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SHORT NOTE

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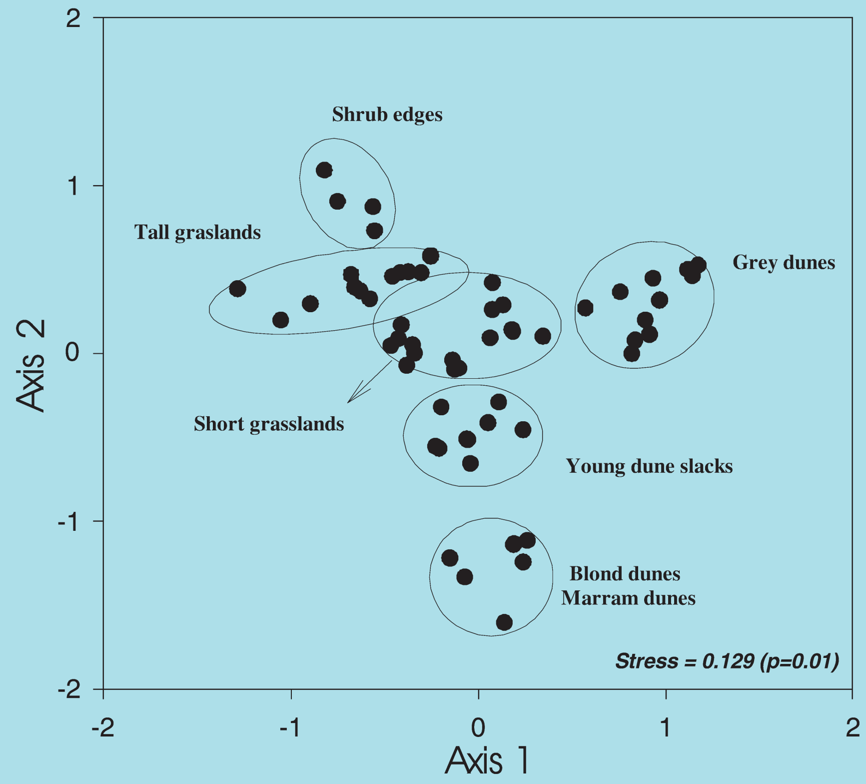

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On the homologies of the skeletal components of catfish (Teleostei: Siluriformes) suspensorium

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ABSTRACT. There has been much controversy concerning the identity of the components of the suspensorium in Siluriformes (catfishes). This confusion has implications not only for comparative morphology, but also for phylogenetic studies. The identity of the suspensorium components in catfish is reviewed here on the basis of: 1) dissections of numerous catfishes, including members of the most primitive group (Diplomystidae), and morphological descriptions in the literature; 2) developmental and paleontological data available; 3) functional morphology; and 4) comparisons with other member of the Ostariophysi, as well as with other teleosts. Our observations and comparisons indicate that catfish suspensorium consists of: 1) a hyomandibula+metapterygoid compound, which corresponds to the hyomandibula plus metapterygoid of other teleosts; 2) a symplectic+quadrate compound, which corresponds to the symplectic+quadrate of other teleosts; 3) an ectopterygoid+ectopterygoid compound, which corresponds to the entopterygoid plus ectopterygoid of other teleost. The small bones present in several catfishes between the anterior portions of the pars quadrata, the palatine, and the ethmoideal region are considered to be sesamoid ossifications.

KEY WORDS: catfish, comparative anatomy, cranium, evolution, ethmoideal region, homologies, morphology, Ostariophysi, suspensorium, Siluriformes, suspensorium.

INTRODUCTION

The division of the suspensorium into rostral (the palatine alone) and caudal (the other skeletal elements) units is a major synapomorphy of catfish (Fink & Fink, 1981; Arratia & Schultze, 1991; Arratia, 1992). This frees the palatine-maxillary system from the more posterior elements, thereby allowing ample movements of the maxillary barbels (Alexander, 1965; Gosline, 1975; Diogo & Chardon, 2000a; in press). The division is ontogenetically present from the first appearance of the splanchnocranium cartilages (Kindred, 1919; Arratia, 1987; 1990; 1992; Howes & Teugels, 1989; Surlemont & Vandewalle, 1990; Kobayakawa, 1992; Vandewalle et al., 1993; 1995a; 1997; Adriaens & Verraes 1998; etc.) and is probably required functionally by the early respiratory pattern of the larva (Vandewalle et al., 1985).

The division results in the lack of an anterior support for the large posterior portion of the suspensorium and the need for compensatory mechanisms, which are probably correlated with numerous synapomorphies in the suspensorium of different catfish lineages. Noteworthy differences between taxa involve several ligaments and small bones between the fore end of the pars quadrata, the palatine, and the ethmoideal region (Gosline, 1975).

There are usually three large bones (not including the preopercular) and some small bones in the pars quadrata, instead of five or six large bones present in that region in the other teleosts. The determination of the identity of the components of the pars quadrata of catfish has long been a matter of controversy. Despite a series of excellent contributions on the topic (see, for example, Regan, 1911; Starks, 1926; Fink & Fink, 1981; Howes, 1983; 1985; Arratia, 1987; 1990; 1992; Howes & Teugels, 1989), comparative and developmental arguments have not yet resulted in a satisfactory consensus as to the identity of the involved ossifications.

In most papers, including Arratia's 1992 well-documented review, the three large bones of the pars quadrata are considered as the hyomandibula, quadrate, and metapterygoid; with the symplectic considered to be totally absent; the smaller anterior bones are interpreted as either the ectopterygoid and/or entopterygoid or as sesamoid bones. Arratia's (1992) opinions appear, how-

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ever, subtler and adapted to particular cases, as will be demonstrated in the discussion. However, many authors have alternative interpretations, of which three are particularly interesting. Howes (1983) hypothesises that, in catfish, the hyomandibula of authors corresponds to the hyomandibula and metapterygoid of other teleosts, and that the so-called metapterygoid is the result of the fusion of the ecto- and entopterygoid sensu stricto, with the small bones being sesamoid ossifications. Howes (1985) suggests that the hyomandibula is the result of the fusion of the hyomandibula sensu stricto and the metapterygoid, with the so-called metapterygoid being the entopterygoid, and the small bones representing sesamoid ossifications. Howes & Teugels (1989) consider that the metapterygoid of authors is homologous to a part of the metapterygoid fused with an ecto- and an entopterygoid. The smaller anterior bones are interpreted as sesamoids and/or fragments of the dermal pterygoids.

On the basis of 1) careful dissections of numerous catfishes, including the most primitive ones (Diplomystidae: see Eigenmann, 1890; Regan, 1911; Alexander, 1965; Chardon, 1968; Lundberg & Baskin, 1969; Gosline, 1975; Fink & Fink, 1981; Arratia, 1987; 1992; Mo, 1991; De Pinna, 1993; 1998; Diogo & Chardon, 2000bc; Diogo et al., 2000b; in press; etc.) and the morphological descriptions in the literature, 2) available developmental and paleontological data, 3) functional morphology and 4) comparisons with other members of the Ostariophysi, as well as with other teleosts, we shall try to propose a comprehensive hypothesis about the homologies of the skeletal components of catfish suspensorium.

MATERIAL AND METHODS

The examined specimens are from the collection of our laboratory (LFEM), the “Musée Royal de l’Afrique Centrale” of (Tervuren: MRAC), the “Université Nationale du Bénin” (Kotonou: UNB), the “Muséum National D’Histoire Naturelle” (Paris: MNHN) and the National Museum of Natural History (Washington: USNM). Anatomical descriptions are made after dissection of fresh, alcohol-fixed or trypsin-cleared and alizarine-stained (following Taylor & Van Dyke’s 1985 method) specimens Dissections and morphological drawings were made using a Wild M5 dissecting microscope equipped with a camera lucida. The cleared and stained (c+s), fresh (fre) or alcohol-fixed (alc) condition of the studied fishes in the list below, is given in parentheses following the number of specimens dissected.

The following specimens were dissected:

Amphilius brevis Boulenger, 1902 (Amphiliidae): MRAC 89-043-P-403, 3 (alc); MRAC 89-043-P-2333, 1 (c+s). *Amphilius jacksonii* Boulenger, 1912 (Amphiliidae): LFEM, 2 (alc). *Andersonia leptura* Boulenger, 1900 (Doumeidae): MNHN 1961-0600, 1 (alc); *Arius herzbergii* (Bloch, 1794) (Ariidae): LFEM, 1 (fre). *Arius heudelotii* Valenciennes, 1840 (Ariidae): MRAC P.56259, 1 (alc); MRAC P.56260, 1 (alc); MRAC P.56261, 1 (alc); *Arius latiscutatus* Günther, 1864 (Ariidae): MRAC 90-057-P-995, 1 (alc). *Auchenoglanis biscutatus* (Geoffroy St. Hilaire, 1809) (Claroteidae): MRAC 73-015-P-999, 2 (alc). *Bagre marinus* (Mitchill, 1815) (Ariidae): LFEM, 1 (alc); LFEM, 1 (c+s). *Bagrus bayad* (Pfaff, 1933) (Bagridae): LFEM, 1 (alc); LFEM, 1 (c+s). *Bagrus docmac* (Forsskål, 1775) (Bagridae): LFEM, 2 (alc); MRAC 86-07-P-512, 1 (alc); MRAC 86-07-P-516, 1 (c+s); UNB, 2 (fre). *Belonoglanis tenuis* Boulenger, 1902 (Doumeinae): MRAC P.60494, 1 (alc). *Clariallabes melas* Boulenger, 1887 (Clariidae): LFEM, 2 (alc). *Clarias gariepinus* (Burchell, 1822) (Clariidae): LFEM, 2 (alc); LFEM, 2 (c+s); MRAC 93-152-P-1356, 1 (alc). *Chrysichthys auratus* (Geoffroy St. Hilaire, 1809) (Claroteidae): LFEM, 2 (c+s); UNB, 2 (alc); UNV, 3 (fre). *Chrysichthys cranchii* (Leach, 1818) (Claroteidae): LFEM, 1 (alc); LFEM, 2 (fre); LFEM, 1 (c+s). *Chrysichthys nigrodigitatus* (Lacepède, 1803) (Claroteidae): UNB, 2 (alc); UNB, 3 (fre); UNB, 2 (c+s). *Doumea typica* Sauvage, 1879 (Doumeidae): MRAC 93-041-P-1335, 1 (alc); MRAC 93-052-P-152, 1 (alc). *Diplomystes chilensis* (Molina, 1782) (Diplomystidae): LFEM, 2 (alc). *Genidens genidens* (Valenciennes, 1840) (Ariidae): LFEM, 2 (alc). *Hemibagrus wycki* (Bleeker, 1858) (Bagridae): LFEM, 1 (alc); LFEM, 1 (c+s). *Heterobranchus longifilis* Valenciennes, 1840 (Clariidae): LFEM, 2 (alc). *Ictalurus punctatus* (Rafinesque, 1818) (Ictaluridae): LFEM, 5 (alc). *Mochokus niloticus* Joannis, 1835 (Mochokidae): MRAC P.119413, 1 (alc); MRAC P.119415, 1 (alc). *Mystus gulio* (Hamilton, 1822) (Bagridae): LFEM, 1 (alc). *Neosilurus rendahli* (Whitley, 1928) (Plotosidae): USNM 173554, 2 (alc). *Paramphilius trichomycteroides* Pellegrin, 1907 (Amphiliidae): LFEM, 2 (alc). *Paraplotosus albilabris* (Valenciennes, 1840) (Plotosidae): USNM 173554, 2 (alc). *Phractura brevicauda* Boulenger, 1911 (Doumeidae): MRAC 90-057-P-5145, 2 (alc); MRAC 92-125-P-386, 1 (c+s). *Phractura intermedia* Boulenger, 1911 (Doumeidae): MRAC 73-016-P-5888, 1 (alc). *Pimelodus clarias* Geoffroy St. Hilaire, 1809 (Pimelodidae): LFEM, 2 (alc), LFEM, 3 (fre); LFEM, 2 (c+s). *Plotosus lineatus* Valenciennes, 1840 (Plotosidae): USNM 200226), 2 (alc). *Pseudomystus bicolor* (Fowler, 1934) (Bagridae): LFEM, 1 (alc), LFEM, 1 (c+s). *Schilbe intermedius* Rüppell, 1832 (Shilbeidae): MRAC P.58661, 1 (alc). *Silurus glanis* Linnaeus, 1758 (Siluridae): LFEM, 2 (alc).

LIST OF ABBREVIATIONS

“ADPT”	“additional pterygoid”
ATLP	additional tooth-plate
AF-	articulatory facet
AF-I	f. a. neurocranium-autopalatinum
C-	cartilago …
C-APAL-A	c. autopalatinus anterior
C-APAL-P	c. autopalatinus posterior
ECT-TE	ectopterygoid teeth
ISUT	imcomplete suture
L-	ligamentum …
L-ANG-“Q”	l. angulo- “quadratum”
L- “ECT”-APAL	l.“ectopterygoideum”-autopalatinum
L-ENT-VM	l. entopterygoideo-vomerale
L-“ENT”-APAL	l.“entopterygoideum”-autopalatinum

L-“ENT”-LETH	l. “entopterygoideo”-lateroethmoideum
L-“ENT”-VM	l. “entopterygoideo”-vomerale
L-“ENT”-PRMX-VM	l. “entopterygoideo”-praemaxillo-vomerale
L-“MP”-APAL	l.“metapterygoideo”-autapalatinum
L-“MP”-“ENT”	l.“metapterygoideo”-“entopterygoideum”
L-“MP”-MX	l.“metapterygoideo”-maxillare
L-“MP”-OSPH-LETH	l.“metapterygoideo”-orbito-lateroethmoideum
L-“MP”-PRMX-LETH	l.“metapterygoideo”-praemaxillo-lateroethmoideum
L-“MP”-PRMX-VM	l.“metapterygoideo”-praemaxillo-vomerale
L-“MP”-VM	l.“metapterygoideo”-vomerale
L-PRMX-MX	l. praemaxillo-maxillare
L-“Q”-“MP”	l. “quadrato”-“metapterygoideum”
L-“Q”-PRMX	l. “quadrato”-praeomaxillare
M-	musculus …
M-AD-AP	m. adductor arcus palatini
M-EX-T	m. extensor tentaculi
M-RE-T	m. retractor tentaculi
MND	mandible
“MP”-TE	“metapterygoid” teeth
MX-B	maxillary barbel
O-	os …
O-APAL	o. autopalatinum
O-ECT	o. ectopterygoideum
O-”ECT”	o. “ectopterygoideum”
O-ENT	o. entopterygoideum
O-”ENT”	o. “entopterygoideum”
O-HM	o. hyomandibulare
O-”HM”	o. “hyomandibulare”
O-IOP	o. interoperculare
O-LETH	o. latero-ethmoideum
O-METH	o. mesethmoideum
O-MP	o. metapterygoideum
O-”MP”	o. “metapterygoideum”
O-MX	o. maxillare
O-OP	o. operculare
O-OSPH	o. orbitosphenoideum
O-PARA	o. parasphenoideum
O-POP	o. praeoperculare
O-PRMX	o. praemaxillare
O-PROT	o. prooticum
O-PSPH	o. pterosphenoideum
O-PT	o. pteroticum
O-Q	o. quadratum
O-“Q”	o. “quadratum”
O-SPH	o. sphenoticum
O-SPOP	o. suprapraeoperculare
O-VM	o. vomerale
O-SY	o. symplecticum
T-M-EX-T	tendon of the musculus extensor tentaculi
VM-TLP	vomerine tooth-plate

RESULTS

We herein describe the suspensorium of representatives of eight catfish families. Recent studies (He, 1998; He et al., 1999; Diogo & Chardon, in preparation), have shown that the “Amphiliidae” as previously delimited are non monophyletic, and that, thus, the subfamilies “Doumeinae” and “Amphiliidae” should be raised to the family level; therefore, the Amphiliidae and Doumeidae of the present study correspond, respectively, to the former “Amphiliinae” and “Doumeinae”). Significant differences between the configuration of the suspensorium of these species and that of other species of the same families are noted.

In the descriptions, we follow the most commonly accepted nomenclature (see, Regan, 1911; David, 1936; Harry, 1953; Nawar, 1955; Tilak, 1961; 1963ab; 1964; 1965; Alexander, 1965; Jayaram, 1966; 1968; 1971; Gosline, 1975; Fink & Fink, 1981; 1996; Gauba, 1969; Skelton, 1981; Skelton et al., 1984; Schaefer, 1987; 1990; Kobayakama, 1989; 1992; Mo, 1991; De Pinna, 1993; 1996; 1998; De Vos, 1995; Vandewalle et al., 1997; He, 1998; Reis, 1998; He et al., 1999; Ng & Kottelat, 1999; etc.). The visual information presented in the figures has preponderance over the text, which will thus be brief.

Diplomystes chilensis Molina, 1782
(Diplomystidae)

Diplomystids are the catfishes richest in archaic characters and thus are considered to be the sister group of all the other siluriforms (Eigenmann, 1890; Regan 1911; Alexander 1965; Chardon 1968; Lundberg & Baskin 1969; Gosline 1975; Fink & Fink 1981; 1996; Arratia, 1987; 1992; Mo 1991; de Pinna, 1993; 1996; etc.). In *Diplomystes chilensis* (Figs 1, 2), the articulation between the suspensorium and the neurocranium is particularly elongated anteroposteriorly on the prootic, pterotic, sphenotic, and pterosphenoid (Fig. 1). The “quadrate” is triangular, being linked with the “hyomandibula” and the “metapterygoid” by cartilage (Fig. 1). Two ligaments originate from the forked anterior end of the “metapterygoid”, and attach respectively to the vomer (Fig. 2A) and to the palatine (Fig. 2B). Only on the right side of the dissected specimens is there an “entopterygoid”, which is imbedded in the ligament that attaches to the vomer (Fig. 2B). In both sides of these specimens the ligament that attaches to the palatine has some fibers in common with the other ligament and with a tendon of the extensor tentaculi muscle, and contains the “ectopterygoid” bone and an “additional pterygoid” (Fig. 2B).

There are some slight discrepancies between our observations and the literature. Alexander (1965: fig. 4A) does not mention the ligament between the “metapterygoid” and the palatine, nor the two “pterygoids” (“ectopterygoid” and “additional pterygoid”) embedded in it. Fink and Fink (1981: fig. 11) omit the same ligament and describe only two small bones anteriorly to the metapterygoid. Arratia’s (1987: fig. 6B) descriptions are

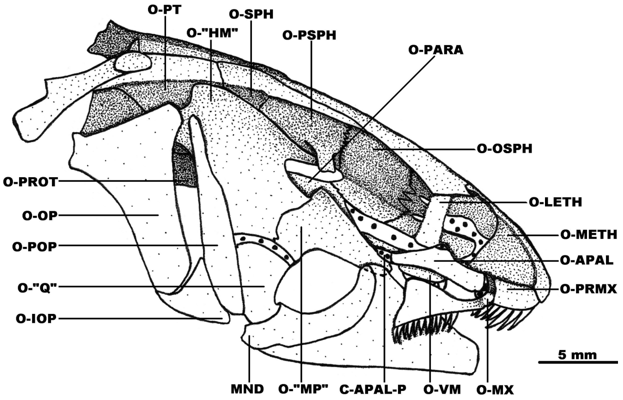

Fig. 1. – Lateral view of the skull of *Diplomystes chilensis*. Infraorbital series and mandibular teeth were removed. Ligaments are not represented.

much closer to our observations, since, although she does not figure the ligament between the "metapterygoid" and the palatine, she does mention in the text an "additional pterygoid" linked with the palatine by a short ligament.

Chrysichthys nigrodigitatus Lacépède, 1803 (Claroteidae)

The "hyomandibula" articulates with the pterotic and sphenotic (Fig. 3). The "quadrate" is associated with the "hyomandibula" and "metapterygoid" by cartilage and bony sutures (Fig. 3). The "metapterygoid" is strongly bifurcated anteriorly (Fig. 4A). Its anterolateral portion bears teeth ventrally and is linked to the vomer and to the premaxilla by a thick ligament in which a small toothed plate is imbedded (Fig. 4A). This is also the case in *Chrysichthys cranchii*, but not in *Chrysichthys auratus*,

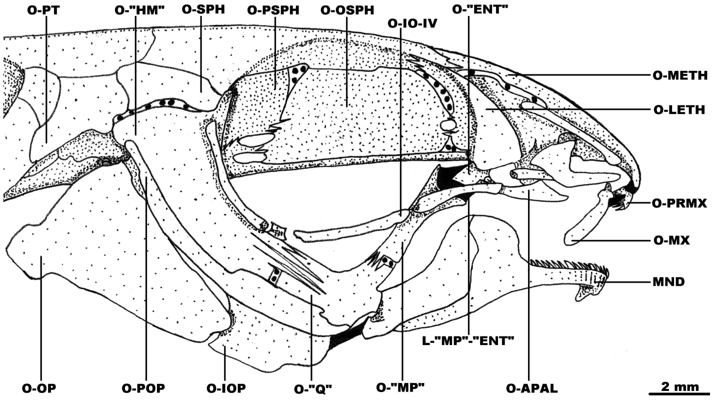

Fig. 3. – Lateral view of the skull of *Chrysichthys nigrodigitatus*. Primordial ligament, palatine cartilage and ligament between the "metapterygoid", vomer and premaxillary were removed.

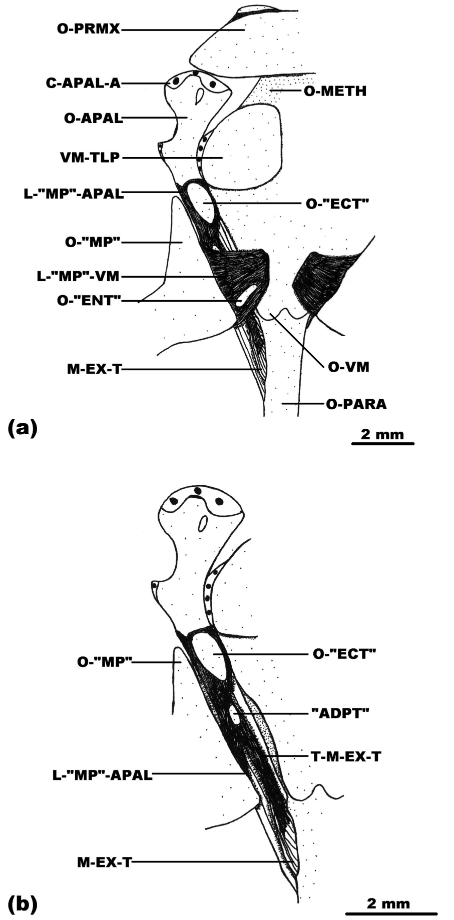

Fig. 2. – Ventral view of the anterior region of the suspensorium of *Diplomystes chilensis*. (A) Vomerine and premaxillary teeth were removed. (B) "Entopterygoid" and ligament between the "metapterygoid" and the vomer were removed.

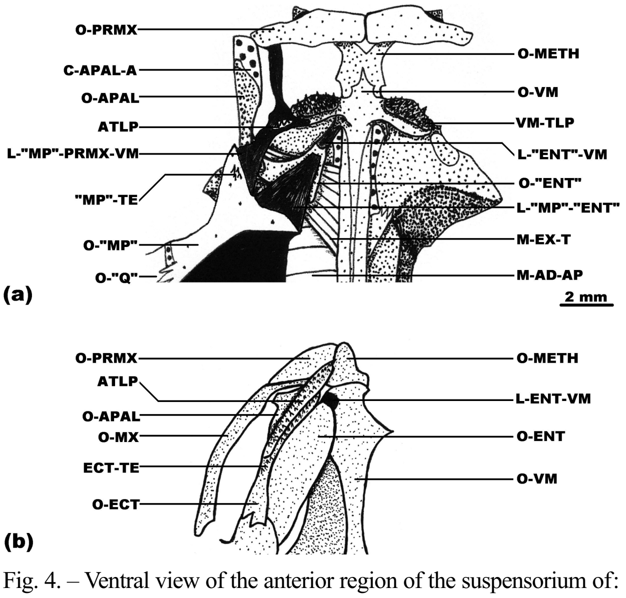

Fig. 4. – Ventral view of the anterior region of the suspensorium of: (A) *Chrysichthys nigrodigitatus*. Premaxillary teeth were removed. (B) *Hoplias* species (modified from Roberts, 1969: the nomenclature used here follows that used in the original illustration).

which lacks “metapterygoid” teeth, or in *Auchenoglanis biscutatus*, in which both these teeth and the small toothed plate are absent. The “entopterygoid” is associated, by means of two ligaments, with the anteromedial part of the “metapterygoid” and the vomer (Figs 4A, 5A). The “ectopterygoid” is firmly attached to the “entopterygoid” and is associated with the palatine by a short, thin ligament (Fig. 5A).

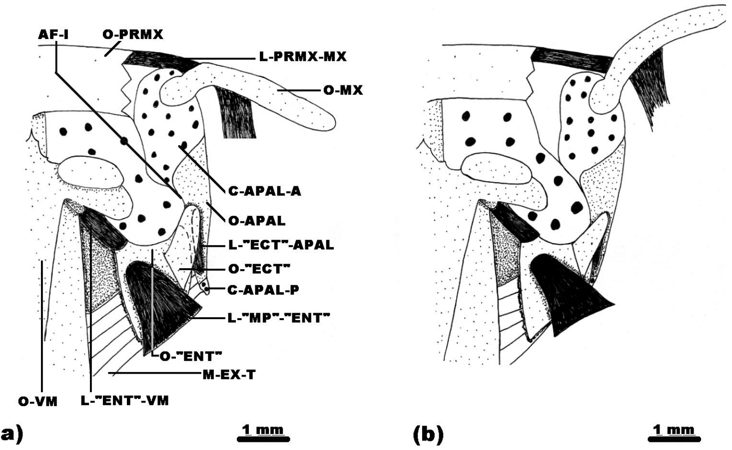

Fig. 5. – Ventral view of the palatine-maxillary system of *Chrysichthys cranchii*. The premaxillary was cut off to show the movements associated with this system. Vomerine and premaxillary teeth, as well as the ligament between the “metapterygoid”, vomer and premaxillary were removed. (A) The maxillary is adducted. (B) The maxillary is abducted.

Neosilurus rendahli Valenciennes, 1840
(Plotosidae)

The “hyomandibula” articulates with both the pterotic and sphenotic (Fig. 6). In the two specimens of *Neosilurus rendahli* dissected, but not in the other plotosid species studied, there is a prominent incomplete suture in the anterodorsal margin of the “hyomandibula” (Fig. 6). The “quadrate” is associated with the “hyomandibula” by cartilage and to the “metapterygoid” by cartilage and a bony suture (Fig. 6). Anteroventrally, the “quadrate” is associated with the posterior margin of the lower jaw by means of a large, strong ligament (Fig. 6). The antero-mesial edge of the “metapterygoid” is firmly attached to both the antero-lateral surface of the orbitosphenoid and the postero-lateral surface of the lateral ethmoid by means of a very short, strong ligament (Fig. 6). Anterolaterally, the “metapterygoid” is also strongly connected, by means of a very short ligament, with the large “entopterygoid” (Fig. 6). However, the roughly dentate aspect of both the anterior and the posterior surfaces of, respectively, the “metapterygoid” and the “entopterygoid”, associated to the very small gap existing between these bones, makes the ligamentous connection between them seem rather as a bony suture. The “ectopterygoid” is absent. The anterior margin of the “entopterygoid” is firmly attached by massive ligamentous tissue to the postero-lateral surface of the vomer.

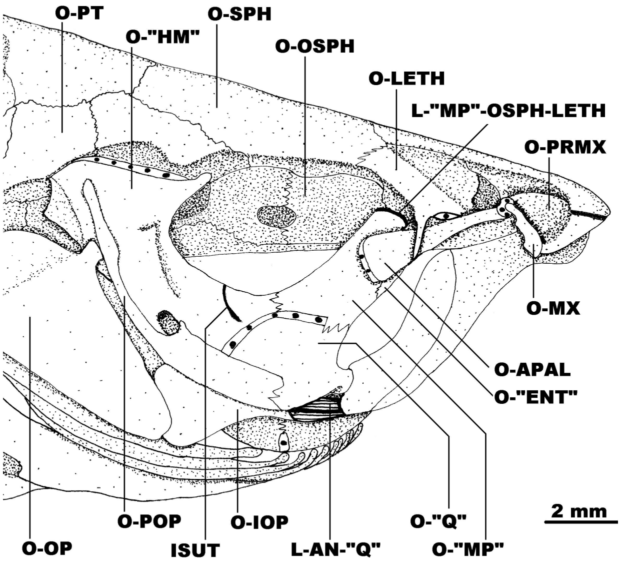

Fig. 6. – Lateral view of the skull of *Neosilurus rendahli*. Primordial ligament and infraorbital series were removed.

