 . . . . *B. fuhrmanni*
29b. Testes number ≤ 10 30
30a. Rostellar hooks 52 in number; anterior rostellar hooks 23-25 long . . . . *B. cylindrica*
30b. Rostellar hooks 48 in number; anterior rostellar hooks 19-22 long . . . . *B. zambiensis*

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