Bagrus docmak Forsskall, 1775
(Bagridae)

The “hyomandibula” articulates with both the sphenotic and pterotic and is linked to the “quadrate” by a cartilaginous band. The “metapterygoid” lies anterodorsally to the “quadrate” and is joined to it by cartilage and a short bony suture. The “entopterygoid” is attached by ligaments to the anteromedial part of the “metapterygoid” and to the lateral ethmoid (Fig. 7). The “ectopterygoid” is firmly attached medially to the “entopterygoid” and laterally, by a short ligament, to the palatine (Fig. 7). A long, thin ligament joins the anterolateral end of the “metapterygoid” to the maxilla (Fig. 7). In addition, there is a long, strong ligament between the upper surface of the “metapterygoid” and the posterior margin of the palatine.

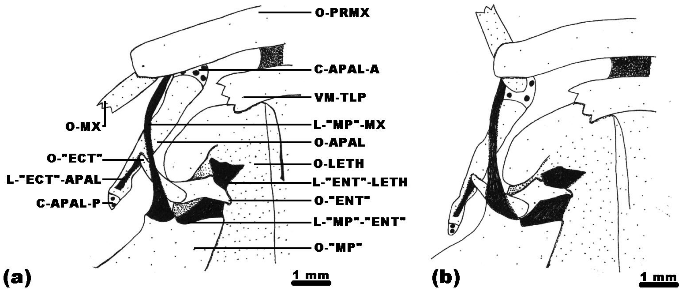

Fig. 7. – Ventral view of the palatine-maxillary system of *Bagrus docmak*. The vomerine tooth-plate was cut off to show the movements associated with this system. Vomerine and premaxillary teeth were removed. (A) The maxillary is adducted. (B) The maxillary is abducted.

Clarias gariepinus Burchell, 1822
(Clariidae)

The “hyomandibula” articulates with the pterotic and sphenotic. The very broad “quadrate” is attached to the “hyomandibula” by bony sutures and to the “metapterygoid” by bony sutures and a small, ventral cartilage band (Fig. 8). The large “entopterygoid” is linked to other bones by five ligaments (Fig. 9): 1) its posterior portion to the anteromesial edge of the “metapterygoid” by a very short, strong ligament; 2) its anterior part to the vomer by a thick ligament; 3) its antero-dorsal border to the lateral ethmoid by a short ligament; 4) its posterodorsal extremity to the palatine by a thin ligament; and 5) its anterolateral edge to the vomer and the premaxilla by a long, massive ligament. The “entopterygoid” of *Clariallabes melas* is much smaller than that of *Clarias gariepinus*, and is firmly associated with the anterolateral, and not with the anteromesial (see above) edge of the “metapterygoid”.

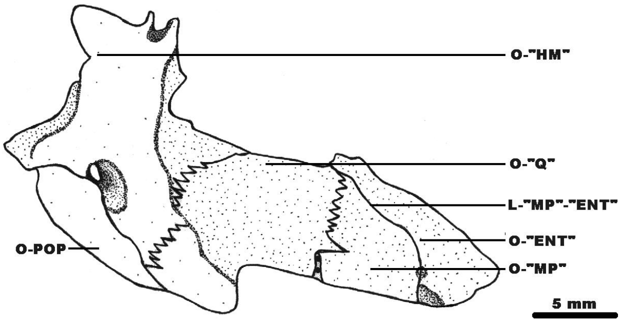

Fig. 8. – Medial view of the suspensorium (palatine not included) of *Clarias gariepinus*.

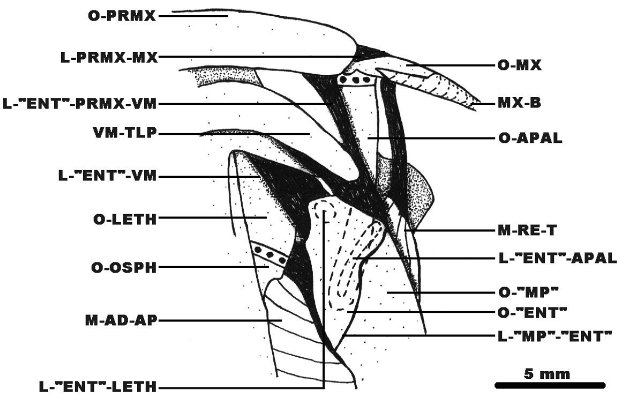

Fig. 9. – Ventral view of the anterior region of the suspensorium of *Clarias gariepinus*. Vomerine and premaxillary teeth are not represented.

Amphilius brevis Boulenger, 1902
(Amphiliidae)

In this species the articulation between the suspensorium and both the sphenotic and pterotic is particularly elongate (Fig. 10). The “quadrate” is associated to the “hyomandibula” and to the “metapterygoid” by bony sutures and cartilage (Fig. 10). The “metapterygoid” is deeply forked anteriorly (Fig. 10). This is also the case in *Amphilius jacksosii*, but not in *Paramphilius trichomycteroides*, in which the “metapterygoid” is a broad, rectangular bone without an anterior bifurcation. The anterolateral margin of the “metapterygoid” is attached by a long, thick ligament to both the lateral ethmoid and the premaxilla (Fig. 10). Its anteromedial portion is firmly linked to the “entopterygoid” by a very short, strong ligament (Fig. 10), and to the “entopterygoid” and the lateral ethmoid by massive ligamentous tissue.

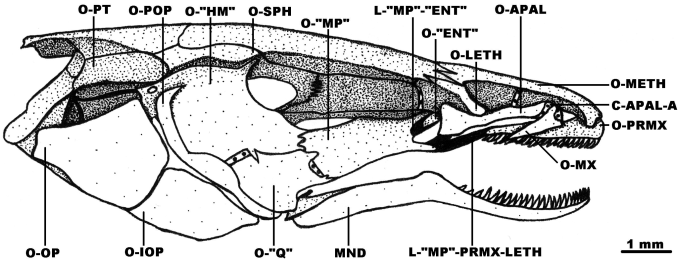

Fig. 10. – Lateral view of the skull of *Amphilius brevis*. Infraorbital series was removed. Only the ligaments associated with the suspensorium are represented.

Arius heudelotii Valenciennes, 1840
(Ariidae)

The “hyomandibula” articulates with the pterotic and sphenotic. It bears a prominent, thick lateral crest to which a medial section of the adductor mandibulae muscle attaches. The “quadrate” is associated with the “hyomandibula” by cartilage and to the “metapterygoid” by bony sutures. The “metapterygoid” is somewhat bifurcate anteriorly (Fig. 11). The “entopterygoid” is a small, triangular bone, which is joined, by means of two long, thick ligaments, with the anterolateral margin of the “metapterygoid” and the anteroventral margin of the vomer (Fig. 11). The main part of the ligament between the “entopterygoid” and the vomer is located dorsal to the well-developed vomerine tooth-plate (Fig. 11). The small, boomerang-shaped “ectopterygoid” is firmly articulated with the “entopterygoid” medially (Fig. 11). Laterally, this little bone is strongly connected by means of connective tissue to the posterior edge of the palatine (Fig. 11). The configuration of the “entopterygoid” of *Genidens genidens* is quite different from that of the “entopterygoid” of *Arius heudelotii*, and of the other ariid species studied, being a long, thin bone significantly larger than the “ectopterygoid”.

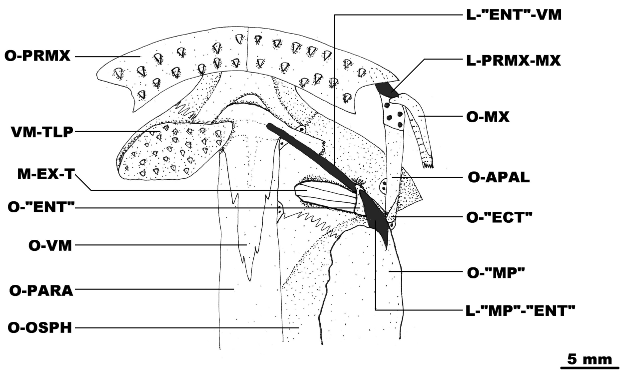

Fig. 11. – Ventral view of the anterior region of the suspensorium of *Arius heudelotii*. In the right side, the vomerine tooth-plate was removed.

Phractura brevicauda Boulenger, 1911 (Doumeidae)

The “hyomandibula” articulates with the sphenotic and pterotic (Fig. 12). The “quadrate” has a large number of pores (true holes). It is connected to the “hyomandibula” by a long cartilaginous strip (Figs 12, 13), to the premaxillary by a long, thick ligament and to the “metapterygoid” by massive connective tissue bands (Fig. 13). The “entopterygoid” is firmly attached to the “metapterygoid” and to the vomer by short, strong ligaments (Fig. 13). The “metapterygoid” is small, being much smaller than the “entopterygoid” (Figs 12, 13). However, it is more developed than that of the specimen of *Andersonia leptura* dissected, in which the “metapterygoid” is a very small, oval bone.

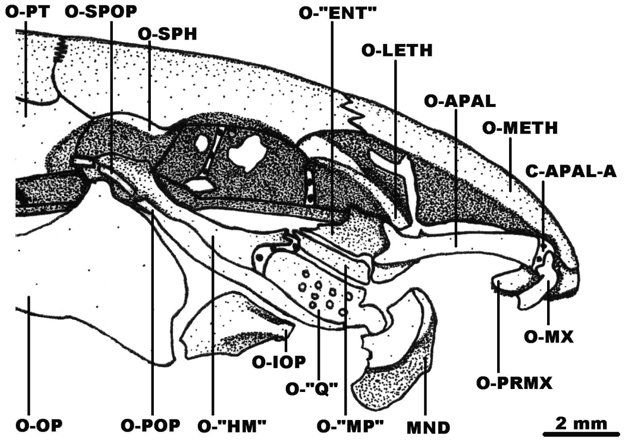

Fig. 12. – Lateral view of the skull of *Phractura brevicauda*. Infraorbital series was removed. Ligaments are not represented.

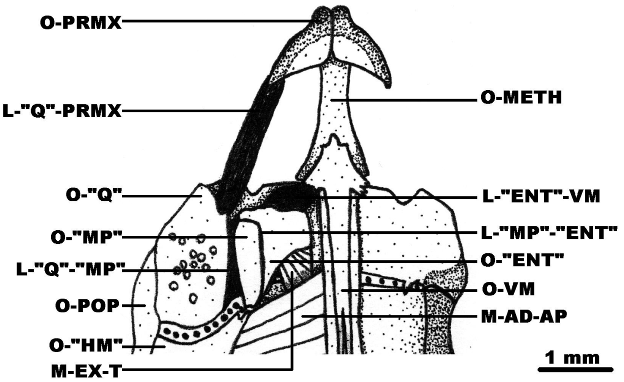

Fig. 13. – Ventral view of the anterior region of the suspensorium (palatine not included) of *Phractura brevicauda*. Premaxillary teeth are not represented.

DISCUSSION

In order to ascertain the true homologies of the ossifications of the suspensorium in catfish we compared the studied catfishes with other Siluriformes, other ostariophysans and even other teleosts. The comparison between catfishes and gymnotiforms, in particular, has proved very interesting. The gymnotiforms are considered to be the closest relatives of the siluriforms (FINK & FINK 1981; 1996; ARRATIA, 1992). The components of the suspensorium in gymnotiforms are easily homologised with those of other teleosts (CHARDON & DE LA HOZ, 1973; 1974; 1977; DE LA HOZ; 1974; MAGO-LECCIA, 1978; FINK & FINK, 1981; DE LA HOZ & CHARDON, 1984; ARRATIA & SCHULTZE, 1991; ARRATIA, 1992), with the exception of the so-called “entopterygoid”, which may represent the entopterygoid or the ectopterygoid or both (DE LA HOZ, 1974) (see below).

The suspensorium of one of the most archaic gymnotiforms, *Sternopygus macrurus* (Bloch & Schneider, 1801) (CHARDON & DE LA HOZ, 1974; 1977; DE LA HOZ, 1974; MAGO-LECCIA, 1978; FINK & FINK, 1981; DE LA HOZ & CHARDON, 1984; but see GAYET et al., 1994; ALBERT & FINK, 1996; ALBERT & CAMPOS DA PAZ, 1998, for a different view), and the South-American trichomycterid catfish *Trichomycterus areolatum* (Valenciennes, 1846) are very similar (Fig. 14), with: 1) a cartilaginous band (A) between two bones; 2) an inverted Y-shaped formation (B) in the middle of the suspensorium; and 3) only one bone (C) situated anterodorsal to this formation and extending up to half the length of the palatine.

Three differences are, however, noteworthy:

1) The A cartilage of *Sternopygus* (Fig. 14A) is prolonged by a clear separation (D) between two bones (hyomandibula and metapterygoid) (DE LA HOZ & CHARDON, 1984). In *Trichomycterus*, there is only a

partial suture between the bones at the same level (see, for example, Fig. 15C), and this is only observed in some species (as, e.g., *Trichomycterus roigi* Arratia & MenuMarque, 1984: see fig. 15C and Arratia & MenuMarque, 1984) of this genus (Arratia & Chang 1975; Arratia et al., 1978; Arratia & MenuMarque, 1981; 1984; Arratia, 1987; 1990; 1992). Complete sutures were however described at the same location in malapterurids (Fig. 15D) (Howes, 1985) and some diplomystids (see, for example, Fig. 15A, B) (Arratia, 1987).

2) In *Sternopygus*, the suspensorium is linked to the neurocranium by an ossified ligament (E), which terminates dorsally in very short fibres (Fig. 14A) (De La Hoz & Chardon, 1984), while *Trichomycterus* (Fig. 14B), like many other catfishes (Mo, 1991; Arratia, 1992), has these bones joined by a non-ossified ligament (Arratia, 1990). However, these ligaments seem to be homologous (see De La Hoz, 1974), and the almost total ossification of the ligament in some gymnotiforms is an unusual situation in this group (Chardon & De La Hoz, 1974; De La Hoz, 1974).

3) *Sternopygus*, like all Gymnotiformes (Chardon & De La Hoz, 1974; 1977; De La Hoz, 1974; Mago-Leccia, 1978; Fink & Fink, 1981; De La Hoz & Chardon, 1984), has a symplectic completely separate from the quadrate (F) (Fig. 14A). In *Trichomycterus* (Fig. 14B), a single ossification occupies the position of these two bones, without any visible separation at the level F. This separation is also lacking in all other catfishes (see, for example, Figs 1, 3, 6, 10, 16) except, perhaps (see below), *Malapterurus* (Fig. 15D) (Howes, 1985).

The above comparison strongly suggests the following homologies for the hitherto discussed skeletal parts of the suspensorium of catfish: *[1]* their "hyomandibula" (Fig. 14B) represents the hyomandibula+metapterygoid of other teleosts (Fig. 14A); *[2]* their "quadrate" (Fig. 14B) represents the quadrate+symplectic of the other teleosts (Fig. 14A); *[3]* their "metapterygoid" (Fig. 14B) corresponds to the "entopterygoid" of gymnotiforms (Fig. 14A). However, as mentioned before, the identity of the "entopterygoid" of the gymnotiforms is somewhat uncertain. In fact, Regan (1911) called this bone the "mesopterygoid" (="entopterygoid") without providing evidence to support its homology with the entopterygoid of other teleosts. This nomenclature was followed by other authors (Chardon & De La Hoz, 1973; 1974; 1977; De La Hoz, 1974; Mago-Leccia, 1978; Fink & Fink, 1981; Arratia & Schultze, 1991; Arratia, 1992; De La Hoz & Chardon, 1984; etc.), but some of them (e.g. Chardon & De La Hoz 1973; De La Hoz, 1974) pointed out that this bone has features typical of the entopterygoid (e.g. ligamentous connection with the neurocranium; relation with the adductor arcus palatini), ectopterygoid (e.g. antero-dorsal relation with the palatine) and entopterygoid+ectopterygoid (spatial position) of other ostariophysine fishes. We are unable, at the present, to determine the identity of the "entopterygoid" in the Gymnotiformes. However, our own observations,

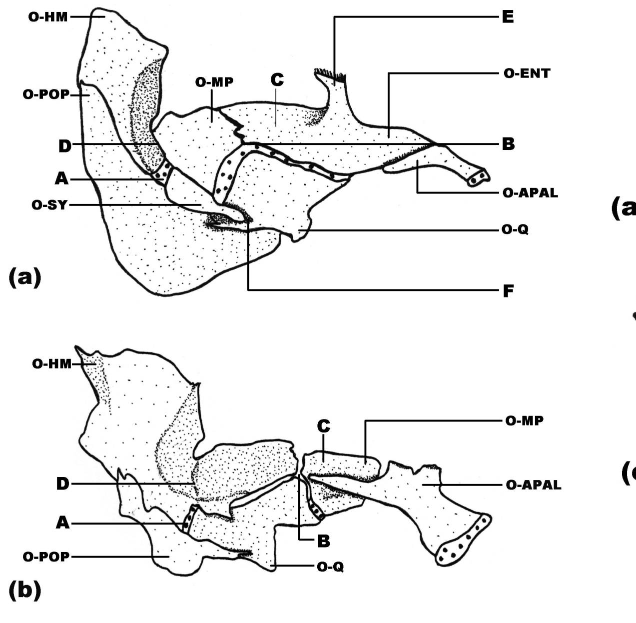

Fig. 14. – Lateral view of the suspensorium of: (A) *Sternopygus macrurus* (modified from De La Hoz & Chardon, 1984). (B) *Trichomycterus areolatum* (modified from Arratia, 1990). The nomenclature used here follows that used in the original illustrations.

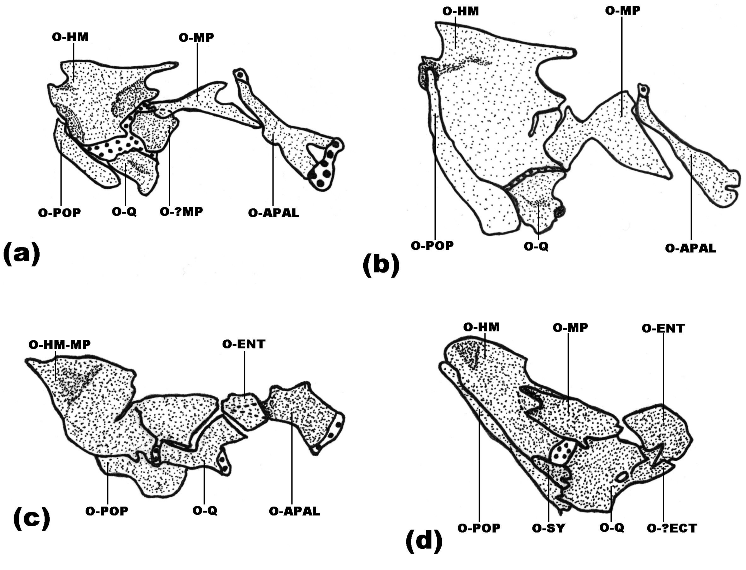

Fig. 15. – Suspensorium of: (A) *Diplomystes camposensis*, young specimen of about 28mm standard length (Modified from Arratia, 1987), lateral view. (B) *Diplomystes camposensis*, large specimen (modified from Arratia, 1987), lateral view. (C) *Trichomycterus roigi* (modified from Arratia & MenuMarque, 1984), dorsal view. (D) *Malapterurus electricus* (modified from Howes 1985), lateral view (the palatine is not represented). The nomenclature used here follows that used in the original illustrations.

together with the anatomical, paleontological and developmental data available in the literature on siluriforms and other groups of fishes, indicate that the "metapterygoid" of the catfish corresponds, very likely, to the entopterygoid+ectopterygoid of other teleosts, and that the small anterior bones present in most catfish (see, for example, Figs 2, 4A, 5, 7) are, in fact, sesamoid ossifications (see below). Further arguments are now presented in favour of this hypothesis.

Hyomandibula and metapterygoid

(1) The metapterygoid of teleosts results from the ossification of the posterodorsal part of the palatoquadrate, thus dorsally and somewhat posteriorly relative to the quadrate (see, for example, Starks, 1926; De Beer, 1937; Bertmar, 1959; Daget, 1964; Hunt Von Herbing et al., 1996; Verraes, 1977). It remains in the same position in almost all adults (see, for example, Starks, 1926; Gregory, 1933; De Beer, 1937; Weitzman, 1962; Daget, 1964; Osse, 1969; Roberts, 1969; De La Hoz, 1974; Taverne, 1974; Vandewalle, 1975; Gijsen & Chardon, 1976; Mago-Leccia, 1978; De La Hoz & Aldunate, 1994), with the exception of very few cases, such as some specialised clupeids such as *Engraulis encrasicholus* (Linnaeus, 1758) (Ridewood, 1904: fig. 135A). In the course of postembryonic development the palatoquadrate fuses and associates with the hyosymplectic, so that the ossifying metapterygoid contacts the future hyomandibula from which it remains separated by a cartilaginous strip, a suture, or a combination of both (Daget, 1964). So, given the position of the metapterygoid in these related groups and primitive teleosts, the true metapterygoid of catfish seems to correspond to the anterior part of the so-called "hyomandibula". The fusion between these two bones may be a consequence of the fact that in catfish the pars quadrata and the hyosymplectic are fused (see, for example, Kindred, 1919; Arratia, 1987; 1990; 1992; Howes & Teugels, 1989; Surlemont & Vandewalle, 1990; Kobayakawa, 1992; Vandewalle et al., 1993; 1995a; 1997; Adriaens & Verraes, 1998; etc.) from the first appearance of the chondrocranium cartilages.

The fact that this true metapterygoid is united by cartilage to the true entopterygoid+ectopterygoid (see below) could lead to the erroneous interpretation that both bones are enchondral and, thus, that the entopterygoid+ ectopterygoid cannot be a dermal compound, as hypothesised above. In fact the cartilage is, probably, the remnant of the pterygoid process of the pars quadrata. Such a cartilage remains present in some adult ostariophysan fishes, such as, for example, *Chanos chanos* (Forsskål, 1775) (Gonorynchiformes), *Opsariichthys uncirostris* Temminck & Schlegel, 1846 (Cypriniformes), *Xenocharax spilurus* Günther, 1867 (Characiformes) and *Sternopygus macrurus* (Gymnotiformes) (see, for example, Fink & Fink, 1981) as well as in some other adult teleosts (see, for example, Daget, 1964).

(2) In some juvenile *Diplomystes camposensis* Arratia, 1987 (Arratia, 1987) a broad, completely independent bone, which lies in the same position and presents the same configuration as the metapterygoid of other teleosts (see above), is present between the "hyomandibula", "metapterygoid" and "quadrate" (Fig. 15A: compare, for example, with Fig. 14A). Arratia (1987) stated that "it does not seem to result from fracture of one of the above ("hyomandibula", "metapterygoid" and "quadrate") mentioned bones". In adult specimens, this bone may be completely independent (Arratia, 1987: fig. 25C), but may be partially fused with the "hyomandibula" as well (Arratia, 1987). In this last case, only a partial suture is present between these two bones (Fig. 15B). Similar sutures also occur in some trichomycterids (see, for example, Fig. 15C) (Arratia & Chang, 1975; Arratia et al., 1978; Arratia & MenuMarque, 1981; 1984; Arratia, 1987; 1990; 1992), plotosids (see, for example, Fig. 6), and malapterurids (see, for example, Fig. 15D) (Howes, 1985). The fact that these partial or complete sutures appear in a position very similar to those between the hyomandibula and the metapterygoid of other teleosts (Fig. 15: compare with Fig. 14A) strongly supports the hypothesis that the so-called "hyomandibula" of catfish corresponds, in fact, to the hyomandibula plus metapterygoid of non-siluriform teleosts.

(3) *Chrysichthys nigrodigitatus*, like some other claroteids (see, for example, Skelton et al., 1984: fig. 15A; Mo 1991: fig. 54), some pimelodids (see, for example, Arratia, 1992: figs 35B, 36A) and some schilbeids (see, for example, Tilak, 1961: figs 7, 8) has a toothed "metapterygoid" (Fig. 4a). The teleost metapterygoid is enchondral and, thus, does not bear dermal toothplates (Jollie, 1986). Arratia (1992) suggested therefore that this toothed bone is "the metapterygoid fused with a dermal toothplate". As a toothed "metapterygoid" is present in some species of three not closely related catfish families (see, for example, Mo, 1991; De Pinna, 1993), Arratia's suggestion requires that the "metapterygoid"+dermal toothplate compound arose at least three times among catfishes, which seems unlikely since the development of such a compound is quite unusual in teleosts (Taverne, 1974). The explanation for the toothed "metapterygoid" of some siluriforms seems to be, thus, that this bone is not the true enchondral metapterygoid, but rather a dermal bone (toothed ectopterygoids and entopterygoids are widely distributed in teleosts: see Taverne, 1974).

(4) Some authors have also expressed opinions, convergent with our hypothesis:

Starks (1926), in a study dedicated to the ethmoideal region of several fishes, suggested that in siluriforms "the metapterygoid, if represented at all, may be incorporated with the pterygoid, but may well be incorporated with the hyomandibula".

Hoedeman (1960), in a work on the development of the skull of some callichthyids, suggested that in catfish the "hyomandibula is ontogenetically fused to the metapterygoid" and that the so-called "metapterygoid" is a dermal bone.

In an extensive work concerning some problems related to catfish anatomy, HOWES (1983: fig. 24) hypothesised that the so-called "hyomandibula" of siluriforms could be the hyomandibula plus metapterygoid of other teleosts.

In his extensive work on the anatomy and phylogeny of catfish, MO (1991) pointed out that "comparing the hyomandibula of siluroids with those of non-siluroid fishes, it is very likely that a large portion of the metapterygoid has joined to the hyomandibula at its lower dorso-medial margin in siluroids".

VANDEWALLE et al. (1993: fig. 2), in an embryological study concerning the suspensorium of *Clarias gariepinus* (Burchell, 1822) interpreted the so-called "metapterygoid" (Figs 8, 9) as dermal bone since "its ossification seems external to and independent of the processus pterygoquadrato" (VANDEWALLE et al., 1997). The dermal origin of the "metapterygoid" of this species was also suggested by POLL (1942).

Entopterygoid and ectopterygoid

It was pointed out above that in catfish the so-called "metapterygoid" is a dermal bone, and that the true metapterygoid is fused with the hyomandibula. We interpret this dermal bone as the entopterygoid+ectopterygoid of other teleosts, since:

(1) As mentioned, for example, by ALEXANDER (1965), HOWES (1983) and ARRATIA (1990; 1992), the "metapterygoid" in catfish occupies the position of the ectopterygoid and entopterygoid in other teleosts. In fact, this similarity is not restricted to the spatial position, but also extends to both the shape of the bone and its relations with other cranium components. The "metapterygoid" is bifurcated anteriorly in most generalised catfishes (see, for example, Figs 3, 4a, 11, 15a, b, 16b, and also TAVOLGA, 1962: Plates 9, 17; ALEXANDER, 1965: fig. 6; HOWES, 1983: figs 23, 24; SKELTON et al., 1984: fig. 4, 14; KOBAYAKAWA, 1989: figs 6, 27, 35; MO, 1991: figs 4, 44, 45, 48; ARRATIA, 1992: figs 16, 22, 25, 27, 33, 35, 36) but also in some specialised groups, as, for example, some amphiliids (Fig. 10) and callichthyids (ALEXANDER, 1965: fig. 15). This configuration is similar to that of the entopterygoid+ectopterygoid of some characiforms (see, for example, ROBERTS, 1969: fig. 18; GIJSEN & CHARDON, 1976: fig. 5; FINK & FINK, 1981: fig. 10A; MIQUELARENA & ARÁMBURU, 1983: fig. 6; ARRATIA, 1992: fig. 10A), cypriniforms (see, for example, VANDEWALLE, 1975: figs 2, 12; TAVERNE & DE VOS, 1997: fig. 6), gonorynchiforms (see, for example, ARRATIA, 1992: fig. 4d) and some "fossil Ostariophysi" – e.g. *Lusitanichthys characiformis* Gayet, 1981 (GAYET, 1985: figs 17, 20) and *Ramallichthys orientalis* Gayet, 1982 (GAYET, 1982: fig. 10). Moreover, the anteromedial and the anterolateral extremities of the "metapterygoid" of catfish have the same anatomical relations as, respectively, the entopterygoid and the ectopterygoid of other teleosts (see, for example, DAGET, 1964): the anteromedial margin is linked by a ligament to the neurocranium and the anterolateral tip is situated ventral to the posterior end of the palatine (see, for example, Figs 4A, 10). Therefore, the anteromedial and anterolateral margins of the "metapterygoid" of catfish seem to correspond, respectively, to the anterior tips of the entopterygoid and ectopterygoid of other teleosts, and, thus, this bone seem to be, in fact, an ento-ectopterygoid compound.

(2) *Chrysichthys nigrodigitatus*, like many other catfishes (EIGENMANN, 1890; STARKS, 1926; TILAK, 1961; ALEXANDER, 1965; GOSLINE, 1975; ARRATIA, 1987; 1992; etc.) possesses an additional tooth-plate (some catfish have more than one) between the anterior portion of the so-called "metapterygoid" and the ethmoideal region (Fig. 4A). The identity of these tooth plates has been a subject of controversy. Some authors (JAYARAM 1966; 1968; 1971; SKELTON, 1981; SKELTON et al., 1984; ARRATIA, 1987; 1992; etc.) suggest that such tooth plates are associated with the palatine. Others (EIGENMANN, 1890; STARKS, 1926; TILAK, 1961; GOSLINE, 1975; FINK & FINK, 1981) interpret them as structures associated with the vomer and to the anterolateral margin of the "metapterygoid". In *C. nigrodigitatus* the tooth plate is embedded in a long ligament between the premaxilla, the vomer, and the toothed anterolateral tip of the "metapterygoid" (Fig. 4A). The similarity between this configuration and that of some characiforms, as, for example, *Hoplias*, is remarkable (Fig. 4A, B). In fact, *Hoplias* (ROBERTS, 1969) has a tooth-plate associated to the toothed anterior portion of the ectopterygoid and to the premaxillary (Fig. 4B). This noticeable resemblance to the noted catfish condition, associated with the fact that such tooth-plates are present in a large number of characiforms (SAGEMEHL, 1885; STARKS, 1926; WEITZMAN, 1962, 1964; ROBERTS, 1969; FINK & FINK 1981; etc.), in some species of archaic or generalised catfish families – e.g. Diplomystidae, Ariidae, Pimelodidae, Claroteidae, Austroglanidae, Cranoglanididae, Bagridae and Schilbeidae – (EIGENMANN, 1890; STARKS, 1926; TILAK, 1961; GOSLINE, 1975; JAYARAM, 1966; FINK & FINK, 1981; SKELTON, 1981; ARRATIA, 1987; 1992; MO, 1991; etc.), and in *Hypsidoris farfonensis* Lundberg and Case, 1970, a fossil catfish from the Eocene (GRANDE, 1987), supports our suggestion that the anterolateral portion of the "metapterygoid" of catfish is homologous to the anterior tip of the ectopterygoid of other teleosts.

(3) HOWES (1983) reported that in *Pinirampus pirinampu* (Spix & Agassiz, 1829) and *Hypophthalmus edentatus* Spix & Agassiz, 1829, two South-American catfish, the usually called "metapterygoid" has "a sharply demarcated ventral portion that articulates with the (so-called*)* quadrate, whilst the dorsal portion articulates with the (so-called) hyomandibula process" (Fig. 16B). This observa-

tion led him to hypothesise that the "metapterygoid" is, in fact, the result of a fusion – which, in the particular case of *P. pirinampu* is incomplete (see Fig. 16B) – between the ectopterygoid and entopterygoid of other teleosts.

(4) Grande (1987), in his reconstruction of *Hypsidoris farsonensis*, a fossil catfish from the Eocene of the Green River formation, reported an "entopterygoid" sutured with a "metapterygoid" (Fig. 16a). However, as Arratia (1992) argued, this "condition is unlikely, when you compare it with other primitive siluroids" (see, for example, *Diplomystes chilensis*: Fig. 2A). Arratia (1992) proposed two alternative hypotheses: 1) that the two bones are not really sutured; 2) that Grande's "entopterygoid" is, in fact, a fragment of the so-called "metapterygoid". However, both of her hypotheses are questionable. First, even if we allow that Grande misinterpreted the presence of a suture between the two bones (which is not the case: see below), it seems unlikely that his "entopterygoid" is homologous to the true entopterygoid, since it does not have the same position and anatomical relations as the latter ossification (Fig. 16A). In reality, this "entopterygoid" has the typical features of the ectopterygoid of other teleosts (the spatial relation between its anterior portion and the posterior tip of the palatine, for example) (Fig. 16A). Moreover, it clearly corresponds to the anterolateral portion of the "metapterygoid" of other catfishes (compare, for example, Fig. 16A to Figs 3, 4A, 10, 15A). With respect to Arratia's second hypothesis, a post-mortem, incidental fracture of the "metapterygoid", resulting in the separation of two parts that present, respectively, the same spatial position and relations as the ectopterygoid and entopterygoid of other teleosts (see above), seems very improbable, especially since a similar fracture is also present in some living catfishes (see above). Moreover, a quite similar, complete fracture is equally present in *Astephus antiquus* (Leidy, 1873), a fossil ictalurid catfish that also occurs in the Eocene of the Green River formation (see Grande & Lundberg, 1988: Fig. 10). We thus agree with Grande's (1987) suggestion that the two parts corresponding to his "metapterygoid" and "entopterygoid" (see Fig. 16A) are, in fact, separated by a suture, and we interpret them as the true entopterygoid and the true ectopterygoid, respectively.

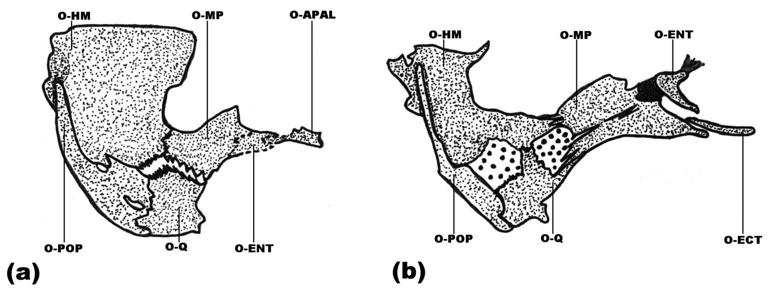

Fig. 16. – Lateral view of the suspensorium of: (A) *Hypsidoris farsonensis*, fossil catfish from the Eocene (modified from Grande, 1987). (B) *Pinirampus pirinampu* (modified from Howes, 1983) (the palatine is not represented). The nomenclature used here follows that used in the original illustrations.

(5) Some opinions, not mentioned above, are convergent with our hypothesis:

After studying the development of the pterygoid bones of some catfishes, Howes & Teugels (1989) pointed out that the true metapterygoid "persists in adult siluroids only as a densely ossified area of the palatoquadrate arch and not as a laminar ossification" and that the so-called "metapterygoid" is composed in great part by the entopterygoid and ectopterygoid of other teleosts.

Sesamoid bones

(1) In *Diplomystes chilensis*, the three anterior small bones of the suspensorium are clearly sesamoid ossifications related to ligaments and, in no way, vestigial bones (Fig. 2). In fact, if we compare them to those of other studied catfishes, it is clear that the larger anterior bones present in some more specialised siluriforms are the result of progressive ossification of these ligaments. The small "entopterygoids" of the generalised *Chrysichthys nigrodigitatus* (Fig. 4A) and *Bagrus docmak* (Fig. 7A) and the relatively wide "entopterygoids" of the specialised *Amphilius brevis* (Fig. 10), *Clarias gariepinus* (Fig. 9) and *Phractura brevicauda* (Fig. 13), for example, are clearly the result of progressive ossification of the "metapterygoid"-neurocranium ligament, which, in *Diplomystes chilensis*, is only slightly ossified (Fig. 2A: "entopterygoid"). This hypothesis is strongly supported by developmental data: a) in a detailed embryological study Adriaens & Verraes (1998) show that the so-called "entopterygoid" of one of the above-mentioned species (e.g. *Clarias gariepinus*) is, in reality, a sesamoid ossification of the ligament between the "metapterygoid" and the vomer; b) after studying the development of some silurids, Kobayakawa (1992) stated that the "entopterygoid" "has ligaments on both its anterior and posterior sides from the onset of its ossification (...), it appears as a small, rod-shaped bone connected by ligaments with the (so-called*)* metapterygoid posteriorly and the ventral surface of the lateral ethmoid anteriorly"; and c) according to Arratia (1990) "the "entopterygoid" in *Nematogenys* arises as an ossification of the ligament extending between the (so-called) metapterygoid and lateral ethmoid, and, late in ontogeny, with the vomer".

(2) The "ectopterygoid" and "entopterygoid" of catfish begin to develop anteriorly to the pterygoid process of the pars quadrata (see, for example, Kobayakawa, 1992: figs 9, 10; Vandewalle et al., 1993: fig. 2; 1995a: figs 9B, 10B; 1997: figs 7B, 8B), while in most teleosts the ectopterygoid and the entopterygoid develop on the processus pterygoideus (see, for example, De Beer, 1937; Daget, 1964; Bertmar, 1959). There is, thus, a difference between the place of origin of the anterior small bones in catfishes and that of the ectopterygoid and entopterygoid in other teleosts.

(3) The so-called "ectopterygoid" and "entopterygoid" of the examined catfish (see, e.g., Figs 2, 4A, 5, 7, 9, 13), as well as those of other siluriforms (see, for example, the descriptions of TILAK, 1963a: figs 6, 15, 21; 1965: figs 13, 14; GAUBA, 1969: fig. 16; HOWES, 1983: figs 23, 24; SRINIVASA RAO & LAKSHMI, 1984: fig. 9B; HOWES & TEUGELS, 1989: fig. 8; ARRATIA, 1990: fig. 12; 1992: figs 25B, 28A, D, 29, 33, 34; MO, 1991: figs 14, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49; KOBAYAKAWA, 1992: fig. 4; DIOGO et al., 1999: figs 3, 4; 2000a: fig. 3) are always associated with ligaments.

(4) HOWES & TEUGELS (1989) clearly show that the two anterior bones of the suspensorium of a 72 mm *Pimelodus blochii* Cuvier & Valenciennes, 1840 result from ossifications in the ligament joining the palatine to the lateral ethmoid, which is already conspicuous in a 40 mm specimen. According to these authors, the "entopterygoid" and "ectopterygoid" of catfish are sesamoid bones and/or fragments of the "metapterygoid".

(5) If the small bones present in the anterior portion of the suspensorium of some catfish are interpreted as reduced or vestigial pterygoids (entopterygoid and/or ectopterygoid), it is expected that they would generally be larger in primitive families than in specialised ones. However, in such primitive catfishes such as diplomystids (see, for example, Fig. 2) and the fossil *Hypsidoris farsonensis* (see, for example, Fig. 16A) these bones are very small or absent, whereas they are not as reduced in generalised siluriforms such as bagrids (see, for example, Fig. 7 and MO, 1991: figs 14, 40, 41, 42, 43, 46, 47; DIOGO et al., 1999: figs 3, 4), claroteids (see, for example, Fig. 4A, 5 and MO: figs 44, 45, 48), pimelodids (see, for example, Fig. 16A and ALEXANDER, 1965: fig. 6; HOWES, 1983: fig. 24; ARRATIA, 1992: fig. 35A, 36), schilbeids (see, for example, ALEXANDER, 1965: fig. 13; DE VOS, 1995: fig. 91), silurids (see, for example, KOBAYAKAWA, 1989: figs 14, 27, 35; 1992: Fig. 4), cranoglanidids (see descriptions of MO, 1991), malapterurids (see, for example, HOWES, 1985: fig. 13), austroglanids (see descriptions of MO, 1991) and ariids (see, for example, Fig. 11 and TILAK, 1965: fig. 14; SRINIVASA RAO & LAKSHMI, 1984: fig. 9). In certain more specialised catfishes, such as clariids (see, for example, Fig. 9 and DAVID, 1936: fig. 4C; TILAK, 1963b: fig. 4), amblycipitids (see, for example, MO, 1991: 28), amphiliids (see, for example, Fig. 10 and HARRY, 1953: fig. 10), doumeids (see, for example, Figs 12, 13 and DIOGO et al., 2000a: fig. 1, 3) and sisorids (see, for example, TILAK, 1963a: figs 6, 21; GAUBA, 1969: fig. 16) these bones are much larger, being sometimes as broad (or even broader) as the so-called "metapterygoid". It is unlikely that, basally among catfishes, the "ectopterygoid" and "entopterygoid" had become reduced or even lost, and, subsequently, re-acquired a large size in some more derived catfish. It is rather more probable that these bones are, in fact, sesamoid ossifications that had begun to develop in some primitive catfishes, and became progressively larger in some siluriform lineages. These ossifications are, probably, functionally related to the decoupling of the palatine from the rest of the suspensorium, as well as to the specialisation of the palatine-maxillary system. In fact, the shape of the sesamoid bones and associated ligaments in the suspensorium of siluriforms seems to be closely associated with the different types of palatine-maxillary system of these fishes. Thus, for example, in siluriforms with a "rocking" palatine-maxillary system (where the abduction of the maxillary is associated with a medial displacement of the back of the palatine: see GOSLINE, 1975) these structures are disposed so as to allow a pronounced medial movement of the rear end of the palatine (see, for example, Fig. 5 A→B), while in catfishes with a "sliding" palatine-maxillary system (where the abduction of the maxillary is associated with a posterior displacement of the palatine: see GOSLINE, 1975), in contrast, their configuration allows a large posterior displacement of this bone (see, for example, Fig. 7 A→B).

(6) Some opinions, not mentioned above, convergent with our hypothesis:

MCMURRICH (1884) interpreted the small bone "lying behind and within the posterior extremity of the palatine" in *Ictalurus catus* Linnaeus, 1758 as a sesamoid bone, which he called "bone number 4".

HOWES (1983, 1985) pointed out that the so-called "entopterygoid" and "ectopterygoid" of catfish are, probably, sesamoid bones.

ARRATIA (1987) stated: "... the position of this bone ("ectopterygoid") in diplomystids is not homologous with that of the ectopterygoid in other teleosts. This small pterygoid appears as an additional element of the series and it could represent a neomorphic feature". Concerning the other small bone present in the anterior portion of the suspensorium of some diplomystids, which corresponds to the "additional pterygoid" we figure in *Diplomystes chilensis* (Fig. 2B), she commented: "... it cannot be interpreted as belonging to the pterygoid series. I interpret it as a neomorphic feature".

According to ARRATIA (1992) the "pterygoid bones in most catfish are highly specialised sesamoid elements, connected by ligaments to cranial bones or other bones of the suspensorium (...) or additional bones whose function is unclear".

Quadrate and symplectic

(1) A 'typical' teleostean quadrate has a posterior notch in which the symplectic inserts on the lateral side (see, for example, TAVERNE, 1974: fig. 4). The inferior arm of the notch, which probably represents the quadratojugal (DEVILLERS, 1958), is lacking in some teleosts, as, for example, some clupeids (see, for example, RIDEWOOD, 1904: figs 124, 132). As for the symplectic, it remains cartilaginous in some mormyriforms (TAVERNE, 1974) and clupeiforms (RIDEWOOD, 1904). However, both the quadrate and the symplectic are present and well ossified

in the Gonorynchiformes (CHARDON & DE LA HOZ, 1974: figs 2, 3, 4, 5, 6; MAGO-LECCIA, 1978: fig. 12; FINK & FINK, 1981: fig. 12; ARRATIA, 1992: fig. 12A, B, D), Cypriniformes (see, for example, VANDEWALLE, 1975: figs 1, 2, 12; ARRATIA, 1992: fig. 8B; TAVERNE & DE VOS, 1997: fig. 6), Characiformes (see, for example, GIJSEN & CHARDON, 1976: fig. 5; ARRATIA, 1992: fig. 10A), Gymnotiformes (see, for example, fig. 14A and ARRATIA, 1992: fig. 12A, B, D) and "fossil Ostariophysi" (see, for example, GAYET, 1982: fig. 10; 1985: figs 2, 19, 20). Catfish have neither a notch nor a distinct symplectic – HOWES (1985) described a "symplectic" in the African catfish *Malapterurus electricus* (Gmelin, 1879) (see Fig. 15D), but this statement was questioned by ARRATIA (1992) – and it is thus plausible that the symplectic is incorporated into the quadrate, filling the notch. In fact, it is difficult to explain the disappearance of the quadrate notch and also the similar shape of the "quadrate" of catfishes and the quadrate+symplectic of other teleosts (see, for example, Fig. 14) if we accept that the "disappearance" of the symplectic in catfish is simply a function of the non-ossification of this element (see below). As in the case of the fusion between the hyomandibula and the metapterygoid (see above), the fusion between the quadrate and symplectic is probably related to the fact that in catfish the pars quadrata and the hyosymplectic are fused from the first appearance of the chondrocranium cartilage.

(2) Most authors (MCMURRICH, 1884; HARRY, 1953; TILAK, 1961; 1963ab; 1964; 1965; SKELTON, 1981; SKELTON et al., 1984; HOWES, 1983; MO, 1991; ARRATIA, 1992; ADRIAENS & VERRAES, 1998; etc.) consider that an ossified symplectic is absent in catfish, and interpret the cartilage between the "hyomandibula", preopercular and "quadrate" (see, for example, Figs 3, 10, 14B) as the remnant of the symplectic cartilage present early in ontogeny, and, thus, as the homologue of the symplectic of other teleosts. However, this cartilage differs from the typical symplectic by its position. Moreover, both the cartilage and the symplectic (which is always situated anteriorly to the cartilage) are present in gymnotiforms (see, for example, Fig. 14A and CHARDON & DE LA HOZ, 1974: figs 2, 3, 4, 5, 6; MAGO-LECCIA, 1978: fig. 12; FINK & FINK, 1981: fig. 12; ARRATIA, 1992: fig. 12a, b, d), characiforms (see, for example, WEITZMAN, 1964: fig. 7; FINK & FINK, 1981: fig. 10), cypriniforms (see, for example, VANDEWALLE, 1975: figs 1, 2; FINK & FINK, 1981: fig. 9; ARRATIA, 1992: fig. 4A), gonorynchiforms (see, for example, FINK & FINK, 1981: fig. 8; ARRATIA, 1990: fig. 2; 1992: fig. 4D) as well as in a large number of other teleosts (see, for example, RIDEWOOD, 1904: figs 123, 132; CHARDON & VANDEWALLE, 1971: fig. 2; VANDEWALLE, 1971: figs 6, 11; VANDEWALLE et al., 1995b: fig. 2), which implies that these structures can not be, in any way, homologous (compare Fig. 14A to Fig. 14B) [if two structures A and B are present at the same time in a certain species X, it cannot be considered that these two structures are homologous within two different species Y and Z: see, for example, GOULD, 1989; HALL, 1994; BEAUMONT, 1998).

General conclusions

The suspensorium of catfish is divided into the separate palatine and a posterior portion composed of the hyomandibulo-metapterygoid, the quadrato-symplectic and the ento-ectopterygoid (see Fig. 17). The smaller anterior bones are sesamoid ossifications. Despite the great diversity in the size and shape of these sesamoid bones (see above), three major types can be distinguished (toothed plates are not considered here) (see Fig. 17): 1) *sesamoid bone 1 of the suspensorium*, which corresponds to the so-called "entopterygoid", being associated, by means of ligaments, to the neurocranium (usually the vomer, lateral ethmoid and/or orbitosphenoid) anteriorly and to the ento-ectopterygoid posteriorly; 2) *sesamoid bone 2 of the suspensorium*, which corresponds to the so-called "ectopterygoid", being usually situated ventral to the palatine and, in most cases, linked to it by a short ligament; 3) *sesamoid bone 3 of the suspensorium*, which corresponds to the "additional pterygoid" figured in *Diplomystes chilensis* (Fig. 2B). It is present only in some diplomystids and is situated between the sesamoid bones 1 and 2, being imbedded in the ligament between the ento-ectopterygoid and the palatine.

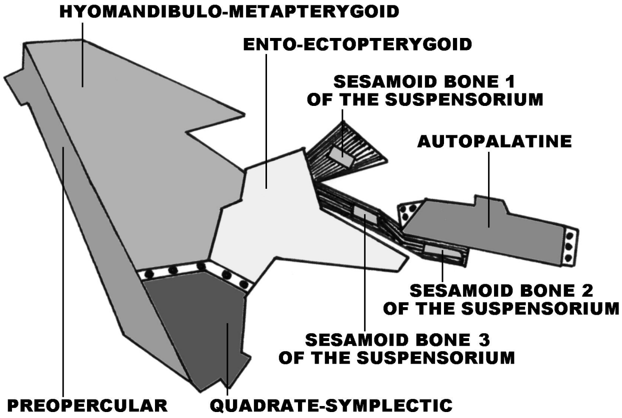

Fig. 17. – Scheme of the suspensorium of *Diplomystes chilensis* illustrating our interpretation of catfish suspensorial bones.

That hypothesis results from data from a variety of sources including comparative morphology, functional morphology, ontogeny, phylogeny and palaeontology, and results in a renewed nomenclature for the bones of the catfish suspensorium. It should be remembered that it was the misinterpretation of the catfish suspensorium that caused (and still causes) great confusion around this subject. It is hoped that the present work will contribute to an emergence from such confusion and facilitate future comparative and phylogenetic studies.

DE PINNA, M.C.C. (1998). Phylogenetic relationships of neotropical Siluriformes: Historical overview and synthesis of hypotheses. In: MALABARNA L.R, R.E. REIS, R.P. VARI, Z.M. LUCENA & C.A.S. LUCENA (eds), *Phylogeny and classification of neotropical fishes*, Edipucrs, Porto Alegre: 279-330.

DEVILLERS, C. (1958). Le crâne des poissons. In: GRASSÉ, P. (ed.), *Agnathes et Poissons, anatomie, éthologie, systématique,* Masson et Cle, Paris: 551-687.

DE VOS, L. (1995). A systematic revision of the African Schilbeidae (Teleostei: Siluriformes). *Ann. Mus. R. Afr. Centr.,* 271: 1-414.

DIOGO, R. & M. CHARDON (2000a). Anatomie et fonction des structures céphaliques associées á la prise de nourriture chez le genre *Chrysichthys* (Teleostei: Siluriformes). *Belg. J. Zool.*, 130: 21-37.

DIOGO, R. & M. CHARDON (2000b). Homologies among different adductor mandibulae sections of teleostean fishes, with special regard to catfishes (Teleostei: Siluriformes). *J. Morphol.,* 243: 193-208.

DIOGO, R. & M. CHARDON (2000c). The structures associated with catfish (Teleostei: Siluriformes) mandibular barbels: origin, anatomy, function, taxonomic distribution, nomenclature and synonymy. *Neth. J. Zool.,* 50: 455-478.

DIOGO, R. & M. CHARDON (in press). The adaptive transformation of the palatine-maxillary system in catfish: Toward freedom and increased mobility for a major sensory device, the maxillary barbel. In: KAPOOR, B.G. (ed.), *Sensory Biology of Jawed Fishes – New Insights*, Oxford & IBH Publishing and Science Publishers, New Delhi and New Hampshire.

DIOGO, R., P. VANDEWALLE & M. CHARDON (1999). Morphological description of the cephalic region of *Bagrus docmac*, with a reflection on Bagridae (Teleostei: Siluriformes) autapomorphies. *Neth. J. Zool*, 49: 207-232.

DIOGO, R., C. OLIVEIRA & M. CHARDON (2000a). On the anatomy and function of the cepahlic structures in *Phractura* (Siluriformes: Amphiliidae), with comments on some striking homoplasies occurring between the Doumeinae and some loricaroid catfishes. *Belg. J. Zool*, 130: 117-130.

DIOGO, R., C. OLIVEIRA & M. CHARDON (2000b). The origin and transformation of the palatine-maxillary system of catfish (Teleostei: Siluriformes): an example of macroevolution. *Neth. J. Zool*, 50: 373-388.

DIOGO, R., C. OLIVEIRA & M. CHARDON (in press). On the osteology and myology of catfish pectoral girdle, with a reflection on catfish (Teleostei: Siluriformes) plesiomorphies. *J. Morphol.*

EIGENMANN, C. (1890). The evolution of the catfish. *Zoe,* 11: 10-15.

FINK, S.V. & W.L. FINK (1981). Interrelationships of ostariophysan fishes (Teleostei). *Zool. J. Linnean Soc.,* 72: 297-353.

FINK, S.V. & W.L. FINK (1996). Interrelationships of ostariophysan fishes (Teleostei). In: STIASSNY, M.L.J., PARENTI, L.R. & JOHNSON, G.D. (eds), *Interrelationships of Fishes*, Academic Press, New York: 209-249.

GAUBA, R.K. (1969). The head skeleton of *Glyptosternum reticulatum* McLelland & Griffith. *Monitore Zool. Ital.,* 3: 1-17.

GAYET, M. (1982). Considération sur la Phylogénie et la Paléobiogéographie des Ostariophysaires. *Geobios,* 6: 39-52.

GAYET, M. (1985). Contribuition à l'Etude Anatomique et Systématique de l'Ichthyofaune Cénomanienne du Portugal. *Comun. Serv. Geol. Portugal,* 71: 91-118.

GAYET, M., F.J. MEUNIER & F. KIRSCHBAUM (1994). *Ellisella kirschbaumi* Gayet & Meunier, 1991, gymnotiforme fossile de Bolivie et ses relations phylogénétiques au sein des formes actuelles. *Cybium*, 18: 273-306.

GIJSEN, L & M. CHARDON (1976). Muscles et ligaments cèphaliques, splanchnocrâne et quelques possibilités de mouvements dans la tête d'*Hoplerythrinus unitaenatus* (Spix) (Teleostei, Ostariophysi, Characoidei). *Ann. Sc. Nat. Zool. Paris,* 18: 251-274.

GOSLINE, W.A. (1975). The palatine-maxillary mechanism in catfishes with comments on the evolution and zoogeography of modern siluroids. *Occ. Pap. Calif. Acad. Sci.,* 120: 1-31.

GOULD, S. J. (1989). The heart of terminology. *Nat. Hist.,* 97: 24-31

GRANDE, L. (1987). Redescription of *Hypsidoris farsonensis* (Teleostei: Siluriformes) with a reassessment of its phylogenetic relationships. *J. Vert. Paleont.,* 7: 24-54.

GRANDE, L. & J.G. LUNDBERG (1988). Revision and redescription of the genus Astephus (Siluriformes: Ictaluridae) with a discussion of its phylogenetic relationships. *J. Vert. Paleont.*, 8: 139-171.

GREGORY, W.K. (1933). Fish skulls. A study of the evolution of natural mechanisms. *Trans. Am. Philos. Soc.,* 23: 75-481.

HALL, B.K. (1994). *Homology, the Hierarchical Basis of Comparative Biology*. Academic, New York.

HARRY, R.R. (1953). A contribuition to the classification of the family Amphiliidae with descriptions of collections from Cameroon. *Rev. Zool. Bot. Afr.,* 47: 178-232.

HE, S. (1998). *Phylogénie et Biogéographie des Sisoridae et des Amphiliidae (Pisces: Siluriformes): deux familles de Poissons-Chats torrenticoles*. PhD. Thesis, Muséum National d'Histoire Naturelle (Paris).

HE, S., M. GAYET & F.J. MEUNIER (1999). Phylogeny on the Amphiliidae (Teleostei: Siluriformes). *Ann. Sci. Nat.,* 20: 117-146.

HOEDEMAN, J.J. (1960). Studies on callichthyid fishes: 4. Development of the skull in *Callichthys* and *Hoplosternum* (1) (Pisces: Siluriformes). *Bull. Aquat. Biol.,* 1: 73-84.

HOWES, G.J. (1983). Problems in catfish anatomy and phylogeny exemplified by the Neotropical Hypophthalmidae (Teleostei. Siluroidei). *Bull. Br. Mus. Nat. Hist. (Zool.),* 45: 1-39.

HOWES, G.J. (1985). The phylogenetic relationships of the electric family Malapteruridae (Teleostei. Siluroidei). *J. Nat. Hist.* 19: 37-67.

HOWES, G.J. & G.G. TEUGELS (1989). Observations and homology of the pterygoid bones in *Corydoras paleatus* and some other catfishes. *J. Zool. (Lond.*), 219: 441-456.

HUNT VON HERBING, I., T. MIYALE, B.K. HALL & R.G. BOUTILIER (1996). Ontogeny of feeding and respiration in larval Atlantic cod *Gadus morhua* (Teleostei, Gadiformes): I. Morphology. *J. Morphol.,* 227: 15-35.

JAYARAM, K.C. (1966). Contributions to study of the fishes of family Bagridae. 2. A systematic account of the African genera with a new classification of the family. *Bull. Inst. Fond. Afr. Noire,* 28: 1064-1139.

JAYARAM, K.C. (1968). Contributions to study of the bagrid fishes (Siluroidea: Bagridae). 3. A systematic account of the

Japanese, Chinese, Malayan and Indonesian genera. *Treubia. Mus. Zool. Bogoriense,* 27: 287-386.

Jayaram, K.C. (1971). Contributions to study of the bagrid fishes. 6. The skeleton of *Rita gogra* (Sykes). *J. Zool. Soc.India,* 22: 117-145.

Jollie, M. (1986). A primer of bone names for the understanding of the actinopterygian head and pectoral girdle skeletons. *Canadian. J. Zool.,* 64: 365-379.

Kindred, J. (1919). The skull of *Ameiurus*. *Illinois Biol. Mono.,* 5: 1-120.

Kobayakawa, M. (1989). Systematic Revision of the Catfish Genus *Silurus*, With Description of a New Species from Thailand and Burma. *Japan. J. Ichthyol.,* 36: 155-186.

Kobayakawa, M. (1992). Comparative Morphology and Development of Bony Elements in the Head Region in Three Species of Japanese Catfishes (*Silurus*: Siluridae; Siluriformes). *Japan. J. Ichthyol.,* 39: 25-36.

Lundberg, J.G. & J.N. Baskin (1969). The caudal skeleton of the catfishes, order Siluriformes. *Am. Mus. Novitates,* 2398: 1-49.

Mago-Leccia, F. (1978). Los peces de la familia Sternopygidae de Venezuela. *Acta Sci. Venez.* 29, Suppl. 1: 1-89.

McMurrich, J.P. (1884). On the osteology of *Amiurus catus* (L.) Gill. *Zool. Anz.,* 168: 296-299.

Miquelarena, A.M & R.H. Arámburu (1983). Osteologia y lepidologia de *Gymnocharacinus bergi* (Pisces Characidae). *Limnobios,* 2: 491-512.

Mo, T. (1991). Anatomy, relationships and systematics of the Bagridae (Teleostei: Siluroidei) with a hypothesis of siluroid phylogeny. *Theses Zoologicae,* 17: 1-216.

Nawar, G. (1955). On the anatomy of *Clarias lazera*: I. Osteology. *J. Morphol.,* 94: 551-586.

Ng, H.H. & M. Kottelat (1999). *Hyalobagrus*, a new genus of miniature bagrid catfish from Southeast asia. *Ichthyol. Explor. Freshwaters*, 9: 335-346.

Osse, J.W.M. (1969). Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.,* 19: 289-392.

Poll, M. (1942). Note sur l'ostéologie de *Dolichallabes microphthalmus* Poll et remarques sur l'evolution des Clariidae. *Ann. Soc. R. Zool. Belg.,* 3-4: 222-235.

Regan, C.T. (1911). The classification of the teleostean fishes of the order Ostariophysi – 2. Siluroidea. *Ann. & Mag. N. Hist.*, 8: 37-577.

Reis, R.E. (1998). Anatomy and phylogenetic analysis of the neotropical callichthyid catfishes (Ostariophysi, Siluriformes). *Zool. J. Linnean. Soc.*, 124: 105-168.

Ridewood, W.G. (1904). On the cranial osteology of the Clupeoid fishes. *Proc. Zool. Soc. Lond.,* 29: 448-493.

Roberts, T.R. (1969). Osteology and relationships of characoid fishes, particularly the genera *Hepsetus*, *Salminus*, *Hoplias*, *Ctenoluclus* and *Acestrorhynchus*. *Proc. Cal.Acad. Sci.,* 36: 91-500.

Sagemehl, M. (1885). Beiträge zur vergleichenden Anatomie der Fische, III. Das Cranium der Characiniden nebst allgemeine Bemerkungen über die mit einem Weber'schen Apparat versehenen Physostomen-familien. *Morphol. Jahrb.,* 10: 1-119.

Schaefer, S.A. (1987). Osteology of *Hypostomus plecostomus* (Linnaeus), with a phylogenetic analysis of the loricariid subfamilles (Pisces: Siluroidei). *Contrib. Sci.,* 394: 1-31.

Schaefer, S.A. (1990). Anatomy and relationships of the scoloplacid catfishes. *Proc. Acad. Nat. Sci. (Phil.),* 142: 167-210.

Skelton, P.H. (1981). The description and osteology of a new species of *Gephyroglanis* (Siluriformes, Bagridae) from the Olifants River, south west Cape, south Africa. *Ann. Cape Prov. Mus.* (Nat. Hist.), 13: 217-250.

Skelton, P.H., L. Risch & L. De Vos (1984). On the generic identity of the *Gephyroglanis* Catfishes from Southern Africa (Pisces, Siluroidei, Bagridae). *Rev. Zool. Afr.,* 983: 337-361.

Srinivasa Rao, K. & K. Lakshmi (1984). Head skeleton of the marine catfish *Arius tenuispinis* Day (Osteichthyes: Siluriformes, Ariidae). *J. Morphol.,* 118: 221-238.

Starks, E.C. (1926). Bones of the ethmoid region of the fish skull. *Stanford Univ. Publications,* 4: 139-338.

Surlemont, C. & P. Vandewalle (1990). Dévelopment postembrionnaire du squelette et de la musculature de la tête de *Clarias gariepinus* (Pisces, Siluriformes) depuis l'éclosion jusqu'à 6.8 mm. *Canadian J. Zool.,* 69: 1094-1103.

Taverne, L. (1974). Ostéologie d'*Elops* Linné, C., 1766 (Pisces, Elopiformes) et son intérêt phylogénétique. *Acad. R. Belg.,* 41: 1-96.

Taverne, L. & L. De Vos (1997). Ostéologie et morphologie d'un bariliné nouveau du bassin de la Malagarasi (système du Lac Tanganyika): *Opsaridium splendens* sp.n. (Teleostei, Cyprinidae). *J. Afr. Zool.,* 111: 281-300.

Tavolga, W.N. (1962). Mechanisms of sound production in the ariid catfishes *Galeichthys* and *Bagre*. *Bull. Am. Mus. Nat. Hist.,* 124: 5-30.

Taylor, W.R. & G.C. Van Dyke (1985). Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium,* 9: 107-119.

Tilak, R. (1961). The osteocranium and the Weberian apparatus of *Eutropiichthys vacha* (Ham.) and *Eutropiichthys murius* (Ham.): a study of inter-relationship. *Zool. Anz.,* 167: 413-430.

Tilak, R. (1963a). The osteocranium and the Weberian apparatus of the fishes of the family Sisoridae (Siluroidea): A study in adaptations and taxonomy. *Z. Wiss. Zool.,* 168: 281-320.

Tilak, R. (1963b). Relationships between the osteocranium and the Weberian apparatus in two Indian catfishes of the genus *Clarias* (Clariidae). *Copeia,* 1963: 623-629.

Tilak, R. (1964). The osteocranium and the Weberian apparatus of the family Schilbeidae. *Proc. Zool. Soc. Lond.,* 143: 1-36.

Tilak, R. (1965). The comparative morphology of the osteocranium and the Weberian apparatus of Tachysuridae (Pisces: Siluroidei). *J. Zool. (Lond.*), 146: 150-174.

Vandewalle, P. (1971). Comparaison ostéologique et myologique de cinc cichlidae Africains et Sud-Américains. *Ann. Soc. R. Zool. Belg.,* 4: 259-292.

Vandewalle, P. (1975). Contribuition à l'étude anatomique et fonctionnelle de la région céphalique de *Gobio gobio* (Pisces, Cyprinidae). 3. Les os, les muscles et les ligaments. *Forma et Functio,* 8: 331-360.

Vandewalle, P. (1977). Particularités anatomiques de la tête de deux Poissons Cyprinidés *Barbus barbus* (L.) et *Leuciscus leuciscus* (L). *Bull. Acad. R. Belg.,* 5: 469-479.

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REFERENCES

ADRIAENS, D. & W. VERRAES (1998). Ontogeny of the Osteocranium in the African Catfish, *Clarias gariepinus* Burchell (1982) (Siluriformes: Clariidae): ossification Sequence as a Response to Functional Demands. *J. Morphol.,* 235: 183-237.

ALBERT, J.S. & W.L. FINK (1996). *Sternopygus xingu*, a new species of electric fish from Brazil (Teleostei: Gymnotoidei), with comments on the phylogenetic position of *Sternopygus*. *Copeia*, 1996: 85-102.

ALBERT, J.S. & R. CAMPOZ-DA-PAZ (1998). Phylogenetic systematics of gymnotiformes with diagnoses of 58 clades: a review of available data. In: MALABARNA L.R, R.E. REIS, R.P. VARI, Z.M. LUCENA & C.A.S. LUCENA (eds), *Phylogeny and classification of neotropical fishes*, Edipucrs, Porto Alegre: 410-446.

ALEXANDER, R.M. (1965). Structure and function in catfish. *J. Zool. (Lond.*), 148: 88-152.

ARRATIA, G. (1987). Description of the primitive family Diplomystidae (Siluriformes, Teleostei, Pisces): morphology, taxonomy and phylogenetic implications. *Bonn. Zool. Monogr*., 24: 1-120.

ARRATIA, G. (1990). Development and diversity of the suspensorium of trichomycterids and comparison with loricarioids (Teleostei: Siluriformes). *J. Morphol.,* 205: 193-218.

ARRATIA, G. (1992). Development and variation of the suspensorium of primitive catfishes (Teleostei: Ostariophysi) and their phylogenetic relationships. *Bonn. Zool. Monogr*., 32: 1-148.

ARRATIA, G. & A. CHANG (1975). Osteología de *Pygidium areolatum* Valenciennes, 1848 (peces Siluriformes, Trichomycteridae). *Publ. Ocasional. Mus. Nac. Hist. Nat. Chile,* 18: 1-12.

ARRATIA, G., A. CHANG, S. MENUMARQUE. & G. ROJAS (1978). About *Bullockia* n. gen. and *Trichomycterus mendozensis* n.sp: revision of the family Trichomycteridae (Pisces, Siluriformes). *Stud. Neotrop. Fauna & Envir.,* 13: 157-194.

ARRATIA, G. & S. MENUMARQUE (1981). Revision of the freshwater catfishes of the genus *Hatcheria* (Siluriformes, Trichomycteridae) with commentaries on ecology and biogeography. *Zool. Anz.,* 207: 88-111.

ARRATIA, G. & S. MENUMARQUE (1984). New catfishes of the genus *Trichomycterus* from the high Andes of South America (Pisces, Siluriformes) with remarks on distribution and ecology. *Zool. Jb. Syst.,* 111: 493-520.

ARRATIA, G. & H.-P. SCHULTZE (1991). Development and homology of the palatoquadrate within osteichthyans. *J. Morphol.,* 208: 1-8.

BEAUMONT, A. (1998). La notion d'homologie. *Bull. Soc. Zool. Fr.,* 123: 311-321.

BERTMAR, G. (1959). On the ontogeny of the chondral skull in Characidae, with a discussion on the chondrocranial base and the visceral chondrocranium in fishes. *Acta Zool.,* 40: 203-364.

CHARDON, M. (1968). Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. *Ann. Mus. R. Afr. Centr.,* 169: 1-273.

CHARDON, M. & P. VANDEWALLE (1971). Comparaison de la région céphalique chez cinq espèces du genre *Tilapia*, dont trois incubateurs buccaux. *Ann. Soc. R. Zool. Belg.,* 101: 3-24.

CHARDON, M. & E. DE LA HOZ (1973). Notes sur le squelette, les muscles, les tendons et le cerveau des Gymnotoïdei. *Ann. Sc. Nat. Zool. Paris*, 15: 1-10.

CHARDON, M. & E. DE LA HOZ (1974). Towards an improved classification of the gymnotoid fishes by the use of splanchnocranium characters. *Ichthyologia,* 6: 15-25.

CHARDON, M. & E. DE LA HOZ (1977). Remarques anatomiques et fonctionnelles à propos du suspensorium et de la série operculaire chez *Sternopygus macrurus* et *Engenmania virescens* (Teleostei Gymnotoidei). *Ann. Soc. R. Zool. Belg.,* 106: 177-191.

DAGET, J. (1964). Le crâne des Téléostéens. *Mém. Mus. Natn. Hist. Nat.,* 31: 163-341.

DAVID, L. (1936). *Uegitglanis*, Silure aveugle de la Somalie italienne. Chainon entre Bagrides et Clariides. *Rev. Zool. Bot. Afr.,* 3: 369-388.

DE BEER, G. R. (1937). *The development of the vertebrate skull.* Clarendon Press, Oxford.

DE LA HOZ, E. (1974). *Définition et classification des poissons Gymnotoidei sur la base de la morphologie comparée et fonctionnélle du squelette et des muscles*. PhD Thesis, University of Liège.

DE LA HOZ, E. & M. CHARDON (1984). Skeleton, muscles, ligaments and swimm-bladder of a gymnotid fish, *Sternopygus macrurus* Bloch & Schneider (Ostariophysi Gymnotoidei). *Bull. Soc. R. Sci. Liège,* 53: 9-53.

DE LA HOZ, E. & R. ALDUNATE (1994). El sistema hioideomandibular de *Cheirodon* (Ostariophysi, Characidae): una innovation functional. *Ann. Mus. Hist. Nat. Valparaíso,* 22: 83-90.

DE PINNA, M.C.C. (1993). *Higher-level phylogeny of Siluriformes, with a new classification of the order (Teleostei, Ostariophysi).* PhD Thesis, University of New York.

DE PINNA, M.C.C. (1996). A phylogenetic analysis of the Asian catfish families Sisoridae, Akysidae and Amblycipitidae, with a hypothesis on the relationships of the neotropical Asprenidae (Teleostei, Ostariophysi). *Fieldiana (Zool)*, 84: 1-82.

VANDEWALLE, P., C. SURLEMONT, P. SANNA & M. CHARDON (1985). Intreprétation fonctionnelle de modifications du splanchnocrâne pendant le développement post-embryonaire de *Clarias gariepinus* (Téléostéens, Siluriformes). *Zool. Jahrb. Anat.,* 113 : 91-100.

VANDEWALLE, P., C. SURLEMONT & M. CHARDON (1993). About the early larval development of the anterior suspensorial ossifications of *Clarias gariepinus* (Burchell, 1822). *Zool. Anz.,* 231 : 11-19.

VANDEWALLE, P., P. LALEYE & B. FOCANT (1995a). Early development of cephalic bony elements in *Chrysichthys auratus*. *Belg. J. Zool.,* 125 : 329-347.

VANDEWALLE, P., P. SAINTIN & M. CHARDON (1995b). Structures and movements of the buccal and pharyngeal jaws in relation to feeding in *Diplodus sargus*. *J. Fish Biol.,* 46 : 623-656.

VANDEWALLE, P., I. GLUCKMANN, E. BARAS, F. HURIAUX & B. FOCANT (1997). Postembryonic development of the cephalic region in *Heterobranchus longifilis*. *J.Fish Biol.,* 50 : 227-253.

VERRAES, W. (1977). Postembryonic ontogeny and functional anatomy of the ligamentum mandibulo-hyoideu and the ligamentum interoperculo-mandibulare, with notes on the opercular bones and some other cranial elements in *Salmo gairdneri* Richardson, 1836 (Teleostei : Salmonidae). *J. Morphol.,* 151 : 111-119.

WEITZMAN, S. H. (1962). The osteology of *Brycon meeki*, a generalised characid fish, with an osteological definition of the family. *Stanford Ichthyol. Bull,* 8 : 1-77.

WEITZMAN, S. H. (1964). Osteology of and relationships of south American characid fishes of subfamilies Lebiasininae and Erythrinae with special reference to subtribe Nannostomina. *Proc. US Natn. Mus.,* 116 : 127-170.

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Morphology of *Tribolium castaneum* male genitalia and its possible role in sperm competition and cryptic female choice

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ABSTRACT. It is now well recognised that sexual selection proceeds after copula via competition between the sperm of different males, and via female influences on sperm storage and usage. The existence of, and potential for, these selection forces have led to the evolution of a wide range of behavioural, anatomical and physiological adaptations for successful reproduction. Males increase fertilization either by enhancing the success of their own sperm, or by negating or eliminating rival sperm. Ultimately, however, sperm are under the potential control of the female. In the red flour beetle, *Tribolium castaneum*, the last male to mate gains fertilization precedence over previous males that have mated. This phenomenon may be due to the morphology of the female sperm storage organ, which could encourage the temporal stratification of sperm through its narrow tubular structure. In addition, males themselves enhance fertilization precedence by removing rival sperm from the female tract. This study examines the detailed external and internal genital morphology of *T. castaneum* using scanning electron microscopy, and relates form to potential function in intrasexual competition and selection. We show that the aedeagus may articulate in a scoop-like manner to remove sperm, and we observe a retractable brush-like structure and discuss its function. In this beetle, a large and unexplained variation in reproductive success is observed between competing males and we suggest that some of this variance may result from mechanisms of selection and competition that are driven by the complex genitalic structure of *T. castaneum* males.

KEY WORDS: aedeagus, sexual selection, courtship, copula, insecta, coleoptera.

INTRODUCTION

Animal genitalia show remarkable diversity in form and function, and male genitalia in particular have evolved into a bewildering array of forms. Sexual selection may account for the evolution of many of these variant and complex structures because genitalic morphology may play a role in post-copulatory fertilization success (Eberhard, 1991). When females mate with two or more males sperm competition for fertilization of the ova can occur (Parker, 1970). Sperm competition is a widespread and influential phenomenon that has been responsible for the evolution of a range of male adaptations at the behavioural, physiological and morphological levels (Smith, 1984; Birkhead & Møller, 1998). For example, the potential for sperm competition has led to the evolution of male genitalia that remove rival sperm from the female reproductive tract (Waage, 1979, 1986; Haubruge et al., 1999). It is becoming increasingly recognised that, in addition to post-copulatory sexual selection arising from sperm competition, females may play an active role in sperm competition and sperm selection (Eberhard, 1991, 1996; Pizzari & Birkhead, 2000). Accordingly, some of the variance we record between males in sperm competition success may arise through female preference for the sperm of particular males. Since fertilization takes place within their bodies, females may be able to influence a male's reproductive success even after the male has achieved intromission, a phenomenon conceptualized by Thornill (1983) as 'cryptic female choice'. Females may implement post-copulatory selection either through mechanisms such as active sperm ejection or preferential

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uptake (Pizzari & Birkhead, 2000), or potentially by more subtle management of ejaculates of different males (Eberhard, 1991, 1996) such as directional movement of sperm to different spermathecae when multiple storage organs have evolved (Otronen, 1997; Otronen et al., 1997). *Tribolium castaneum* (Herbst) has a single spermatheca but this consists of multiple tubules (Sinha, 1953), which could be used to accommodate sperm of different males in different spermathecal sites.

Just as there are a number of signals that males have evolved to influence female willingness to mate, males may employ similar signals to influence cryptic female choice. In the red flour beetle *T. castaneum* male fertilization success in sperm competition is influenced by the rate that males rub the female elytra with their tarsi during copula (Edvardsson & Arnqvist, 2000). Leg rubbing may therefore provide honest signals of some aspects of male fitness upon which females subsequently base their sperm selection decisions. In this study, we investigate the detailed morphology of *T. castaneum* male genitalia in relation to intrasexual selection and cryptic female choice. *T. castaneum* provides excellent opportunities for such a study. The outcome of sperm competition between different males in this species is well described and reveals that the last male to mate achieves precedence by fertilizing two-thirds of the ova (Schlager, 1960; Wool & Bergerson, 1979; Lewis & Austad, 1990, 1994; Lewis & Jutkiewicz, 1998; Arnaud et al., 2001). The mechanism behind this pattern of fertilization precedence may be indirectly driven by the morphology of the female tract since sperm are stored in a tubular spermatheca, which could encourage a last-in first-out mechanism of sperm competition due to the temporal stratification of different ejaculates within the narrow cul-de-sac storage tubules. There is also evidence that male *T. castaneum* have evolved genitalia capable of removing rival sperm from the bursa copulatrix of recently-mated females (Haubruge et al., 1999).

Despite detailed studies of the mechanisms of sperm competition, an important feature of the *T. castaneum* mating pattern has not been explained, namely that there is significant variation between males in fertilization precedence, and these differences are consistent for individual males (Lewis & Austad, 1990). Accordingly, there are as yet unrecognised mechanisms influencing fertilization precedence that may proceed within the environment of the female reproductive tract. An obvious trait that could be used to influence female management of sperm is male genitalic morphology, and we therefore conducted a detailed examination of the aedeagal morphology of *T. castaneum* with particular respect to traits that could have evolved to function in intrasexual competition and/or cryptic female choice.

MATERIAL AND METHODS

Beetles were cultured in dark incubators at 30 ± 3°C and 65 ± 5% RH with wheat flour and brewer's yeast (10/1-wt/wt) as rearing medium. Males were sexed as pupae and maintained individually in small vials with rearing medium.

Males were weighed to the nearest 10^{-4} mg on a Cahn electro balance. After anaesthesia and decapitation, genitalia were carefully removed intact. Dissected genitalia were mounted on glass slides (0.75mm diameter) and then critical-point dried through a series of dehydrating alcohol washes before being Au/Pd (60/40) coated.

Morphometric observations. Beetles originating from different geographic areas (Canada, Ivory Coast, Japan, Mozambique, Nigeria, Pakistan, Philippines, UK and USA) were examined to provide a range of body sizes. A total of 14 populations were examined and five males were observed per population. Genitalia for measurement were mounted on their side to present a lateral and perpendicular viewpoint for measurement. Since genitalia can articulate (see Discussion and Fig. 2), total aedeagal length was calculated by summing the lengths of the basal and lateral lobes (between which the articulation occurs, Fig. 2). Measurements were made from micrographs so that two-dimensional images were presented.

External and internal genital morphology. 20 male *T. castaneum* originating from Ivory Coast were used in this study. Genitalia were deliberately mounted in a range of positions so that a three-dimensional image of the aedeagus could be perceived. We also dissected some aedeagi further to observe their internal morphology.

RESULTS

Mean penis length averaged across all populations was 368.8 ± 2.8 µm (mean ± se, n=70). Total aedeagal length was significantly correlated with body weight across 70 males (r=0.351, P=0.003) (Fig. 1). Detailed morphometric measures of aedeagal dimensions showed that residual penis length did not differ significantly between the males of the 14 different populations ($F_{13,56}$= 1.80, P=0.065).

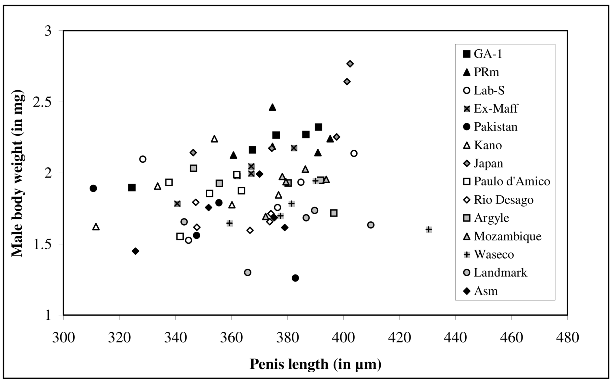
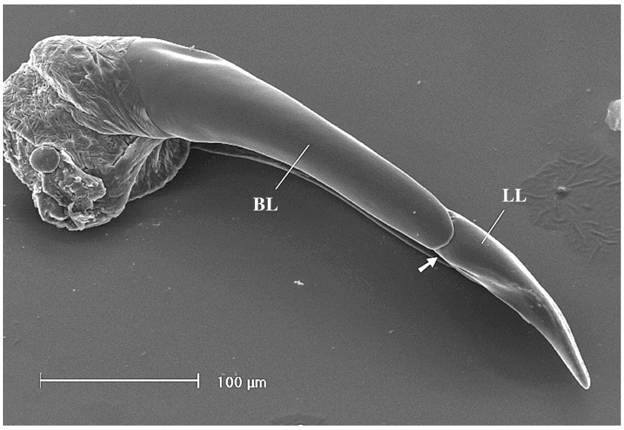
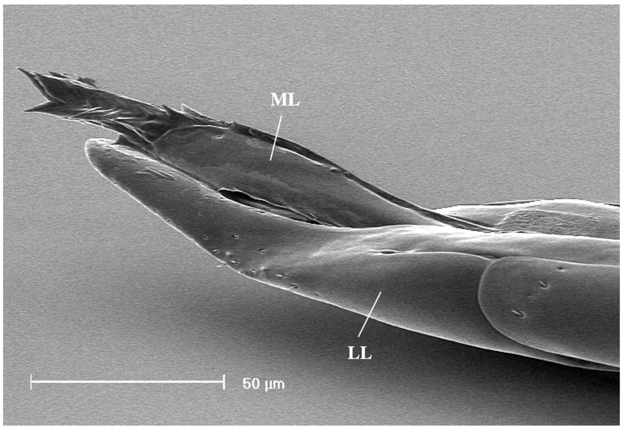


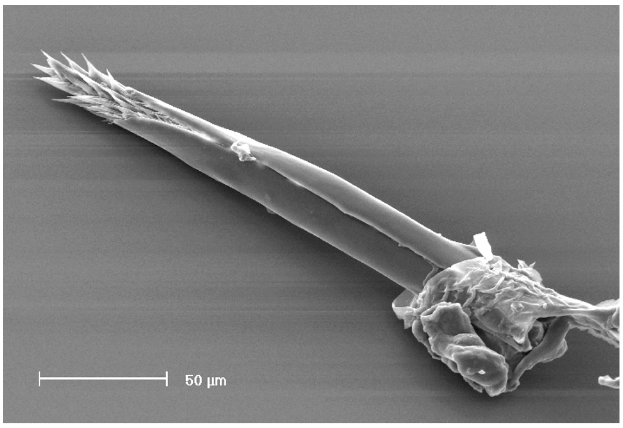
Fig. 1. – Allometric relationship between male body weight (in mg) and penis length (in µm) in *T. castaneum* (r= 0.351, P= 0.003). Data were obtained from 70 males of 14 populations (five males per population).

The detailed external and internal structures of the male genitalia of *T. castaneum* are illustrated in micrographs (Figs 2-5). A total of 20 aedeagi were examined for anatomical purposes. The aedeagus consists of a chitinous organ with a concave scoop lined with sclerotised spines, previously shown to trap and remove rival sperm (Haubruge et al., 1999). The aedeagus appears able to articulate about a central axis (marked on Fig. 2), which may enable the distal part of the aedeagus to swing up and down within the female bursa copulatrix and effect a scooping mechanism.

The internal morphology of the aedeagus reveals a significant brush-like organ encased within the aedeagal valves (Figs 3 and 4). This brush appears to be retractable and able to move in-and-out of the distal end of the aedeagus.







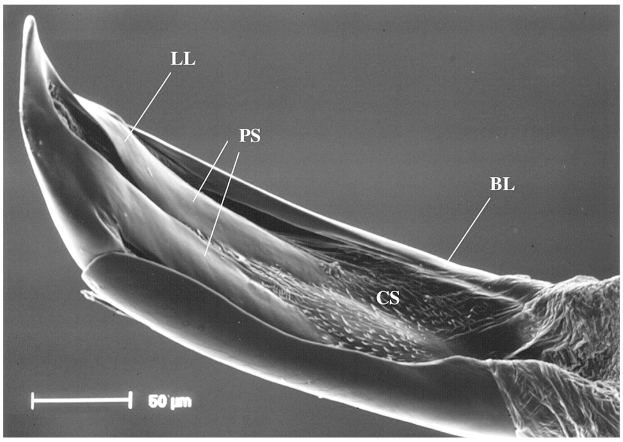


Fig. 2 (upper left). – Lateral view of *T. castaneum* male genitalia showing the two components that have been measured separately (BL: basal lobe and LL: lateral lobe) and are combined to produce a total length measure. The white arrow shows the articulation.

Fig. 3 (upper right). – Side view of *T. castaneum* male genitalia showing the median lobe (ML) expressed. This lobe is comprised of a brush-like structure, which emerges from an aperture in the lateral lobe (LL) (see Fig. 5).

Fig. 4 (lower left). – Detailed view of the internal and retractable brush-like structure within the aedeagus of *T. castaneum*.

Fig. 5 (lower right). – Ventrolateral view of *T. castaneum* male genitalia with the concave furrow running dorsally. The movement of the lateral lobe (LL) appears to be effected by the sliding of paired struts (PS). An array of chitinous spines (CS) line the proximal half of the basal lobe (BL). The brush-like structure on the median lobe (Fig. 4) emerges from an aperture (see Fig. 3) near the distal tip of the aedeagus.

DISCUSSION AND CONCLUSIONS

Our examinations reveal a detailed picture of the male genitalia of *T. castaneum*. We found an allometric relationship between aedeagal dimension and body size across 70 males. Lewis & Austad (1990) recorded that the relative body size of *T. castaneum* males influenced the degree of second-male fertilization success in sperm competitions. Furthermore, there was a consistent, but unexplained, level of variance between males in the degree of sperm precedence they achieved (Lewis & Austad, 1990). Larger males could achieve an advantage in sperm competition if aedeagal dimensions influence sperm removal ability (Haubruge et al., 1999) and/or ability to stimulate cryptic female choice (Eberhard, 1991).

Microdissections and different orientations suggest that the aedeagus is able to articulate about a central axis. This articulation appears to be effected by the sliding of paired chitinous struts (Fig. 5) along the base of the aedeagus. A forward movement by these struts appears to generate a rise in the distal tip of the aedeagus about the fulcrum at the central axis. Accordingly, this articulation results in a scooping action of the aedeagus that may function to move sperm from the bursa copulatrix back onto the aedeagal spines where the sperm are trapped and removed from the fertilization set at the end of copula (HAUBRUGE et al., 1999). This mechanism may contribute to the fertilization advantage bestowed upon spermatozoa of the last male to mate (SCHLAGER, 1960).

Internal microdissections reveal a retractable brush-like structure within the aedeagus. This brush appears able to slide in-and-out of the aedeagus. This apparatus does not appear adapted to function in sperm transfer as it is non-tubular and could impede the movement of sperm from the male into the female tract. The brush-like apparatus may somehow interfere with previously-deposited rival sperm in the bursa or spermatheca akin to the actions of the secondary genitalia evolved by odonates (WAAGE, 1979). Alternatively, the brush may be used as a sexually-selected signal to which the female is sensitive. More vigorous stimulation of the female's elytra by a mating male's forelimbs encourages sperm selection and increased sperm competition success in *T. castaneum* (EDVARDSSON & ARNQVIST, 2000), and courtship stimulation of females is widespread in insects (EBERHARD, 1994). Similarly, the aedeagal brush may directly stimulate the female reproductive tract. Female insects have evolved sensory structures in the reproductive tract (OBARA et al., 1975 ; SUGAWARA, 1979 ; LUM & ARBOGAST, 1979 ; CORDOBA-AGUILAR, 1999) that are sensitive to the morphology and / or behaviour of male genitalia or ejaculates. For example, in the damselfly, *Calopteryx haemorrhoidalis asturica* (Vander Linden), males stimulate mechano-receptive sensilla of the female genital tract with their aedeagus. This stimulation results in sperm ejection from the spermatheca (CORDOBA-AGUILAR, 1999) and therefore a fertilization advantage for the stimulating male. The multiple-tubule spermatheca of *T. castaneum* provides a mechanistic opportunity for preferential sperm storage and usage, as is claimed for other insects (YUVAL et al., 1996, OTRONEN, 1997 ; OTRONEN et al., 1997). In *Scatophaga stercoraria* (L.), OTRONEN et al. (1997) observed significant interactions between male and female characters on the pattern of sperm storage. Moreover, in the fly *Dryomyza anilis* Fallén, which has multiple sperm storage sites, the single spermatheca is central for male fertilization success, and male-female interactions during copula, such as male leg-tapping on the female, influence the quantity of sperm stored in this spermatheca (OTRONEN, 1997). Similarly, if complex genitalic structures such as retractable aedeagal brushes have evolved as sexually-selected signals, enhanced and direct stimulation of the female reproductive tract during copula could influence sperm storage or usage.

ACKNOWLEDGEMENTS

We are extremely grateful to Kess Veltkamp for scanning electron microscopy expertise. This work was funded by the FRIA (Fonds pour la formation à la Recherche dans l'Industrie et dans l'Agriculture) and "la Communauté française Belgique" to L. Arnaud and the Royal Society to M. Gage.

REFERENCES

ARNAUD, L., E. HAUBRUGE & M.J.G. GAGE (2001). The dynamics of second- and third-male fertilization precedence in *Tribolium castaneum*. *Entomol. Exp. Appl.*, 99 : 55-64.

BIRKHEAD, T.R. & A.P. MÖLLER (Eds) (1998). *Sperm competition and sexual selection.* Academic Press, London, UK, 826 pp.

CORDOBA-AGUILAR, A. (1999) Male copulatory sensory stimulation induces female ejection of rival sperm in a damselfly. *Proc. R. Soc. Lond. B*, 266 : 779-784.

EBERHARD, W.G. (1991). Copulatory courtship and cryptic female choice in insects. *Biol. Rev.*, 66 : 1-31.

EBERHARD, W.G. (1994). Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. *Evolution*, 48 : 711-733.

EBERHARD, W.G. (1996). *Female control : sexual selection by cryptic female choice.* Princenton University Press, Princenton, USA, 472 pp.

EDVARDSSON, M. & G. ARNQVIST (2000). Copulatory courtship and cryptic female choice in red flour beetles *Tribolium castaneum*. *Proc. R. Soc. Lond. B*, 267 : 559-563.

HAUBRUGE, E., L. ARNAUD, J. MIGNON & M.J.G. GAGE (1999). Fertilization by proxy : rival sperm removal and translocation in a beetle. *Proc. R. Soc. Lond. B*, 266 : 1183-1187.

LEWIS, S.M. & S.N. AUSTAD (1990). Sources of intraspecific variation in sperm precedence in red flour beetles. *Am. Nat.*, 135 : 351-359.

LEWIS, S.M. & S.N. AUSTAD (1994). Sexual selection in flour beetles : the relationship between sperm precedence and male olfactory attractiveness. *Behav. Ecol.*, 5 : 219-224.

LEWIS, S.M. & E. JUTKIEWICZ (1998). Sperm precedence and sperm storage in multiply mated red flour beetles. *Behav. Ecol. Sociobiol.*, 43 : 365-369.

LUM, P.T.M. & R.T. ARBOGAST (1979). Ultrastructure of setae in the spermathecal gland of *Plodia interpunctella* (Hübner) (Lepidoptera : Pyralidae). *Int. J. Insect Morphol. Embryol.* 9 : 251-253.

OBARA, Y., H. TATEDA & M. KUWABARA (1975). Mating behavior of the cabbage white butterfly, *Pieris rapae crucivora* Boisduval. V. Copulatory stimuli inducing changes of female response patterns. *Zool. Mag. (Tokyo)*, 84 : 71-76.

OTRONEN, M. (1997). Sperm numbers, their storage and usage in the fly *Dryomyza anilis*. *Proc. R. Soc. Lond. B*, 264 : 777-782.

OTRONEN, M., P. REGUERA & P.I. WARD. (1997). Sperm storage in the yellow dung fly *Scatophaga stercoraria* : identifying the sperm of competing males in separate female spermathecae. *Ethology*, 103 : 844-854.

PARKER, G.A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biol. Rev.*, 45 : 525-567.

PIZZARI, T. & T. BIRKHEAD (2000). Female feral fowl eject sperm of subdominant males. *Nature*, 405: 787-789.

SCHLAGER, G. (1960). Sperm precedence in the fertilization of eggs in *Tribolium castaneum*. *Ann. Entomol. Soc. Am.*, 53: 557-560.

SINHA, R.N. (1953). The spermatheca in the flour beetle (*Tribolium castaneum* herbst). *J. New York Entomol. Soc.*, 61: 131-134.

SMITH, R.L. (Ed.) (1984). *Sperm competition and the evolution of animal mating systems.* Academic Press, Tucson, Arizona, USA., 687 pp.

SUGAWARA, T. (1979) Stretch reception in the bursa copulatrix of the butterfly, *Pieris rapae* crucivora, and its role in Behaviour. *J. Comp. Physiol. A*, 130: 191-199.

THORNILL, R. (1983). Cryptic female choice and its implication in the scorpion fly *Harpobittacus nigriceps*. *Am. Nat.*, 122: 765-788.

WAAGE, J.K. (1979). Dual function of the damselfly penis: sperm removal and transfer. *Science*, 203: 916-918.

WAAGE, J.K. (1986). Evidence for widespread sperm displacement ability among Zygoptera (Odonata) and the means for predicting its presence. *Biol. J. Linn. Soc.*, 28: 285-300.

WOOL, D. & O. BERGERSON (1979). Sperm precedence in repeated mating of adults *Tribolium castaneum* (Coleoptera, Tenebrionidae). *Entomol. Exp. Appl.*, 26: 167-160.

YUVAL, B., S. BLAY & R. KASPI (1996). Sperm transfer and storage in the Mediterranean fruit fly (Diptera: Tephritidae). *Ann. Entomol. Soc. Am.*, 89: 486-492.

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The creodonts (Mammalia, Ferae) from the Paleocene-Eocene transition in Belgium (Tienen Formation, MP7)

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ABSTRACT. Study of the dental remains of creodont mammals from the Paleocene-Eocene transition in Belgium (Tienen Formation, reference-level MP7) allows seven species to be recognized, four of which belong to the family Hyaenodontidae and three to the Oxyaenidae. The four hyaenodontid species, which are new to science, present numerous symplesiomorphic characteristics. They represent the oldest hyaenodontids of northern Europe and are shown to be the most primitive representatives of the sub-family Hyaenodontinae known so far. They are closely related to the oldest North American species but the morphological differences between them demonstrate that they are not vicariant species. Thus, the Belgian species could be at the origin of the American hyaenodontid lineages or belong to lineages already distinct but recently differentiated from common ancestors slightly older than both of these species groups. As for oxyaenids, their dental morphology shows that they could originate from the North American Paleocene lineages, although their small size does not support this hypothesis. The smallest Belgian creodont, *Prototomus minimus* n. sp. is remarkable in that it may present sexual dimorphism in mandibular morphology.

KEY WORDS: mammals, creodonts, Paleocene-Eocene transition, MP7, Belgium.

INTRODUCTION

At the Paleocene-Eocene transition, about 55 million years ago, most of the placental mammal orders of modern type appear simultaneously in western Europe, North America and central Asia. The most typical groups are the rodents, euprimates, perissodactyls, artiodactyls, bats, miacid carnivorans and hyaenodontid creodonts. On the other hand, persisting archaic type groups from the Paleocene begin to decline, such as condylarths, arctocyonids, plesiadapiform "primates", cimolestids, viverravid carnivores and oxyaenid creodonts.

The mammal faunas from the outcrop sections of Dormaal, Orp-le-Grand and Hoegaarden in the Brabant province, and those of Erquelinnes and Leval in the Hainaut province, belonging all to the Tienen Formation (Upper "Landenian", Landen Group), representing the Paleocene-Eocene transition in Belgium, have been the subject of detailed study (SMITH, 1999, 2000). Among these, the important Dormaal fauna (see SMITH & SMITH, 1996; STEURBAUT et al., 1999) was specified for reference-level MP7 of the mammalian biochronological scale for the European Paleogene (SCHMIDT-KITTLER, ed., 1987).

In this first part of the study we analyse the order Creodonta, which is classified with the Carnivora and the Cimolesta in the grand-order Ferae Linnaeus, 1758 (MCKENNA & BELL, 1997). The creodonts form a group of carnivorous mammals that persisted from the Middle Paleocene to the Late Miocene (60-10 million years ago). They are characterised by the presence of at least two pairs of shearing carnassial teeth (generally M1/ and M/2, M2/ and M/3), whereas the carnivorans have only one pair of shearing carnassial teeth (P4/ and M/1). Two large families are included in the creodonts: the oxyaenids and the hyaenodontids. The oxyaenids, which are known from the Paleocene to the Middle Eocene, have two molars per half-jaw. The hyaenodontids, which appear at the beginning of the Eocene and persist to the Late Miocene, present three molars per half-jaw.

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MATERIAL AND METHODS

For the sake of homogeneity, the mammal systematic classification in this work is that proposed by McKenna & Bell (1997). The terminology of the dental cusps and crests used here (see Smith, 1996, fig. 1) is based on that defined by Van Valen (1966) to describe the tribosphenic tooth of the therian mammals.

ABBREVIATIONS

Institutions:

AMNH: American Museum of Natural History, New York.
BMNH: Natural History Museum, London.
IRSNB: Institut royal des Sciences naturelles de Belgique, Bruxelles.
MNHN: Muséum National d'Histoire Naturelle, Paris.
UC (MP): University of California (Museum of Paleontology), Berkeley.
UM (VP): University of Michigan (Vertebrate Paleontology), Ann Arbor.

Localities and collections:

AC: Meudon, collections of the MNHN.
Al, ARP: Argiles à lignites du Soissonnais, collections of the MNHN.
CL: Dormaal, collection J-C. Lepage (IRSNB).
D: Dormaal, general collection of the IRSNB.
DIRS, DIIARS, DIICRS, DIIIRS: Dormaal, collection R. Smith.
DMG: Dormaal, collection M. Girardot (R. Smith).
DC, DD, DL: Dormaal, collection D. Delsate (IRSNB).
Do: Dormaal, general collection of the IRSNB; numbering of P. Gigase.
DoPG: Dormaal, collection P. Gigase.
Eq: Erquelinnes, general collection of the IRSNB.
IRSNB M: Mammals, collection of types and figured specimens of the IRSNB.
L, Louis: Collection P. Louis (MNHN).
Mu: Mutigny.
RI: Rians, collection of the MNHN.
TS: Dormaal, general collection of the IRSNB, numbering of T. Smith.
WL: Dormaal, collection G. Wouters (IRSNB).

SYSTEMATIC PALAEONTOLOGY

Order CREODONTA Cope, 1875
Family HYAENODONTIDAE Leidy, 1869
Subfamily HYAENODONTINAE Leidy, 1869

Genus *Prototomus* Cope, 1874
Type species *Prototomus viverrinus* Cope, 1874

***Prototomus minimus* n. sp.**

(Figs 1 and 2)

1927: Créodontes indéterminés; Teilhard de Chardin, p. 20, figs. 16c-d, pl. V, figs. 1, 6, 11, 12.
1927: Miacidés; Teilhard de Chardin, p. 21, fig. 18d.
1966: Proviverrinae, Cat. I.; Quinet, p. 37, pl. V, figs. 7-9.
1966: Proviverrinae, Cat. II.; Quinet, p. 37, pl. V, figs. 10-11.
1966: Proviverrinae, Cat. III.; Quinet, p. 37, pl. V, figs. 12-13.
1978: cf. *Prolimnocyon*; Godinot et al., p. 1273.
1987: *Prolimnocyon* sp.; Lange-Badré *in* Godinot et al., p. 275.

Material

Holotype: IRSNB M1287, LM/1.

Paratypes: IRSNB M1285, RDP/4; IRSNB M1286, RP/4; IRSNB M1288, LM/2; IRSNB M1289, RM/3; IRSNB M1356, RDP4/; IRSNB M1290, LP4/; IRSNB M1291, LM1/; IRSNB M1292, RM2/; IRSNB M1293, LM3/; IRSNB M1294, edentulous fragment of left mandible; IRSNB M1295, edentulous fragment of left mandible.

Referred material: DI1471RS, RP/3?; DIIC1389RS, RDP/4; TS5, RDP/4; TS6, LDP/4; Do1713PG, RDP/4; DIIA2296RS, RP/4; CL706, RP/4; TS7, RP/4; TS8, LP/4; TS9, RP/4; IRSNB M919, RM/1; DI1429RS, LM/1; DIIC1681RS, LM/1; DIII325RS, RM/1; DIII80RS, RM/1; DIIC1574RS, LM/1; DIII82RS, RM/1; TS10, LM/1; TS11, RM/1; TS12, LM/1; TS13, LM/1; DIII258RS, LM/1; WL167, LM/2; WL158, LM/2; CL102, LM/2; TS14, LM/2; TS15, RM/2; TS16, LM/2; TS17, RM/2; TS18, LM/2; DIII81RS, LM/2; DIII264RS, RM/2; DIII79RS, RM/2; DIIA1910RS, RM/2; DIII364RS, LM/2; IRSNB M917, RM/3; TS19, RM/3; TS20, RM/3; CL379, LDP4/; DIIC624RS, RDP4/; DIIC625RS, RDP4/; DIIC1557RS, LDP4/; DIIA1912RS, LDP4/; TS21, RDP4/; IRSNB M72, RM1/; IRSNB M80, LM1/; DIII363RS, LM1/; TS22, LM1/; TS23, RM1/ (broken); TS24, LM1/ (broken);

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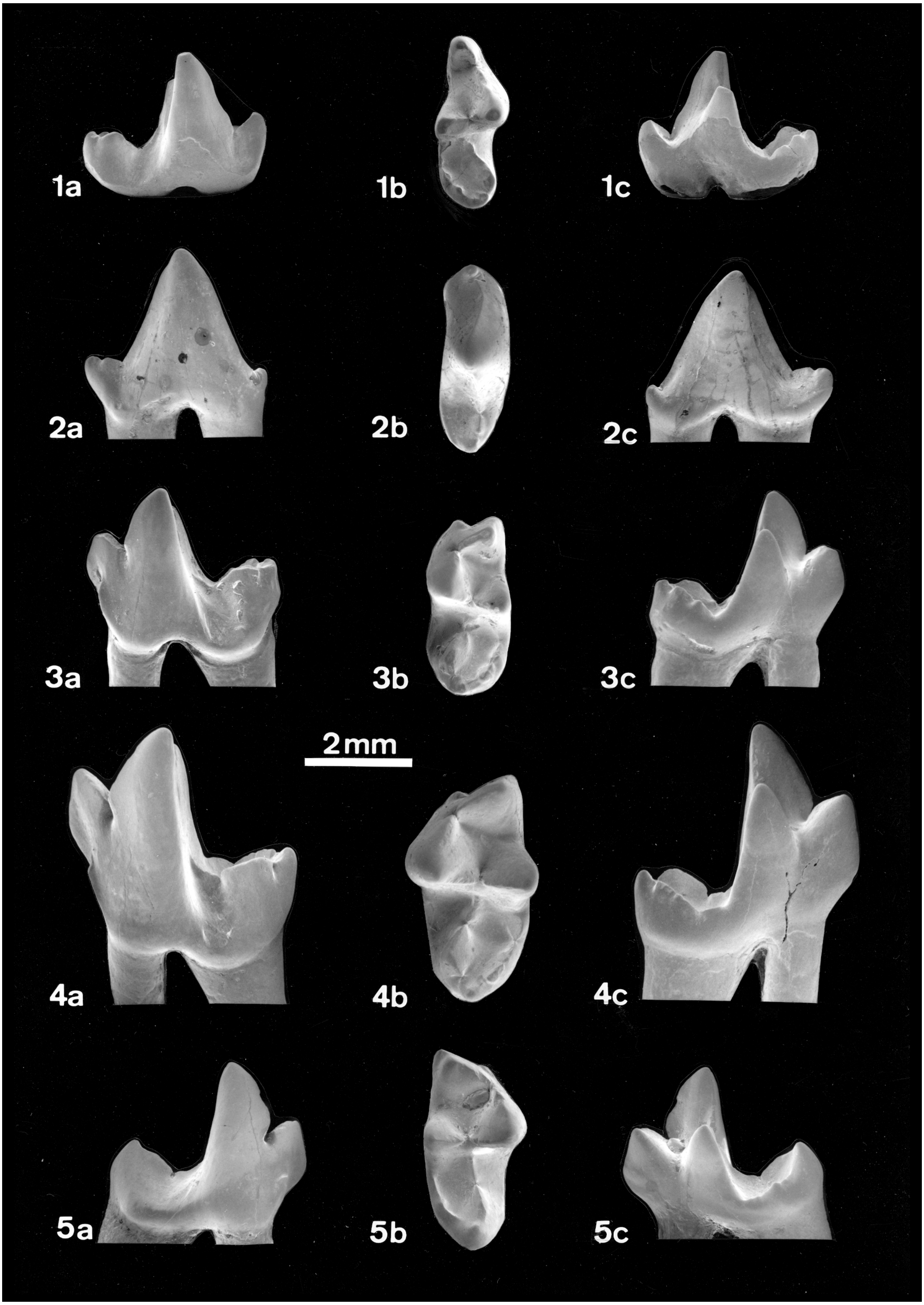
Fig. 1. – *Prototomus minimus* n. sp. – 1. IRSNB M1285, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1286, RP/4. a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1287, LM/1 (holotype). a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1288, LM/2. a: labial view, b: occlusal view, c: lingual view. – 5. IRSNB M1289, RM/3. a: labial view, b: occlusal view, c: lingual view.


1a
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DIII312RS, RM2/ (broken); DIII72RS, LM2/ (broken); DIIA1782RS, RM3/; TS25, RM3/; TS26, RM3/ (broken); TS29, edentulous fragment of right mandible.

Type locality

Dormaal.

Diagnosis

Smallest species of the genus, differing from all the other species, except maybe *P. giraroti*, by M/3 smaller than M/2 (the ratio M/3:M/2 length is 0.87) and proportionally smaller M3/, and by M2/ with more labially oriented parastyle and with a pronounced ectoflexus.

Etymology

The name refers to the extremely small size of this species. B. Lange-Badré (Université Paris VI), in her unfinished study of the Dormaal creodonts, intended the name *minimus* for this species, which she believed to belong to the genus *Prolimnocyon*. However, the latter is characterized by developed P/4 and P4/, reduction of M2/, and extreme reduction of M/3 and M3/, which it is not the case in the present taxa. We validate here the species name *minimus* as a tribute to her work.

TABLE 1

Measurements (in mm) of cheek teeth of *Prototomus minimus* n. sp. from Dormaal. L: length; l: width; n: number of specimens; OR: observed range of variation; M: mean; σ: standard deviation; V: coefficient of variation.

		n	OR		M	σ	V
DP4/	L	6	2.95	3.25	3.16	0.11	3.53
	l	6	2.85	3.05	2.94	0.10	3.47
P4/	L	1	2.95		-	-	-
	l	1	3.05		-	-	-
M1/	L	5	3.10	3.65	3.48	0.22	6.31
	l	5	3.60	3.80	3.71	0.08	2.21
M2/	L	1	3.65		-	-	-
	l	1	4.95		-	-	-
M3/	L	3	2.00	2.25	2.12	0.13	5.94
	l	3	2.27	2.95	2.85	0.13	4.64
P/3	L	1	3.10		-	-	-
	l	1	1.25		-	-	-
DP/4	L	5	3.30	3.60	3.44	0.13	3.76
	l	5	1.40	1.55	1.47	0.08	5.16
P/4	L	6	3.45	3.80	3.61	0.13	3.55
	l	6	1.30	1.45	1.37	0.05	3.78
M/1	L	9	3.35	3.90	3.62	0.20	5.57
	l	9	1.65	1.95	1.82	0.12	6.45
M/2	L	15	3.90	4.45	4.12	0.17	4.15
	l	15	2.15	2.6	2.43	0.13	5.21
M/3	L	3	3.45	3.80	3.60	0.18	5.01
	l	3	1.85	2.00	1.90	0.08	3.98

Description

Lower dentition

The trigonid of DP/4 (Fig. 1. 1a-c) is wider than the talonid. The paraconid is narrow and well distinct. The metaconid is slightly posterior to the protoconid. The latter is slender.

The P/4 (Fig. 1. 2a-c) is tall with a simple morphology. A small paraconid is present. The talonid is narrow with a central crest (slightly shifted labially) bearing two small cusps.

The M/1 (Fig. 1. 3a-c) is the same length as P/4. It is also relatively narrow. Trigonid and talonid have about the same width. On some specimens the trigonid is even somewhat narrower than the talonid.

The M/2 (Fig. 1. 4a-c) is much larger than M/1. The trigonid is wide, particularly developed and elevated.

The M/3 (Fig. 1. 5a-c) is a little larger than M/1. The trigonid is not as wide as on M/2. The talonid basin is long and narrow. The hypoconulid is the most developed cusp of the talonid.

Three edentulous fragments of mandible belonging to *Prototomus minimus* n. sp. from Dormaal have been identified by comparison with the mandible UM79612 of *Prototomus deimos*. The alveoli indicate that P/1 was single-rooted. It is worth noting that the fragment of mandible IRSNB M1294 is higher and more elongated than in IRSNB M1295 and TS29, the alveoli for the canine is larger, the diastemata on each side of P/2 are longer and the mental foramina are larger (Fig. 3).

Upper dentition

The parastyle of DP4/ (Fig.2. 1a-b) is wide labio-lingually, and anteriorly developed. Paracone and metacone are labio-lingually compressed. The protocone is relatively anterior. The postmetacrista is short. The two conules present weak postparaconule crista and premetaconule crista.

The P4/ (Fig. 2. 2a-b) is small. The paracone is relatively low and it has a central position. The relatively short metastylar crest is somewhat developed in height. The protocone is weakly developed, as is the entire lingual part of the tooth.

On M1/ (Fig. 2. 3a-b) as on DP4/, the paracone is slightly higher than the metacone. The parastyle is anteriorly oriented. The postmetacrista is of medium length and labio-posteriorly orientated. The paraconule is protruded

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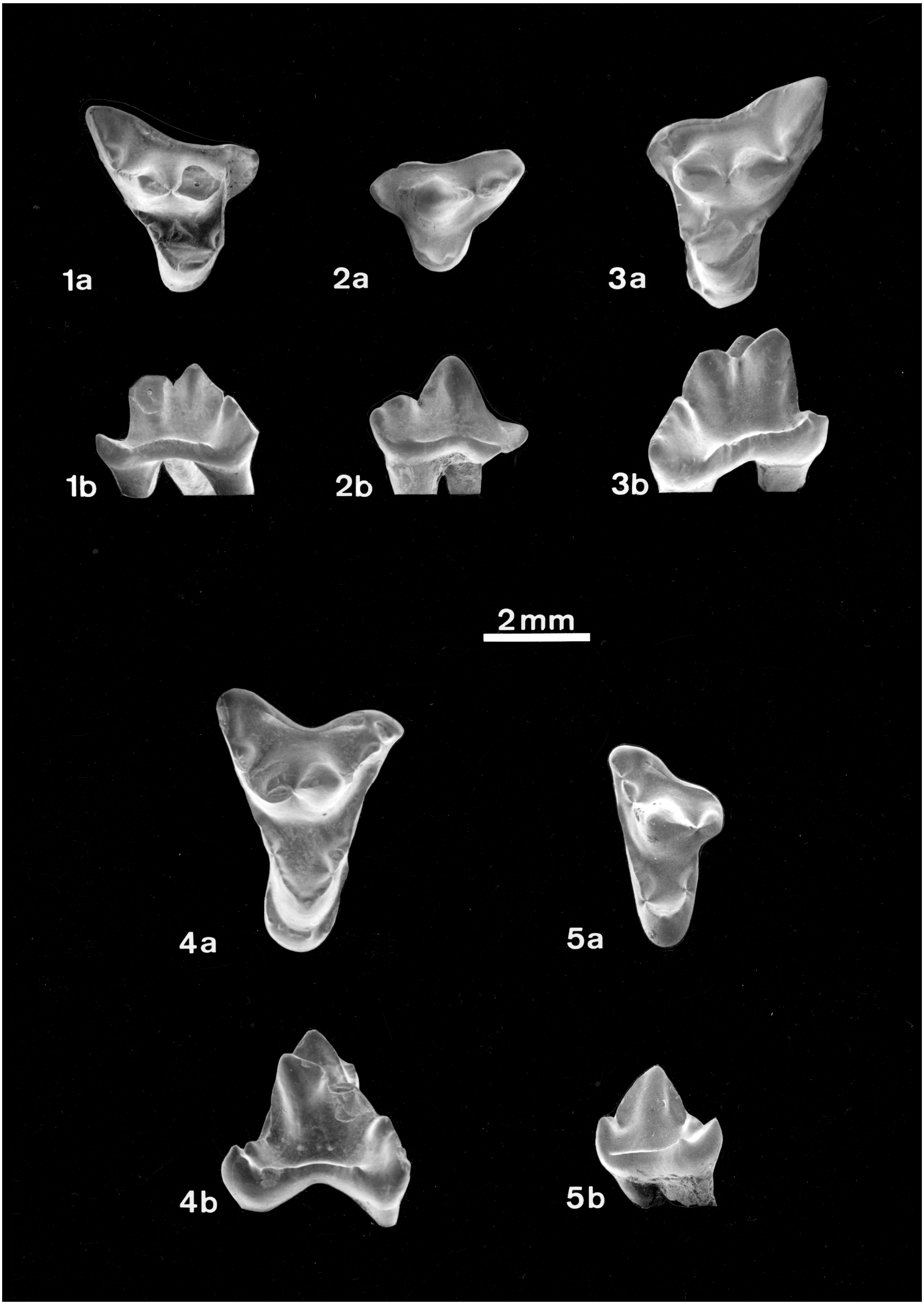
Fig. 2. – *Prototomus minimus* n. sp. – 1. IRSNB M1356, RDP/4. a: occlusal view, b: labial view. – 2. IRSNB M1290, LP4/; a: occlusal view, b: labial view. – 3. IRSNB M1291, LM1/; a: occlusal view, b: labial view. – 4. IRSNB M1292, RM2/; a: occlusal view, b: labial view. – 5. IRSNB M1293, LM3/; a: occlusal view, b: labial view.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4b
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and is connected to the base of the paracone by a postparaconule crista. Weak pre- and postcingula border the protocone. The latter is thicker on M1/ than on DP4/.

The M2/ (Figs. 2. 4a-b) is a wide tooth labio-lingually and larger than M1/. The ectoflexus is pronounced. The paracone and metacone are close to one another. The parastyle is more developed than on M1/ and antero-labially orientated. The postmetacrista is the same length as on M1/ or is slightly shorter. The protocone is nearly median with respect to the paracone and the metacone. The pre- and postcingula are slightly more developed than on M1/ and the protocone is somewhat larger.

The M3/ (Fig. 2. 5a-b) is small in comparison with M2/. It has a small metacone and two conules. The protocone is poorly developed labio-lingually and has no cingula. The preparacrista is present as a labially stretched cusp.

Discussion

The upper molars of this taxon present a series of primitive characters recalling the Paleocene didelphodontid Cimolesta such as *Cimolestes* species : close paracone and metacone, protocone median with respect to the paracone and the metacone (scarcely shifted anteriorly), postmetacrista labially orientated and with little elongation, parastyle anteriorly orientated. However, this taxon corresponds well with hyaenodontid creodonts in the narrow stylar shelf, the different morphology of the P4/ and the poorly developed talonid cusps of the lower molars.

This mammal is the smallest creodont in the Belgian fauna. It belongs to the genus *Prototomus* by having simple P/4 and P4/, narrow lower molars, M/1 and M1/ distinctly smaller than M/2 and M2/, only slightly reduced M/3 and M3/, and the metaconid slightly higher than the paraconid on M/1-2.

The teeth are morphologically close to those of *P. deimos* Gingerich & Deutsch, 1989 (Wa0-3), *P. phobos* Gingerich & Deutsch, 1989 (Wa1-4) and *P. martis* Gingerich & Deutsch, 1989 (Wa2-3), which are the oldest known representatives of the genus in North America. However, the Belgian species differs from the three American species by its clearly smaller size, proportionally shorter P/4 and P4/, and smaller M/3 et M3/ with a hypoconulid less developed on M/3. *P. deimos*, the smallest and oldest species, is, according to its M/1 and M/2 measurements, 20-30% larger than *Prototomus minimus* n. sp. from Dormaal.

The DP4/ of *P. minimus* have been identified by comparison with DP4/ of *P. martis* (UM67138, two fragments of maxilla with DP4/-M1/ and DP4/-M2/). These teeth present a series of plesiomorphies : absence of cingulum around the protocone, considerable development of the parastyle, presence of para- and metaloph.

The postparaconule crista on M1/ (plesiomorphic character) is also present in *P. deimos* (UM46642) and *P. martis* (UM67138). It seems to be absent or strongly attenuated in *P. phobos* (UM74134).

The molars of *Prototomus minimus* n. sp. are fairly similar to those of the smallest North American hyaenodontid, *Acarictis ryani* Gingerich & Deutsch, 1989 (UM79081), but they are slightly smaller. One of the main diagnostic characteristics of the genus *Acarictis*, known from only four specimens, is the singularity of its P3/. However, this tooth (UM86291) more closely resembles a DP3/ by its low length/width ratio, its protruding parastyle, the presence of a protocone and of three roots. The validity of the genus *Acarictis* could therefore be questioned, and the species *A. ryani* should probably be attributed to the genus *Prototomus* or *Prolimnocyon*. An objection to the synonymy *Acarictis-Prototomus* could be argued to be the absence of diastema between P/2 and P/3 in *Acarictis*. On the other hand, *Prolimnocyon haematus* Gingerich & Deutsch, 1989 is close in size to *Acarictis ryani* and does not possess a diastema, either. Moreover, both come from the same stratigraphic level.

The respective alveoli of the three edentulous fragments of mandible attributed to *Prototomus minimus* n. sp. have the same dimensions and cannot correspond to the large teeth of *Prototomus girardoti* n. sp. (see following pages). The mandibular variability seems to result from sexual dimorphism comparable to those of the extant red fox *Vulpes vulpes* (GINGERICH & WINKLER, 1979). The more developed mandible (IRSNB M1294) belongs probably to a male individual (Fig. 3).

Among the rare teeth of European Proviverrini, those of *Proviverra palaeonictides* (Lemoine, 1880) from Epernay (MNHN Al5515, MP8+9, upper Ypresian, Champagne) and of *Proviverra eisenmanni* Godinot, 1981 from Rians (RI 400, MP7, Early Eocene, Provence) present a well-developed and individualised entoconid on a relatively large talonid, while the entoconid is reduced and crestiform on the lower molar of *Prototomus minimus* n. sp. This apomorphic character is not shared by *Prototomus* cf. *P. palaeonictides* (RICH, 1971, p. 14) from Grauves (MNHN Louis195, MP10). Moreover, the alveoli of its mandible indicate that P/1 was double-rooted. It is thus justified to consider this last taxon as belonging to the genus *Proviverra* Rütimeyer,

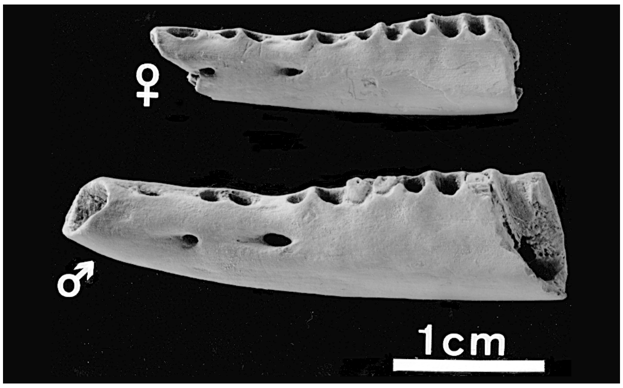


Fig. 3. – *Prototomus minimus* n. sp. – ♀. IRSNB M1294, edentulous fragment of left mandible belonging to a female individual ; in labial view. – ♂. IRSNB M1295, edentulous fragment of left mandible belonging to a male individual ; in labial view.

1862. On the other hand, the RM3/, named cf. *Proviverra* or *Prototomus* sp. (Rich, 1971, p. 16) from Mutigny (MNHN Mu6464, MP8+9), has two small conules, a somewhat reduced metacone and a marked ectoflexus like that on M3/ of *Prototomus minimus* n. sp. These characters bring these teeth rather closer to the genus *Prototomus*, M3/ of *Proviverra* being clearly more developed.

***Prototomus girardoti* n. sp.**

(Fig. 4)

Material

Holotype: IRSNB M1297, RM/1

Paratypes: IRSNB M1296, RDP/4; IRSNB M1298, RM/3; IRSNB M1299, RP4/; IRSNB M1300, RM3/.

Type locality

Dormaal.

Diagnosis

Species similar in size to *P. deimos* but differing by smaller M/3 (11 to 26 % smaller).

Etymology

Named after Michel Girardot who contributed to the Dormaal collections.

TABLE 2

Measurements (in mm) of cheek teeth of *Prototomus girardoti* n. sp. from Dormaal. Abbreviations as in Table 1.

		n	OR	M	σ	V
P4/	L	1	4.55	-	-	-
	l	1	3.00	-	-	-
M3/	L	1	2.05	-	-	-
	l	1	3.45	-	-	-
DP/4	L	1	4.05	-	-	-
	l	1	1.85	-	-	-
M/1	L	1	4.40	-	-	-
	l	1	2.25	-	-	-
M/3	L	1	4.45	-	-	-
	l	1	2.40	-	-	-

Description

Lower dentition

The trigonid of DP/4 (Fig. 4. 1a-c) is slightly wider than the talonid. The metaconid is posterior to the protoconid.

The M/1 (Fig. 4. 2a-c) also presents a trigonid slightly wider than the talonid. Three small cusps are set in the lingual edge of the talonid.

The talonid of M/3 (Fig. 4. 3a-c) is relatively long and narrow. A small antero-labial cingulum is visible and the trigonid is somewhat closed.

Upper dentition

The P4/ (Fig. 4. 4a-b) has a long and narrow labial part. The relatively tall paracone has a central position. The lingual part of the tooth is weakly developed, and the protocone is insignificant.

The M3/ (Fig. 4. 5a-b) is labio-lingually elongated. It presents a developed metacone and 2 conules. The protocone is relatively massive.

Discussion

The few teeth of this taxon are distinctly larger than those of *Prototomus minimus* n. sp. but relatively similar in morphology. They differ also in having P4/ more antero-posteriorly elongated, the preparacrista of M3/ longer and the protocone more developed. The dimensions are nearly the same as those of *P. deimos* from Wyoming (Wa0-3), only M/3 is here smaller than on the American species.

Genus *Arfia* Van Valen, 1965
Type species *Arfia opisthotoma* (Matthew, 1901)

***Arfia gingerichi* n. sp.**

(Figs 5 and 6)

1982: *Arfia woutersi* n. sp.; Lange-Badré & Godinot, p. 295-300, pl. 1, figs. 2-4; *non* pl. 1, fig. 1.
1989: *Arfia junnei*; Gingerich, p. 36.

Material

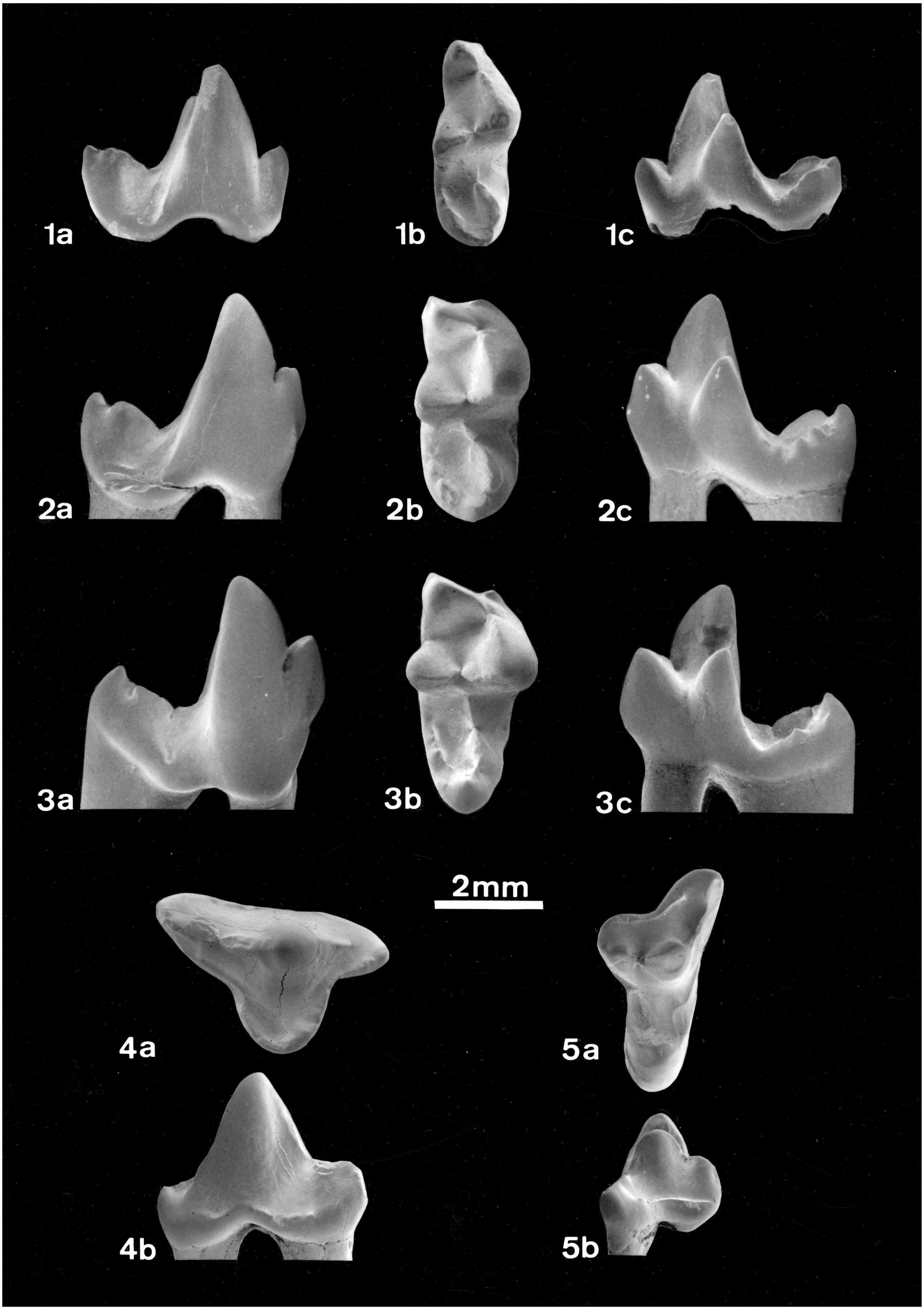
Holotype: IRSNB M1275, RM/3, figured as CL13 by Lange-Badré & Godinot (1982; pl. I, fig. 4a-c).

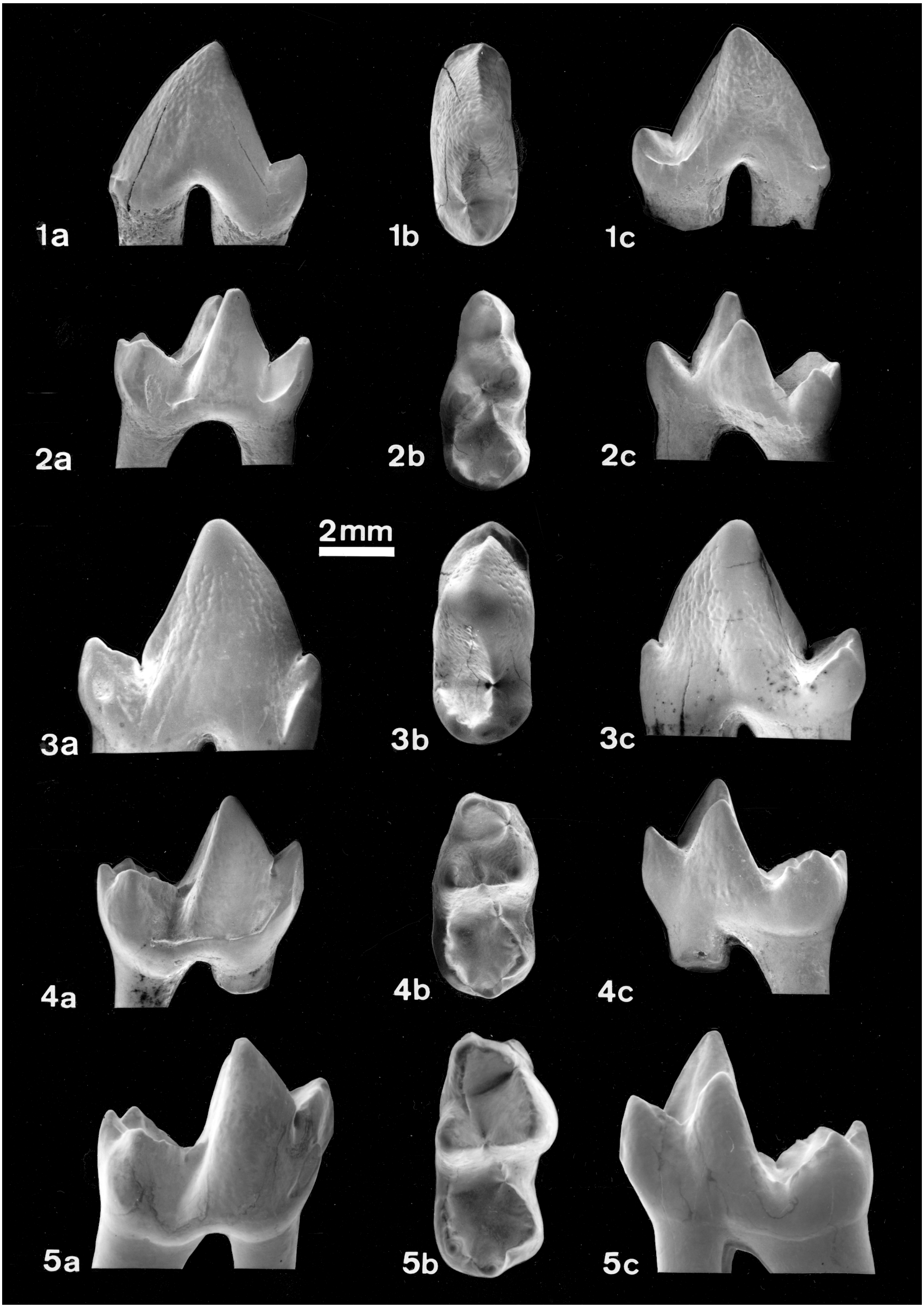
Paratypes: IRSNB M1301, LP/3; IRSNB M1302, RDP/4; IRSNB M1303, RP/4; IRSNB M1304, RM/1 (CL14 in Lange-Badré & Godinot, 1982, pl. I, fig. 3b, e, h); IRSNB M1305, RM/2; IRSNB M1306, LM/3;

Legends to the figures (see next pages)

Fig. 4 – *Prototomus girardoti* n. sp. – 1. IRSNB M1296, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1297, RM/1 (holotype). a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1298, RM/3. a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1299, RP4/. a: occlusal view, b: labial view. – 5. IRSNB M1300, RM3/. a: occlusal view, b: labial view.

Fig. 5. – *Arfia gingerichi* n. sp. – 1. IRSNB M1301, LP/3. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1302, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1303, RP/4. a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1304, RM/1. a: labial view, b: occlusal view, c: lingual view. – 5. IRSNB M1305, RM/2. a: labial view, b: occlusal view, c: lingual view.


1a
1b
1c
2a
2b
2c
3a
3b
3c
2mm
4a
5a
4b
5b


1a
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3b
3c
4a
4b
4c
5a
5b
5c

IRSNB M1307, RP3/; IRSNB M1358, RDP4/; IRSNB M1308, LP4/; IRSNB M1309, RM1/; IRSNB M1310, RM2/ (labial part); IRSNB M1311, LM3/.

Referred material: CL44, LP/3; CL46, LP/3; CL47, LP/3; DIII173RS, RP/3; DIIC643RS, LP/3; TS30, LP/3; TS31, RP/3; TS32, LP/3 (broken); D83, LDP/4 (trigonid); DC143, RDP/4; DIIC641RS, RP/4; DIIC1687RS, LP/4; IRSNB M1276, RM/1 (WL169 in Lange-Badré & Godinot, 1982, pl. I, fig. 3a, d, g); IRSNB M1277, LM/1 (CL22 in Lange-Badré & Godinot, 1982, pl. I, fig. 3c, f, i); DIII1315RS, LM/1; DIIC250RS, LM/1; TS34, RM/2; TS35, RM/2 (trigonid); TS36, RM/3 (trigonid); DIII177RS, RM/3; DIII261RS, RM/3; TS42, LM/3 (worn); Do1712PG, RM/3 (trigonid); TS37, RP2/?; Do832, LP3/; DI1426RS, LP3/; CL37, LP4/ (labial part); DL1, RM1/; DD8, LM1/; TS39, RM1/ (lingual part); DI1849RS, LM3/; TS41, LM3/; Eq1, LM/3 (trigonid); Eq2, RP/4.

Type locality

Dormaal

Other localities

Erquelinnes, Try (MP7, Early Eocene, Marne, France), Kyson (MP7, Early Eocene, Suffolk, England).

Diagnosis

Smallest species of the genus, differing from all the other species by M/3 with distinctly less developed talonid cusps, by the absence of postcingulum on lower molars, and by proportionally smaller M3/.

Etymology

Named after Prof. Philip Gingerich (University of Michigan, Ann Arbor) who contributed to the knowledge of the Wa0 faunas. He was the first to show the similarities between *A. junnei* from Wyoming and the Belgian species here described (Gingerich, 1989, p. 33-36).

Description

Lower dentition

As for all the teeth of this new species, the P/3 (Fig. 5. 1a-c) presents a finely crenulated enamel surface. The paraconid is generally absent or reduced to a tiny spherical cusp (CL47). The crest that descends the posterior wall of the trigonid and the central crest of the talonid delimit the labial edge of a slight basin.

The molariform DP/4 (Fig. 5. 2a-c) has well-developed metaconid and talonid cusps. The metaconid is strongly posterior in comparison with the position of the protoconid. The paraconid is prominent. The talonid is relatively high.

TABLE 3

Measurements (in mm) of cheek teeth of *Arfia gingerichi* n. sp. from Dormaal. Abbreviations as in Table 1.

		n	OR		M	σ	V
DP4/	L	1	4.85		-	-	-
	l	1	4.20		-	-	-
P3/	L	2	5.75	5.80	5.78	0.04	0.61
	l	2	2.90	3.10	3.00	0.14	4.71
P4/	L	1	6.75		-	-	-
	l	1	5.80		-	-	-
M1/	L	1	5.45		-	-	-
	l	1	5.90		-	-	-
M3/	L	3	2.95	3.5	3.22	0.28	8.56
	l	3	7.95	8.5	8.32	0.32	3.82
DP/3	L	2	5.05	5.05	5.05	0.00	0.00
	l	2	1.85	1.90	1.88	0.04	1.89
DP/4	L	1	5.50		-	-	-
	l	1	2.50		-	-	-
P/3	L	8	5.55	5.8	5.64	0.09	1.55
	l	8	2.2	2.35	2.29	0.06	2.80
P/4	L	4	5.85	6.90	6.25	0.45	7.24
	l	4	2.65	3.05	2.88	0.17	5.94
M/1	L	4	5.60	6.00	5.89	0.19	3.28
	l	4	3.00	3.25	3.11	0.11	3.56
M/2	L	1	6.90		-	-	-
	l	1	3.45		-	-	-
M/3	L	4	6.35	7.40	6.79	0.47	6.92
	l	4	3.45	3.90	3.65	0.20	5.36

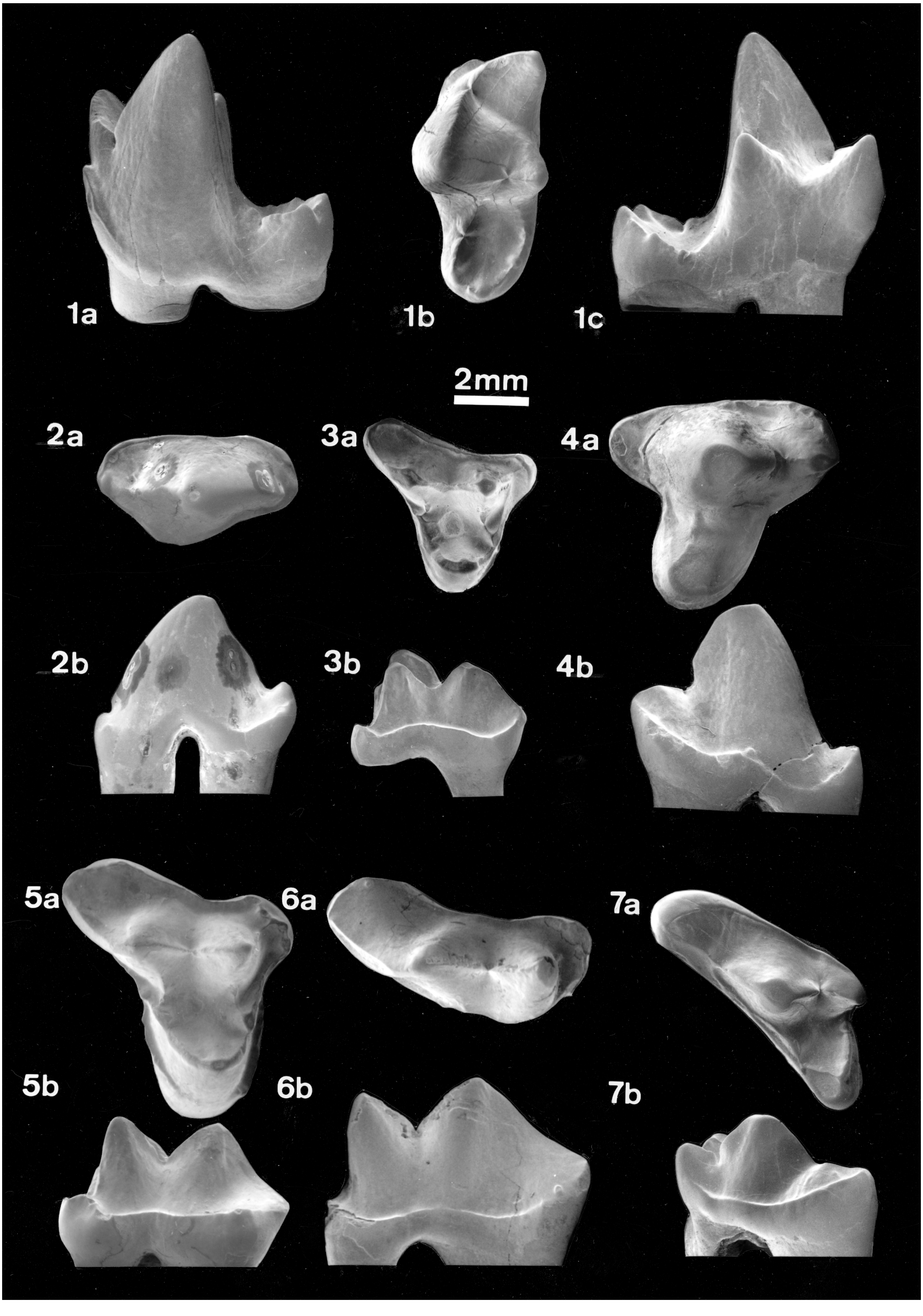
The P/4 (Fig. 5. 3a-c) is large with a massive wide protoconid. An antero-labial cingulum and an antero-lingual fold are situated on either sides of a small paraconid.

The M/1 (Fig. 5. 4a-c) is a little shorter than P/4 and slightly wider. The metaconid is more developed than the paraconid. In addition to the three talonid cusps (hypoconid, hypoconulid, entoconid), an entoconulid is developed on the entocristid. An incomplete labial cingulum is present: the postcingulum is absent. The specimen IRSNB M1277 is slightly larger than the others and shows a somewhat more developed talonid.

The M/2 (Fig. 5. 5a-c) is distinctly larger than M/1. The trigonid is proportionally larger than on M/1. The metaconid is also more developed than the paraconid. Only an antero-labial cingulum is visible, the labial cingulum being absent. A crest descends the postero-lingual edge of the paraconid on specimen IRSNB M1305. This crest is absent on the specimens TS34 and TS35.

Legend to the figures (see opposite page)

Fig. 6. – *Arfia gingerichi* n. sp. – 1. IRSNB M1306, LM/3. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1307, RP3/. a: occlusal view, b: labial view. – 3. IRSNB M1358, RDP/4. a: occlusal view, b: labial view. – 4. IRSNB M1308, LP4/. a: occlusal view, b: labial view. – 5. IRSNB M1309, RM1/. a: occlusal view, b: labial view. – 6. IRSNB M1310, RM2/ (labial part). a: occlusal view, b: labial view. – 7. IRSNB M1311, LM3/. a: occlusal view, b: labial view.


1a
1b
1c
2mm
2a
3a
4a
2b
3b
4b
5a
6a
7a
5b
6b
7b

The M/3 (Fig. 6. 1a-c) is a little shorter than M/2 (except maybe for the specimen IRSNB M1306). The metaconid is more reduced than on M/1 and M/2, but still sub-equal to the paraconid. The protoconid is well developed and taller than on the other molars. The talonid cusps are less differentiated than on M/1 and M/2.

Upper dentition

The P3/ (Fig. 6. 2a-b) is slightly wider anteriorly than posteriorly. It presents an antero-labial bulge and a posterior cusp.

The DP4/ (Fig. 6. 3a-b) presents a parastylar lobe extended anteriorly. The metacone has almost the same height as the paracone.

The P4 / (Fig. 6. 4a-b) is large and its lingual part is particularly developed. The paracone is massive and the metastylar crest is relatively thick.

The M1/ (Fig. 6. 5a-b) and M2/ (Fig. 6. 6a-b) show a considerable development of the metastylar lobe. Their paracone and metacone are approximately of the same height but the paracone is shorter. Although the unique M2/ (IRSNB M1310) is broken, its preserved labial part has a morphology similar to that of M1/ but it is definitely larger.

The parastylar lobe of M3/ (fig. 6. 7a-b) is very elongated antero-labially. The metacone is reduced compared with that of M1/ and M2/. The protocone is short anteroposteriorly.

Discussion

The presence of the genus *Arfia* was announced for the first time in Europe with *Arfia woutersi* from Dormaal (Lange-Badré & Godinot, 1982). Subsequently, three M/1 (IRSNB M1304, IRSNB M1277, IRSNB M1276), among the six teeth described in 1982, were referred to *A. junnei* from the Wa0 of Willwood Formation, Wyoming (Gingerich, 1989). Thus, *A. junnei* was one of the rare species reported on the two continents. The validity of *A. woutersi* was questioned because one of the two syntypes designated by Lange-Badré & Godinot (1982) was recognized by Gingerich (1989) as belonging to a genus other than *Arfia* and he voluntarily selected it as the lectotype of "*A.*" *woutersi* (LM1/, IRSNB M1319). The latter is an oxyaenid creodont; it is described further on.

We have today about 30 teeth collected at Dormaal and Erquelinnes that we attribute to the genus *Arfia*. This material indicates that the Belgian species is indeed closely related to *Arfia junnei* from the Willwood Formation Wa0 (M/1, M1/ and DP4/ are nearly identical). However, it is characterized by the absence of postcingulum on the lower molars and by M/3 probably a little shorter than M/2, a reverse situation to that of *A. junnei* and the other American species (*A. shoshoniensis* Matthew, 1915 and *A. opisthotoma* Matthew, 1901). It should be noted that a similar observation was already made for the M/3 at the time of the comparison of *Prototomus minimus* n. sp. from Dormaal with *P. deimos* from the Wa0. Moreover, the talonid cusps of the lower molars are less differentiated and individualized than in *A. junnei*. It is M/3 that presents the least developed talonid (observation on four complete specimens). This character, which affects preferentially the entoconid, is found to a lesser extent on the specimen AMNH15745 of *A. shoshoniensis*. The protocone of M3/ of *Arfia gingerichi* n. sp. is proportionally shorter than that of *A. opisthotoma* (AMNH99). We could not compare the M3/ with that of *A. junnei*, the M3/ of the latter being as yet unknown.

The Belgian taxon belongs to another species than *A. junnei*. By its incomplete labial cingulum on the lower molars and its less developed M/3, it differs somewhat from the American lineage and is at its origin or close to its origin. At all events, there is no doubt that the two species are very close.

Genus *Galecyon* Gingerich & Deutsch, 1989
Type species *Galecyon mordax* (Matthew, 1915)

Emended diagnosis: hyaenodontid with robust canines, short deep dentary, single-rooted P/1, large and sharp posterior cusp on P/4, short basined talonids on M/1-3 with reduced entoconid and hypoconulid which form a lingual crest, reduced M/3, high metastylar and parastylar crests on P4/, tall cusps and very short postmetacrista on upper molars.

***Galecyon morloi* n. sp.**
(Fig. 7)

Material

Holotype: IRSNB M1314, LM/1.

Paratypes: IRSNB M1312, RDP/4; IRSNB M1313, RP/4; IRSNB M1315, RM/2; IRSNB M916, RM/3; IRSNB M1316, RP4/; IRSNB M1317, LM1,2/.

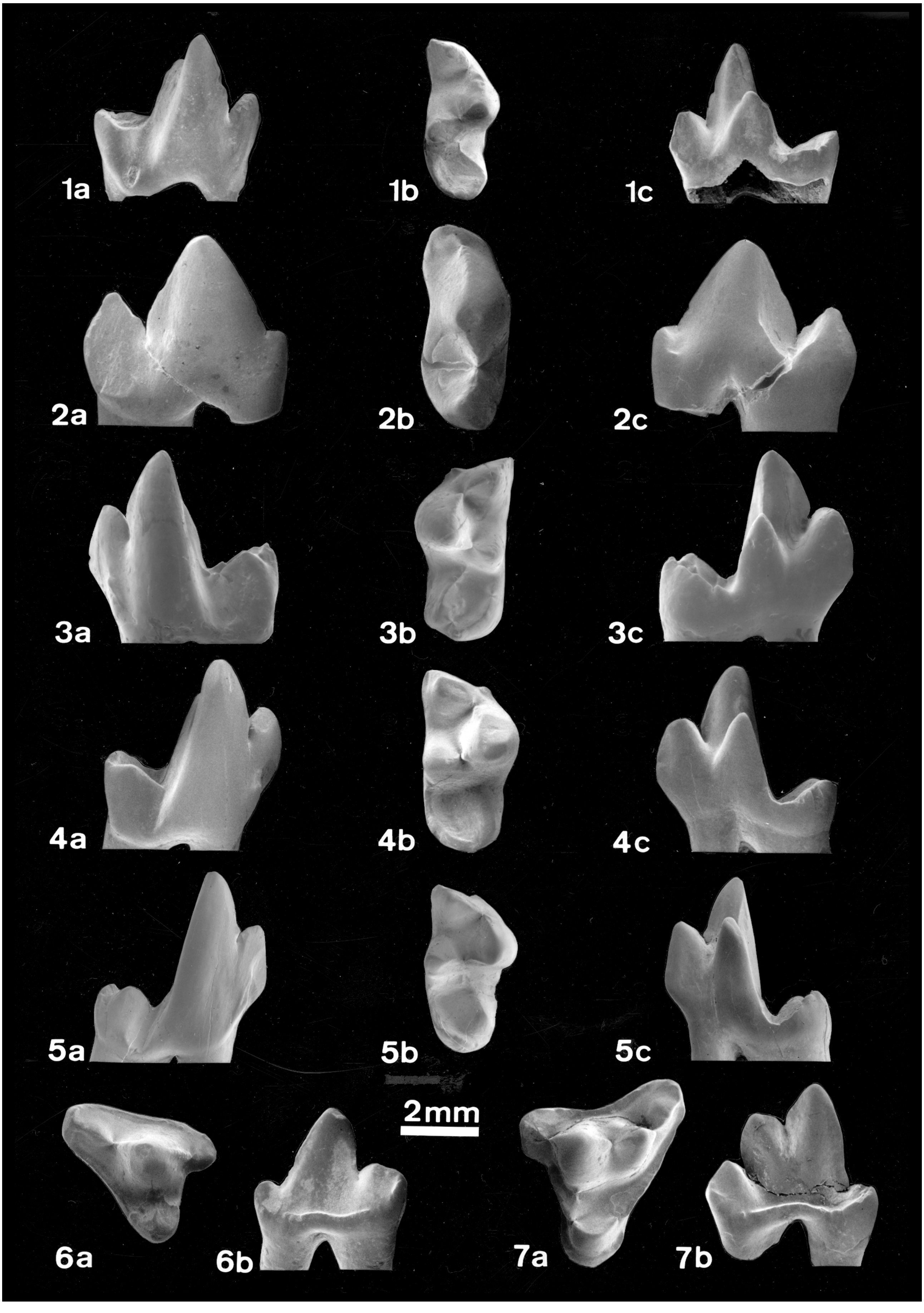
Referred material: DIII175RS, LP/4; D137, LM/1; CL89, RM/1; DIII176RS, LM/1; Do291PG, RM/1; Do306PG, RM/1?; TS44, LP4/ (labial part); DIII478RS, RDP4/?; IRSNB M1357, M1,2/d; CL94, LM1,2/.

Type locality

Dormaal.

Legend to the figures (see opposite page)

Fig. 7. – *Galecyon morloi* n. sp. – 1. IRSNB M1312, RDP/4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1313, RP/4. a: labial view, b: occlusal view, c: lingual view. – 3. IRSNB M1314, LM/1 (holotype). a: labial view, b: occlusal view, c: lingual view. – 4. IRSNB M1315, RM/2. a: labial view, b: occlusal view, c: lingual view. – 5. IRSNB M916, RM/3. a: labial view, b: occlusal view, c: lingual view. – 6. IRSNB M1316, RP4/. a: occlusal view, b: labial view. – 7. IRSNB M1317, LM1,2/. a: occlusal view, b: labial view.


1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c
5a
5b
5c
2mm
6a
6b
7a
7b

Diagnosis

Smallest species of the genus, differing from *Galecyon mordax* in being about 20 % smaller, by the higher ratio M/3:M/2 length (0.93 for *G. morloi*; 0.75 for *G. mordax*), and by the less developed lingual crest of the talonid and hypoconulid.

Etymology

Named after Dr. Michael Morlo (Frankfurt) who has contributed to the knowledge of the hyaenodontid creodonts of Europe.

TABLE 4

Measurements (in mm) of cheek teeth of *Galecyon morloi* n. sp. from Dormaal. Abbreviations as in Table 1.

		n	OR		M	σ	V
P4/	L	1	4.30		-	-	-
	l	1	3.40		-	-	-
M1,2/	L	2	4.60	4.85	4.73	0.18	3.74
	l	2	4.75	4.90	4.83	0.11	2.20
DP/4	L	2	4.50	4.65	4.58	0.11	2.32
	l	2	2.20	2.25	2.23	0.04	1.59
P/4	L	2	5.70	6.15	5.93	0.32	5.37
	l	2	2.55	2.80	2.68	0.18	6.61
M/1	L	4	5,00	5.60	5.36	0.26	4.78
	l	4	2.45	2.75	2.65	0.14	5.11
M/2	L	1	4.85		-	-	-
	l	1	2.65		-	-	-
M/3	L	1	4.50		-	-	-
	l	1	2.60		-	-	-

Description

Lower dentition

The DP/4 (Fig. 7. 1a-c) presents a high and wide paraconid. The trigonid is longer than the talonid, and the metaconid has a posterior position relative to the protoconid.

The P/4 (Fig. 7. 2a-c) is large and its protoconid is massive. The paraconid is relatively extended lingually. A lingual crest delimits a small talonid basin. The central crest of the talonid rises posteriorly to end in a large sharp cusp.

The lower molars (fig. 7. 3-5) have the trigonid longer than the talonid, a developed and massive paraconid and protoconid, a posterior metaconid, as well as a wide talonid basin. The entoconid is absent and is replaced by a crest that extends from the back of the metaconid to the hypoconulid. The M/1 (Fig. 7. 3a-c) differs from the M/2 (fig. 7. 4a-c) in its narrower trigonid. The M/3 (Fig. 7. 5a-c) is shorter anteroposteriorly than M/1 and M/2 and its talonid is narrower.

Upper dentition

The P4/ (Fig. 7. 6a-b) has an oblique labial edge. The lingual part of the tooth is not reduced. The metastylar and parastylar crests are developed in height. The paracone is high. The postcingulum ascends to the tip of the metastyle.

The M1,2/ (Fig. 7. 7a-b) is a robust tooth, relatively narrow labio-lingually. The paracone is much broader and taller than the metacone. The postmetacrista is very short. The protocone is relatively powerful and is surrounded by a weak but complete lingual cingulum. The postcingulum extends to the metastyle as on P4/.

Discussion

Before being attributed to the new genus *Galecyon*, *G. mordax* was referred to *Sinopa* (Matthew, 1915; MacIntyre & Guthrie, 1979) and to *Prototomus* (Van Valen, 1965). *Galecyon* is indeed close to *Sinopa* according to the fusion of the lingual cusps and the hypoconulid, which form a curved crest delimiting the talonid basin of the lower molars (derived character). It presents also relatively narrow lower molars and an important difference in height between the trigonid and the talonid.

The differences between *Galecyon mordax* Matthew, 1915 (Wa1-3, Willwood Formation, Wyoming) and *Galecyon morloi* n. sp. from Dormaal lie primarily in the larger size of the American species (15-30%), the more developed lingual crest of the talonid and hypoconulid, and the lower length/width ratio of the molars. *G. mordax* is known from only six specimens. Most of them are damaged and they all belong to lower dentitions. However, an upper molar ascribed to *Prototomus martis*, UM86399 from the Wa2 of Willwood Formation (Gingerich & Deutsch, 1989), is quite similar to M1,2/ of *Galecyon morloi* n. sp. Indeed, its thick and very short postmetacrista does not correspond to the genus *Prototomus*. It should probably be referred to *G. mordax*.

On the other hand, the two specimens RI275 and RI276 of *Prototomus* cf. *mordax* from Rians (Godinot, 1981) belong actually to the genus *Galecyon*. They present 10 to 25% larger lower molars than those of the Belgian species. Moreover, the paraconid of P/4 is clearly less developed than in *Galecyon morloi* n. sp.

The discovery, in Dormaal, of the upper molars of *Galecyon* reveals a very short postmetacrista. This character is particularly primitive for the creodonts. It thus seems that *Galecyon morloi* n. sp. preserves symplesiomorphic characters while already developing some synapomorphic characters, which could give it a position between *Prototomus* and *Sinopa* in the cladogram of the early Hyaenodontidae proposed by Polly (1996, fig. 12).

Family OXYAENIDAE Cope, 1877
Subfamily OXYAENINAE Cope, 1877
Genus *Oxyaena* Cope, 1874
Type species *Oxyaena lupina* Cope, 1874

Oxyaena woutersi (Lange-Badré & Godinot, 1982) comb. nov.

(Fig. 8. 1-3)

1982: *Arfia woutersi* n. sp.; Lange-Badré & Godinot, p. 295-300, pl. 1, fig. 1.; non pl. 1, figs. 2-4.

1989: "*Arfia*" *woutersi*; GINGERICH, p. 36.

Material

Lectotype: IRSNB M1319, LM1/ (or LDP4/?), figured as WL1147 by LANGE-BADRÉ & GODINOT (1982; pl. I, fig. 1a-b).

Referred material: IRSNB M1318, RP/3,4; IRSNB M1320, LM1/.

Type locality

Dormaal.

Diagnosis

Smallest species of the genus. Differs from *Oxyaena transiens* by the shorter postmetacrista on M1/; from *O. krausei* and *O. aequidens* by its lower and spindlier cusps.

TABLE 5

Measurements (in mm) of cheek teeth of *Oxyaena woutersi* (Lange-Badré & Godinot, 1982) from Dormaal. Abbreviations as in Table 1.

		n	OR		M	σ	V
M1/	L	2	6.35	7.00	6.68	-	-
	l	2	8.20	9.45	8.83	-	-
P/3,4	L	1	6.40		-	-	-
	l	1	3.05		-	-	-

Description

Lower dentition

The single lower tooth is a P/3,4 (fig. 8. 1a-c) the surface of the enamel of which is finely crenulated. The paraconid is weak. The central crest of the talonid is very high and its tip is round. A lingual cingulum delimits a weak basin on the talonid.

Upper dentition

Both M1/ (fig. 8. 2-3) have somewhat different dimensions primarily because of labio-lingual shortening of the tooth IRSNB M1319. Paracone and metacone are fairly closely set and have appreciably the same height. The postmetacrista is little extended and the protocone is short antero-posteriorly.

Discussion

GINGERICH (1989) designated the M1/ IRSNB M1319 as the lectotype of "*Arfia*" *woutersi*. The morphology of this tooth agrees not with that of the hyaenodontid *Arfia*, but with that of an oxyaenid. Indeed, the proximity of the paracone and metacone, the relatively short and massive postmetacrista, and the well-developed metacone characterize the Oxyaeninae. The different length/width proportions between IRSNB M1319 and IRSNB M1320 result probably from a simple intraspecific variation but we can not exclude that the lectotype IRSNB M1319 is in fact a DP4/.

The morphology of the P/3,4 confirms the presence, at Dormaal, of a species of Oxyaeninae attributable to the genus *Oxyaena* Cope, 1874 or *Dipsalidictis* Matthew, 1915. *Oxyaena*, a large animal, was considered as ranging through the entire Wasatchian, whereas *Dipsalidictis*, smaller in size, characterized the Clarkforkian and the early Wasatchian. It is to be noted that *D. platypus* Matthew, 1915, the smallest oxyaenine of North America, is still approximately 40% larger than the Belgian species. The characters separating the genera *Dipsalidictis* and *Oxyaena* are poor and some of them are probably related to differences in body size (GUNNELL & GINGERICH, 1991, p. 165). Besides, *Dipsalidictis* was recently included in the genus *Oxyaena* (MCKENNA & BELL, 1997, p. 226). Considering the paucity of the material from Dormaal, it is still difficult to specify the phylogenetic relations of *Oxyaena woutersi*. However, the rather short postmetacrista on M1/ (symplesiomorphic character) distinguishes it from *O. transiens* Matthew, 1915 (Wa0-2). This character is found on the two oldest American species: *O. krausei* (Gunnell & Gingerich, 1991) (Cf1-3) and *O. aequidens* Matthew, 1915 (Cf2-3). *O. krausei* has taller cusps and the teeth of these two species are clearly more massive than those of *O. woutersi*. *O. platypus* (Cf2-Wa1), of a slender aspect, seems to be the closest to the Belgian species. A fragment of the right maxilla with P3/-M2/ (UM66137, Wa0) well shows a relatively short but a little posteriorly tilted postmetacrista.

Among the European Oxyaenidae, *Oxyaena* sp. (LM/1, UCMP83754) from Sinceny (MP10, Aisne, Paris Basin) described by RICH (1971) is similar to *O. transiens* (Wa0-2) from Wyoming (GUNNELL & GINGERICH, 1991). Moreover, for HOOKER (1998) it would belong to the same species as *Oxyaena* sp. (trigonid of LM/1, MNHN AC656) recognized at Meudon (Ypresian, Hauts-de-Seine, France) by GUNNELL & GINGERICH (1991, p. 177). A small species represented by the lingual part of a RM1/ (BMNH15128) and a large species known by a RM/2 (BMNH13778), both from Abbey Wood (lower Ypresian, England) and described by VAN VALEN (1965), were also referred as *Oxyaena* sp. (GUNNELL & GINGERICH, 1991). These authors relate the large species to *O. aequidens* (Cf2-3) from Wyoming, whereas HOOKER (1998) names it *O. gulo* Matthew, 1915 known also from Wyoming (Wa2-3). All these taxa are larger than that from Dormaal. Only that from Meudon could possibly be related to *Oxyaena woutersi* considering its small size. However, owing to the very scarce material currently available, it is difficult, for the time being, to make any more detailed comparisons.

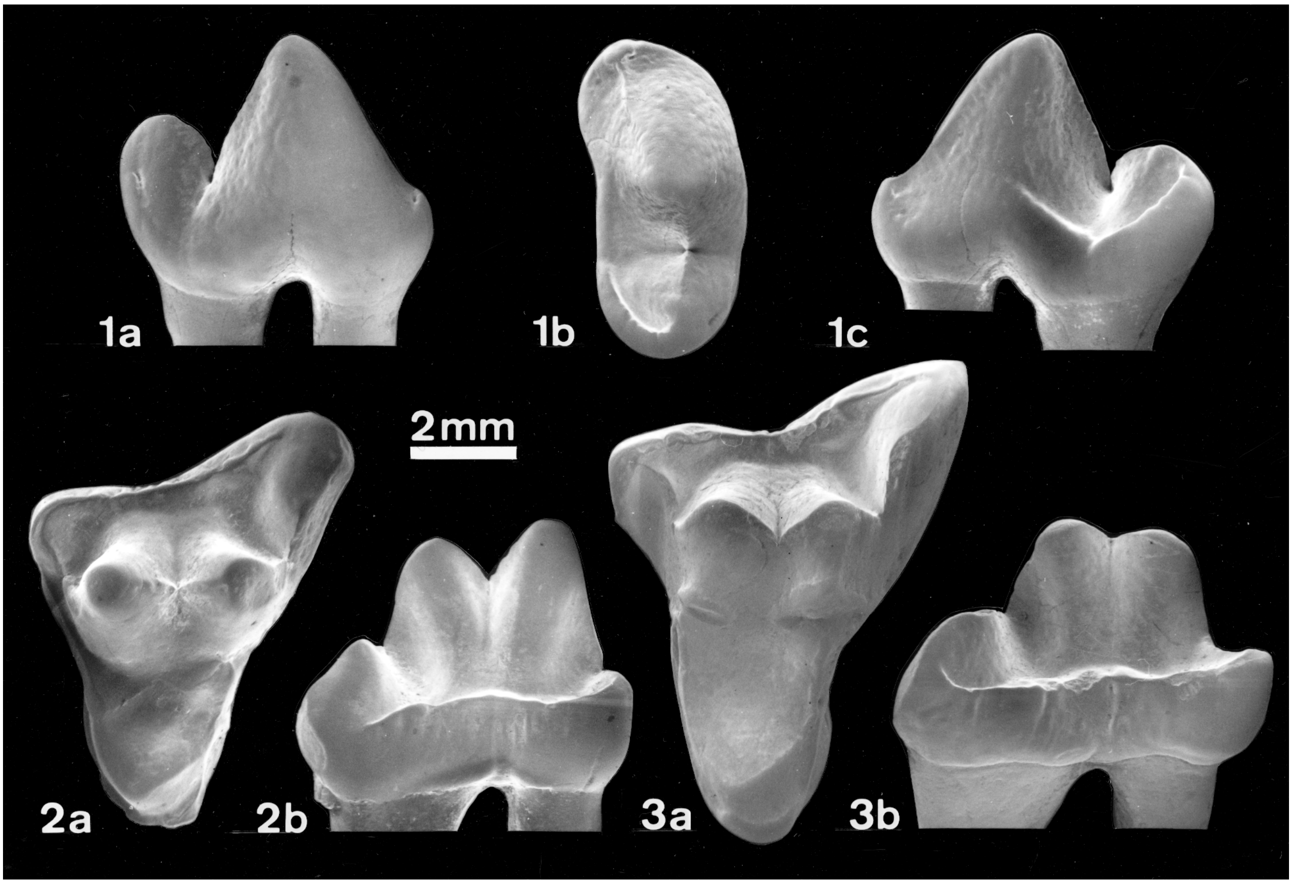


Fig. 8. – *Oxyaena woutersi* (Lange-Badré & Godinot, 1982) – 1. IRSNB M1318, RP/3,4. a: labial view, b: occlusal view, c: lingual view. – 2. IRSNB M1319, LM1/ (Lectotype). a: occlusal view, b: labial view. – 3. IRSNB M1320, LM1/. a: occlusal view, b: labial view.

Subfamily AMBLOCTONINAE Cope, 1877

Genus *Palaeonictis* de Blainville, 1842

Type species *Palaeonictis gigantea* de Blainville, 1842

Palaeonictis gigantea **de Blainville, 1842**

1966: *Oxyaena* (?) *casieri* n. sp.; QUINET, p. 35, pl. V, figs 4-6.
1978: cf. *Palaeonictis*; GODINOT et al., p. 1273.
1987: *Palaeonictis gigantea*; LANGE-BADRÉ, p. 831.

Material

Syntypes: ARP52, fragment of left mandible with P/3, P/4 (talonid), M/1 (talonid); ARP53, canine; ARP54, upper premolar (Argiles à lignites du Soissonnais).

Referred material: IRSNB M1355, LP/4 (Dormaal); IRSNB M1797, LDP/4 (Hoegaarden).

Type locality

Not specified, area of Soisson (Argiles à lignites du Soissonnais).

Other localities

Dormaal, Hoegaarden, Meudon?

Discussion

No new material can be referred to *Palaeonictis gigantea*. The DP/4 discovered at Hoegaarden was identified by comparison with DP/4 of the American species *Palaeonictis occidentalis* Osborn, 1892 (UM73459, Wa1-4) and *P. peloria* Rose, 1981 (UM65640, Cf3) (SMITH & HOOKER, 1996). These two species are larger than *P. gigantea* (*P. occidentalis*: 20%, *P. peloria*: 50%). Considering the less reduced M/2 with a larger metaconid, *P. peloria* would be more plesiomorphic than *P. occidentalis,* and would be closer to *P. gigantea* (ROSE, 1981). In addition, the holotype of *P. gigantea* shows that P/4 had to be a little larger than the IRSNB M1355, which does not exclude the possibility that the taxon from Dormaal could belong in fact to a new species. In the absence of additional material, we thus refer to the work of LANGE-BADRÉ (1987). *P. gigantea* is currently one of the most primitive oxyaenid creodonts of Europe.

Genus *Dormaalodon* Lange-Badré, 1987
Type species *Dormaalodon woutersi*
Lange-Badré, 1987

Dormaalodon woutersi Lange-Badré, 1987

Material

Holotype: IRSNB M1474, RM/1.

Referred material: IRSNB M1466, LM/1 (worn).

Type locality

Dormaal.

Discussion

The state of the knowledge on *Dormaalodon woutersi* remains unchanged because no other tooth has been found since its study by Lange-Badré (1987). This enigmatic species is characterized by many apomorphies: the retreat of the metaconid and its integration in the talonid, the communication between the trigonid basin and the hypoflexid, the relative fusion of the hypoconid and the hypoconulid, the disappearance of the entoconid.

RELATIONSHIPS OF NORTH AMERICAN AND EUROPEAN LATE PALEOCENE AND EARLY EOCENE CREODONTS

The creodonts of the Paleocene-Eocene transition are well represented in Belgium: two families and three subfamilies for six genera. Such an observation is a priori unexpected since, not only are the creodonts rare in the Early Eocene of Europe (Lange-Badré *in* Godinot et al., 1987), but, in addition, they represent in Dormaal one of the first occurrences of this group in Europe.

The hyaenodontid creodonts (Fig. 9) are closely related to those of the Wasatchian Wa0 of the North American Willwood Formation (Wyoming) from which *Arfia* and *Prototomus* can be distinguished primarily by M/3 and M3/. In both Belgian taxa, M/3 and M3/ are proportionally smaller and the talonid of M/3 is less developed, whereas among the various species of *Arfia* and *Prototomus* of the higher Wasatchian levels, the size of M/3 remains at least equal to M/2. P/4 and P4/ of *Prototomus* are less developed in the Belgian species, and the upper molars show primitive evolutionary stages, particularly M2/. Thus, two hypotheses can be drawn from our study. The Belgian species could either be at the origin of the American lineages, or belong already to distinct lineages but of recent differentiation.

The Belgian oxyaenid creodonts (Fig. 10) seem to resemble more the primitive species of the North American Clarkforkian than those already more derived from the Wasatchian. This would indicate that the north European species could be originating from the Paleocene lineages as presently documented by the North-American record. However, this does not explain their very small size as compared to the oxyaenids of the New World.

In conclusion, the phylogenetic relations between the Belgian and North American creodonts of the Paleocene-Eocene transition are narrow and any way relatively recent.

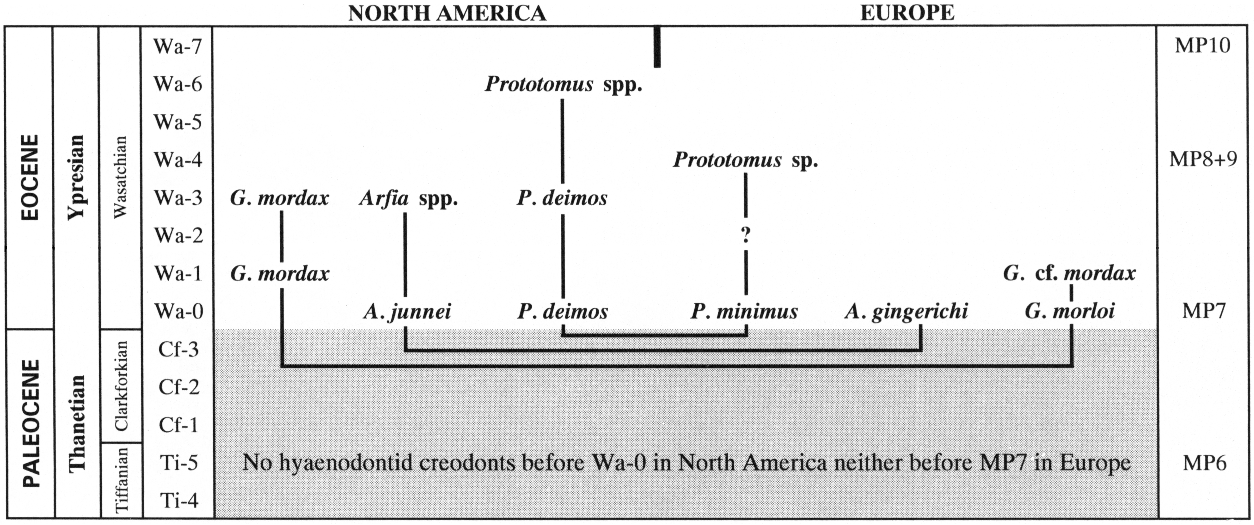


Fig. 9. – Spatial and temporal distribution of hyaenodontid creodonts in Europe and North America that have phylogenetic relationships with those of Belgium (the lines connect the closely related species). The left columns indicate the international stratigraphic scale and the equivalent stages in the continental stratigraphic scale of North America. The right columns indicate the reference levels of the mammalian biochronological scale for the European Paleogene (MP: Mammal Paleogene, MP6 to 10).

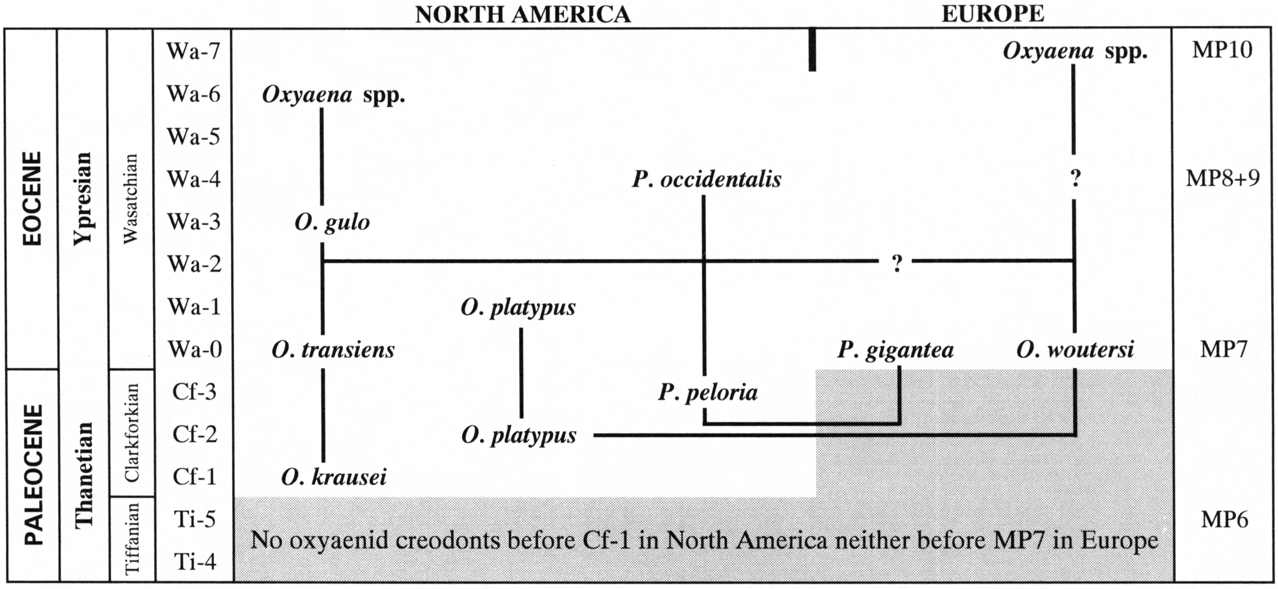


Fig. 10. – Spatial and temporal distribution of oxyaenid creodonts in Europe and North America that have phylogenetic relationships with those of Belgium (the lines connect the closely related species).

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REFERENCES

Cope, E.D. (1874). *Report upon the Vertebrate fossils dicovered in New Mexico, with description of new species.* Extracted from Appendix FF of the Annual Report, Chief of Engineers. Government Printing Office, Washington 1874: 3-18.

Cope, E.D. (1875). Systematic catalogue of Vertebrata of the Eocene of New Mexico, collected in 1874. *Geographical Explorations and Suveys West of the 100th Meridian*, Geo. M. Wheeler, Corps of Engineers, in charge. Government Printing Office, Washington 1875: 5-37.

Cope, E.D. (1877). Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. *Report upon United States Geographical Surveys West of the 100th Meridian*, in charge of First Lieutenant Geo. M. Wheeler, Corps of Engineers, US Army. Volume IV. – Paleontology. Part III. Government Printing Office, Washington 1877: 1-370.

de Blainville, H.M.D. (1842). *Ostéographie ou description iconographique comparée du squelette et du système dentaire des mammifères récents et fossiles pour servir de base à la zoologie et à la géologie.* Livraison 10: Des Viverras. J.B. Baillière et Fils, Paris: 1-100.

Gingerich, P.D. (1989). New Earliest Wasatchian Mammalian Fauna from the Eocene of Northwestern Wyoming: Composition and Diversity in a rarely sampled high-floodplain assemblage. *University of Michigan, Papers on Paleontology*, 28: 97 p.

Gingerich, P.D. & H.A. Deutsch (1989). Systematics and Evolution of Early Eocene Hyaenodontidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming. *Contributions from the Museum of Paleontology*, University of Michigan, 27 (13): 327-391.

Gingerich, P.D. & D.A. Winkler (1979). Patterns of variation and correlation in the dentition of the red fox *Vulpes vulpes. Journal of Mammalogy,* 60: 691-704.

Godinot, M. (1981). Les Mammifères de Rians (Eocène inférieur, Provence). *Palaeovertebrata,* 10 (2): 43-126.

Godinot, M., F. de Broin, E. Buffetaut, J.-C. Rage & D.E. Russell (1978). Dormaal: une des plus anciennes faunes éocènes d'Europe. *Comptes rendus de l'Académie des Sciences,* Paris, Série D, 287: 1273-1276.

Godinot, M., J.-Y. Crochet, J.-L. Hartenberger, B. Lange-Badré, D.E. Russell & B. Sigé (1987). Nouvelles données sur les mammifères de Palette (Eocène inférieur, Provence). *Münchner Geowissenschaftliche Abhandlungen,* (A) 10: 273-288.

Gunnell, G.F. & P.D. Gingerich (1991). Systematics and Evolution of Late Paleocene and Early Eocene Oxyaenidae (Mammalia, Creodonta) in the Clarks Fork Basin, Wyoming.

Contributions from the Museum of Paleontology, University of Michigan, 28 (7): 141-180.

HOOKER, J.J. (1998). Mammalian faunal change across the Paleocene-Eocene transition in Europe. In: AUBRY, LUCAS & BERGGREN (eds), *Late Paleocene-Early Eocene climatic and biotic events in the marine and terrestrial records*. Columbia University Press, New York: 428-450.

LANGE-BADRÉ, B. (1987). *Dormalodon woutersi*, n. g., n. sp., un Créodonte Paléonictiné nouveau de l'Eocène inférieur de Dormaal (Belgique). *Comptes rendus de l'Académie des Sciences*, Paris, Série II, 305: 829-832.

LANGE-BADRÉ, B. & M. GODINOT (1982). Sur la présence du genre nord-américain *Arfia* Van Valen (Creodonta, Mammalia) dans la faune de Dormaal (Eocène inférieur de Belgique). *Comptes rendus de l'Académie des Sciences,* Paris, Série II, 294: 471-476.

LEIDY, J. (1869). The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. *Journal of the Academy of Natural Sciences*, Philadelphia, Series 2, 7: 8-472.

LEMOINE, V. (1880). Communication sur les ossements fossiles des terrains tertiaires inférieurs des environs de Reims. *Association française pour l'avancement des Sciences, Congrès de Montpellier*, 1879: 585-594.

LINNAEUS, C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines genera, species cum characteribus, differentis, locis, editis decima, reformata*. Stockholm, Laurentii Salvii.

MACINTYRE, G.T. & D.A. GUTHRIE (1979). *Paeneprolimnocyon* Guthrie, 1967, a junior synonym of *Oodectes* Wortman, 1901. *Journal of Paleontology*, 53: 1034-1036.

MATTHEW, W.D. (1901). Additional observations on the Creodonta. *Bulletin of the American Museum of Natural History*, 14: 1-38.

MATTHEW, W.D. (1915). A revision of the lower Eocene Wasatch and Wind River faunas. Part 1. Order Ferae (Carnivora). Suborder Creodonta. *Bulletin of the American Museum of Natural History*, 34: 4-103.

MCKENNA, M.C. & S.K. BELL (1997). *Classification of Mammals Above the Species Level*. Columbia University Press, New York, 631 p.

POLLY, P.D. (1996). The skeleton of *Gazinocyon vulpeculus* gen. et comb. nov. and the cladistic relationships of Hyaenodontidae (Eutheria, Mammalia*). Journal of Vertebrate Paleontology*, 16 (2): 303-319.

QUINET, G.E. (1966). Les Mammifères du Landénien continental belge, second tome. Etude de la morphologie dentaire comparée des Carnivores de Dormaal. *Mémoire de l'Institut royal des Sciences naturelles de Belgique,* 158: 1-64.

RICH, T.H.V. (1971). Deltatheridia, Carnivora, and Condylarthra (Mammalia) of the Early Eocene, Paris Basin, France. *University of California Publications in Geological Sciences,* 88: 1-72.

ROSE, K.D. (1981). The Clarkforkian Land-Mammal Age and Mammalian Faunal Composition across the Paleocene-Eocene Boundary. *University of Michigan*, *Papers on Paleontology*, 26: 196 p.

RÜTIMEYER, L. (1862). Eocäne Säugethiere aus dem Gebiet des schweizerischen Jura. *Neue Denkschriften der Allgemeinen schweizerischen Gesellschaft für die gesammten Naturwissenschaften*, Zurich, 19 (3): 1-98.

SCHMIDT-KITTLER, N., éd. (1987). International Symposium on Mammalian Biostratigraphy and Paleoecology of the European Paleogene, Mainz, February 18th-21st 1987. *Münchner Geowissenschaftliche Abhandlungen*, Munich, (A), 10: 312 p.

SMITH, R. & J.J. HOOKER (1996). Sur la présence de dents de mammifères (Creodonta, Perissodactyla) près de la Limite Paléocène-Eocène à Hoegaarden, Belgique. *Palaeovertebrata,* Volume Jubilaire D.E. Russell, 25 (2-4): 115-124.

SMITH, T. (1996). *Leptacodon dormaalensis* (Mammalia, Lipotyphla), un nyctithère primitif de la transition Paléocène-Eocène de Belgique. *Belgian Journal of Zoology*, 126 (2): 153-167.

SMITH, T. (1999). *Les mammifères de la transition Paléocène-Eocène de Belgique (Formation de Tienen, MP7): systématique, phylogénie, paléoécologie, paléobiogéographie et biostratigraphie*. Thèse de doctorat, Université de Louvain, 311 p.

SMITH, T. (2000). Mammals from the Paleocene-Eocene transition in Belgium (Tienen Formation, MP7): Palaeobiogeographical and biostratigraphical implications. *GFF*, 122 (1): 148-149.

SMITH, T. & R. SMITH (1996). Synthèse des données actuelles sur les vertébrés de la transition Paléocène-Eocène de Dormaal (Belgique). *Bulletin de la Société belge de Géologie*, 104 (1-2): 119-131.

STEURBAUT, E., J. DE CONINCK, E. ROCHE & T. SMITH (1999). The Dormaal Sands and the Paleocene-Eocene boundary in Belgium. *Bulletin de la Société Géologique de France*, 170 (2): 217-227.

TEILHARD DE CHARDIN, P. (1927). Les Mammifères de l'Eocène inférieur de la Belgique. *Mémoires du Musée royal d'Histoire naturelle de Belgique,* 36: 1-33.

VAN VALEN, L.M. (1965). Some European Proviverrini (Mammalia, Deltatheridia). *Palaeontology,* 8 (4): 638-665.

VAN VALEN, L.M. (1966). Deltatheridia, a new order of Mammals. *Bulletin of the American Museum of Natural History*, 132 (1): 1-126.

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Chicken Luteinizing Hormone-Releasing hormone-I and -II are located in distinct fiber terminals in the median eminence of the quail: a light and electron microscopic study

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ABSTRACT. Using highly specific antibodies directed towards the avian luteinizing hormone-releasing hormones-I and –II (cLHRH-I and –II), we were able to show the presence of both peptides in the median eminence of the quail. In order to examine in more detail the morphological organization of both gonadotropin-releasing hormone systems in the median eminence, the present paper describes the results from a light and ultrastructural immunocytochemical double labeling study. These results demonstrate the presence of cLHRH-I and cLHRH-II in distinct fiber systems in the median eminence of the quail. Moreover, close associations between cLHRH-I or –II- immunoreactive neurons and glial cells were observed, suggesting glial-neuronal interactions.

KEY WORDS: LHRH-I, LHRH-II, immunocytochemistry, LM, EM, double staining, bird, median eminence, quail.

INTRODUCTION

In birds two luteinizing hormone-releasing hormones, cLHRH-I and cLHRH-II have been described (for a review see KING & MILLAR, 1995). MIKAMI et al. (1988) published the immunocytochemical distribution of both cLHRH variants in the hypothalamus of both chicken and quail. In 1993, Millam and co-workers used antibodies directed against the full amino acid sequences of cLHRH-I and cLHRH-II to study their distribution in the turkey hen (MILLAM et al., 1993).

In our laboratory, highly specific antibodies were developed directed against polypeptides corresponding to the C-terminal portion of cLHRH-I and –II. After exhaustive specificity testing, these polyclonal antisera were applied in an immunocytochemical study on chicken and quail (VAN GILS, ABSIL, GRAUWELS, MOONS, VANDESANDE & BALTHAZART, 1993). The most striking observation in that study was the presence of not only cLHRH-I, but also of cLHRH-II immunoreactive (ir) fibers in the median eminence (ME) of both species. This finding remained very controversial, since no other study, with any other antibody, had ever reported the presence of densely labeled cLHRH-II fibers in the ME of birds. The latter conviction has always been fundamental for ascribing cLHRH-II a neurotransmitter/neuromodulator role instead of a gonadotropin-releasing function. However, very recently, the final positive identification of cLHRH-II in the ME of birds was provided by affinity purification of the anti-cLHRH-II antiserum, in combination with nano flow quadrupole time of flight mass spectrometry (D'HONDT et al., unpublished data).

The first aim of the present study was to investigate whether cLHRH-I and –II are present in separate fiber systems or not. For this purpose, we performed immunocytochemical double stainings at the light and ultrastructural level.

Secondly, we examined the morphological features of the cLHRH-I and –II -containing fibers and terminals in

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Corresponding author: L. Arckens, e-mail: lut.arckens@bio.kuleuven.ac.be the median eminence to obtain more information about the functioning and regulation of the LHRH system in birds. Although several physiological studies in mammals indicate that LHRH release might be regulated at the level of the ME by neuropeptides, neurotransmitters or excitatory amino acids, electron microscopic studies often fail to find synaptic contacts on LHRH neurons (KAWAKAMI, HIRUNAGI, TSUKAMURA & MAEDA, 1998). Therefore it was suggested that the LHRH release in the ME might be regulated, at least in part, in a non-synaptic manner. Since at present no information is available about the ultrastructural organization of the cLHRH-I and –II systems, the present study aimed to provide more data on this subject in birds.

MATERIAL AND METHODS

Animals and tissue preparation

Three adult female quails were used in this study. These animals were kept under a lighting schedule of 16 hours light/8 hours dark and had feed and water available ad libitum. For light microscopy, the birds were transcardially perfused with 200 ml saline solution containing 1% $NaNO_2$, followed by 200 ml Zamboni's fixative (4% paraformaldehyde + 0.2% (w/v) picric acid). For electron microscopy, median eminences were postfixed for 24 hours with modified Zamboni (Zamboni's fixative containing 0.1% glutaraldehyde). After the brains were embedded in 20% (w/v) gelatin, transverse vibratome sections (50 µm) were cut and serial sections containing the ME were collected in 12-well plates containing 0.15M phosphate buffer (pH=7.4).

Immunocytochemical procedures

Light microscopy

Basically, the immunocytochemical procedure for the double staining of cLHRH-I and –II was the same as the one described by MOONS et al. 1988. All antiserum incubations and washing steps were performed in 0.01 M Tris-HCl buffer pH 7.4, containing 0.9% (w/v) NaCl and 0.1% Triton X-100 (v/v) (TBST). After blocking of the endogenous peroxidase activity (blocking solution, Envision$^+$, DAKO, 10 min) and preincubation with 5% normal goat serum (30 min), the first primary antiserum, Ra cLHRH-II (1/10 000), was applied for an overnight incubation. After extensive rinsing, the sections were incubated with a secondary goat anti-rabbit polyclonal antiserum linked to a peroxidase-coupled dextran chain (Envision$^+$, DAKO, 30 minutes), and peroxidase activity was visualized using diaminobenzidine (20µl/ml substrate solution, Envision$^+$, DAKO) as a chromogen. The staining was stopped in distilled water. Prior to processing the sections through the second sequence, all antibodies of the first sequence were electrophoretically eluted (Moons et al. 1988). To subsequently reveal cLHRH-I immunoreactivity, the stained sections were pre-incubated in 5% normal goat serum, followed by an overnight incubation in Ra-cLHRH-I antiserum, diluted 1/15 000. Subsequent incubations steps in biotinylated goat anti-rabbit secondary antiserum (DAKO, 1/400, 30 min) and streptABComplex (DAKO, 30 min) were performed, followed by the fast blue BB staining procedure.

Electron microscopy

To detect simultaneously cLHRH-I and cLHRH-II, a pre-embedding double-labeling technique was optimized. DAB was used as the first chromogen while the second staining sequence was a silver intensified immunogold technique. Free floating vibratome sections were prepared for ICC by treatment in a solution of 0.1% sodium borohydride in 0.15M PBS, pH 7.4 for 15 minutes, followed by thorough rinsing in 0.15M PBS. To reduce aspecific staining, sections were blocked with a solution of 5% acetylated BSA (BSA-c, Aurion, the Netherlands), 0.1% CWFS (cold water fish) gelatin (Aurion, the Netherlands) and 1% normal goat serum in 0.15M PBS, pH 7.4. Unless otherwise mentioned, all subsequent incubation and rinsing steps were performed in BSA-c buffer (0.15M PBS + 0.1% BSA-c). Apart from this different buffer incubation system, all steps for the first staining sequence were the same as for light microscopy. After the DAB staining, sections were rinsed in BSA-c buffer, prior to the second staining procedure. The second primary antiserum was again applied in an overnight incubation step. After intensive rinsing in BSA-c buffer, the sections were incubated with a 1nm gold-conjugated secondary antibody (Aurion, the Netherlands). The gold was intensified with the R-Gent kit (Aurion, the Netherlands) for 15 minutes, in the dark at room temperature.

Tissue preparation for electron microscopy

Following ICC pre-embedding double labeling, sections were rinsed in 0.15M PBS buffer, pH 7.2 and fixed for 1 hour in 1% osmium tetroxide in the same buffer. Sections were then prepared for embedding in Embed 812 resin (Electron microscopy Sciences) by immersion for 10 minutes in each of a series of ethanol solutions as follows: 50%, 70%, 98%, 100%. They were infiltrated with araldite by immersion in (1) propylene oxide (PO) 100%, 10 min., (2) PO 50% + Embed 812 50% 2 hours, (3) Embed 812, overnight and (4) fresh Embed 812, 2 hours. Infiltrated sections were flat mounted between glass slides and plastic coverslips coated with liquid release agent (Electron microscopy Sciences) and cured. Pieces of the embedded ME tissue were mounted onto blocks and ultrathin sections were cut from the surface with an ultramicrotome. These sections were mounted on mesh grids and stained with lead citrate and uranyl acetate and finally viewed and photographed with a Zeiss 109 transmission electron microscope.

Immunocytochemical specificity tests

Because the two primary antisera used in this study were raised in the same species, we included a number of control experiments to prevent false positive or negative staining. For light microscopy, all antibodies of the first sequence were removed by electrophoretic elution. The efficiency of this elution step and the specificity of the double labeling procedure has been tested by omitting the DAB reaction from the first sequence and the primary or the secondary antibody from the second sequence. As a further validation of our co-localization method, two double staining sequences were performed. A first series of sections was double stained using Ra cLHRH-I as primary antibody in the first staining sequence, while a second series of sections was double stained using Ra cLHRH-II as primary antibody in the first staining sequence. In the double stainings performed for electron microscopy, no electrophoresis was performed, to obtain better preservation of the ultrastructure. To ensure the specificity of the stainings we performed two control procedures: (1): stainings omitting the DAB reaction and the primary or secondary antibody of the second sequence and (2) performance of stainings in both directions as for light microscopy.

Light microscopic data analysis

The sections stained for light microscopy were examined and photographed using a DMR-Leitz microscope. To obtain additional information, we performed some computerized image processing on the double stained vibratome sections. The Leitz microscope was connected to a personal computer, through a CCD camera (Sony ICX38AK). Several images of the same microscopic field were digitized at different focal planes. Subsequently, the brown or blue colors, respectively, were eliminated with a combination of red/green/blue optical filters on the microscope and the resulting images were digitized. These images were reversed into grey scale and optimized by means of the ADOBE Photoshop graphical software, and subsequently stored for printing.

RESULTS

Light microscopic observations

Since our anti-cLHRH-I and -II were both raised in rabbits, we included a number of control experiments to avoid unwanted false positive or negative results. The efficiency of the electrophoretic elution step has already been proven in a number of other double labeling studies (Moons, Cambré, Marivoet, Batten, Vanderhaeghen, Ollevier & Vandesande, 1988; D'Hondt, Eelen, Berghman & Vandesande, 2000). However, since the present study included a different combination of primary antisera, we included the classical control sections (omitting DAB staining as well as the primary or secondary antisera of the second sequence) to exclude definitively all assumptions of false positive results. All control sections were negative. As a second control procedure, double stainings were performed in both directions and revealed similar results.

Fig. 1 shows a typical double labeling for cLHRH-I (blue) and cLHRH-II (brown). Both peptides are quite densely stained, but cLHRH-I ir fibers are more abundant. At a higher magnification it becomes clear that cLHRH-I and cLHRH-II ir are not co-localized but are present in distinct fibers; the blue and brown reaction products do not appear to overlap.

For both peptides the staining is the most pronounced in the lateral and external zone of the median eminence. cLHRH-I and -II -ir fibers are often found perpendicular to the basal lamina of the ME.

The density of the staining makes it often difficult do distinguish double from single labeled fibers. Moreover, the thickness of the vibratome sections complicates the interpretation. To obtain additional data, we performed some computerized image processing on the stained sections. From the same microscopic field, several images at different focal plains through a vibratome section were digitized in order to get a better view of overlaying structures (Fig. 2). To distinguish single- from double- labeled fibers, we filtered one color at a time (blue or brown, respectively) from the same sections and recorded the resulting images (Fig. 3). Comparison of the three different images that were generated in this way revealed that the cLHRH-II fibers were not double stained: after elimination of the brown color from the image, the cLHRH-II fiber profiles disappeared completely (Fig. 3 D, E ,F) and vice versa, after elimination of the blue color all cLHRH-I ir fibers vanished from the image (Fig 3 A,B,C). These results indicate that cLHRH-I and –II immunoreactivities are located in different fibers in the ME.

Electron microscopic observations

Since our light microscopic observations indicated separate cLHRH-I and –II fiber terminals in the median eminence of the quail, we wanted to confirm these data at the electron microscopic level. Therefore, we conducted a pre-embedding double labeling experiment on quail ME tissue. The best results were obtained when the DAB staining for cLHRH-II was combined with the immunogold labeling for cLHRH-I.

Control sections, on which the DAB staining and the second primary or secondary antibody were omitted, showed no immunogold labeling, thereby demonstrating the specificity of the staining.

Many neuronal profiles in the quail median eminence were labeled with DAB (cLHRH-II) or immunogold (cLHRH-I). A profile was considered to be a cross-section through a cLHRH-II axon when it contained three or more densely stained vesicles and was considered cLHRH-I-

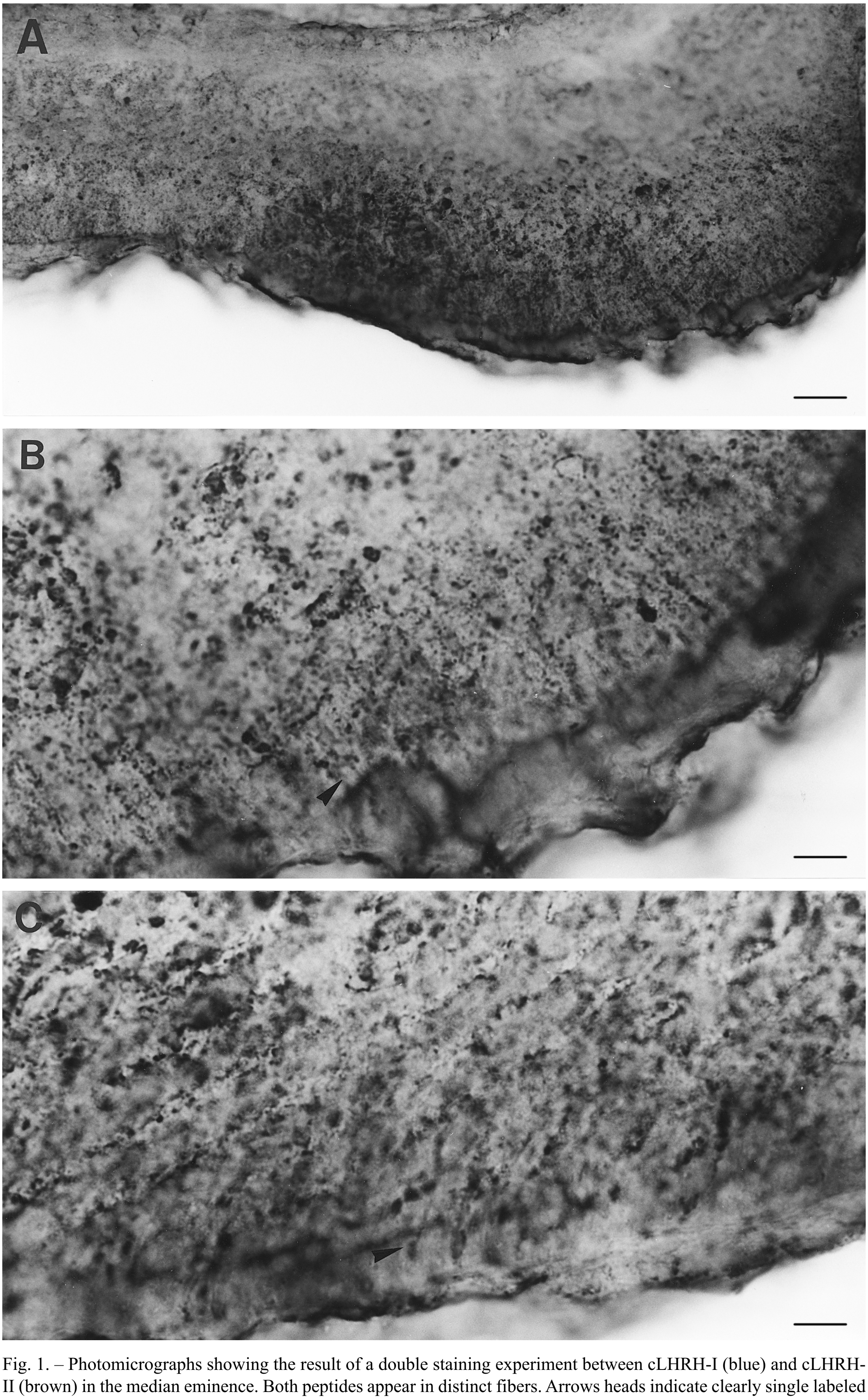

Fig. 1. – Photomicrographs showing the result of a double staining experiment between cLHRH-I (blue) and cLHRH-II (brown) in the median eminence. Both peptides appear in distinct fibers. Arrows heads indicate clearly single labeled cLHRH-II fibers. B and C are enlargements of A (magnification bars are 40 µm in A, 10 µm in B and C).

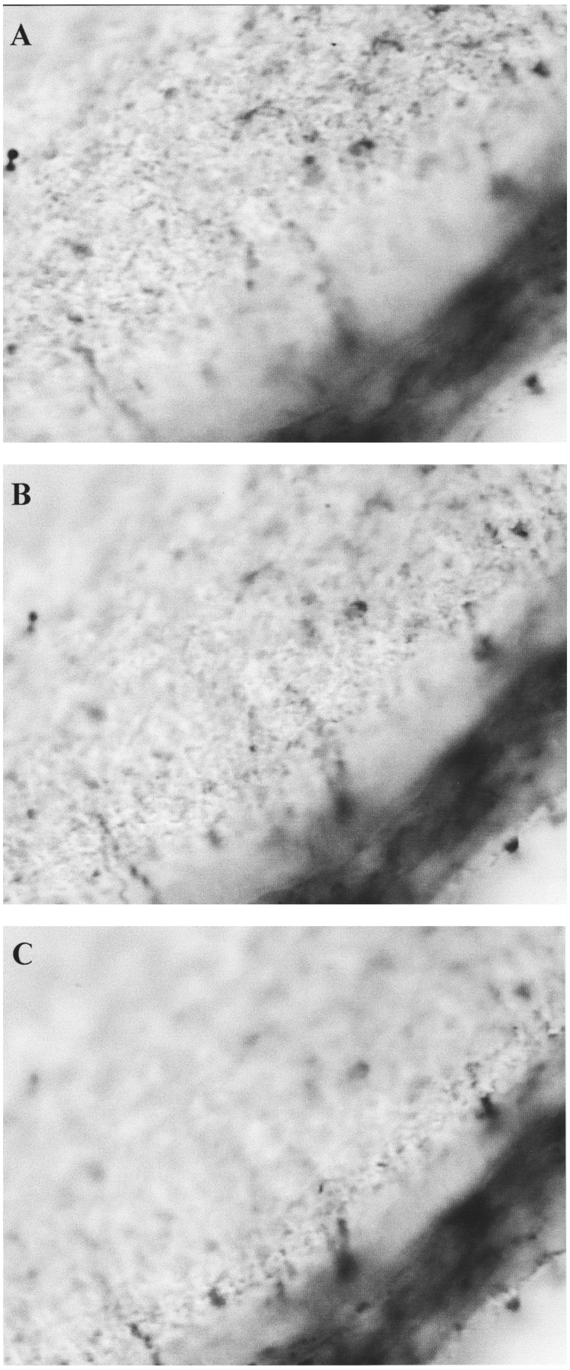

Fig. 2. – Computerized color image of a double staining between cLHRH-I (blue) and cLHRH-II (brown) in the median eminence of the chicken. A, B and C represent three images of the same microscopic field, taken at different focal planes.

positive when several gold particles were located within these fiber profiles. Double labeled profiles were never found (Fig. 4). cLHRH-I ir axons, in close contact with glial cells, were frequently observed. This was also the case for cLHRH-II ir axons but to a lesser extent (Fig 5).

Occasionally, intimate contacts were found between cLHRH-I and –II-ir axons and unlabeled axons.

DISCUSSION

The results of our double stainings at the light and ultrastructural level clearly show that cLHRH-I and –II are confined to separate fibers in the median eminence of the quail. These data together with the fact that cLHRH-I and cLHRH-II ir cell bodies are present in distinct hypothalamic nuclei, point to the existence of two separate avian gonadotropin-releasing systems.

Since the presence of cLHRH-II in the ME has always been denied, the present study is the first to provide information about its morphological characteristics. No ultrastructural data are available for cLHRH-I fibers in the ME of birds, and the morphological features of its regulation still remain to be elucidated. However, a number of studies indicate that cLHRH-I release can be regulated at the level of the ME in hens (Contijoch et al*.,* 1992; 1993a; 1993b). This has not only been demonstrated by physiological experiments, but light microscopic double stainings have shown that dopamine- (Contijoch, Gonzalez, Singh, Malamed, Troncoso & Advis, 1992), ß-END- (Contijoch, Malamed, Sarkar, & Advis, 1993b) and NPY- (Contijoch, Malamed, McDonald & Advis, 1993a) immunoreactivities coincide with cLHRH-I ir fibers in the external layer of the ME in hens. These authors suggest the existence of synaptic contacts between these neurotransmitter/neuropeptide–containing axons and cLHRH-I nerve terminals, since dopaminergic synaptic contacts on LHRH-containing processes have been described in the ewe (Kuljis & Advis, 1989). However, more recently the possibility of a non-synaptic regulation of LHRH secretion from ME terminals has been posed by a number of ultrastructural studies which report only few synaptic contacts on mLHRH terminals in the rat median eminence (Kawakami, Hirunagi, Tsukamura & Maeda, 1998).

In the present study, performed in quail, synaptic contacts on cLHRH-I ir nerve terminals were found, although not frequently. This is in agreement with the last study and indicates that cLHRH-I release could, at least in part, be regulated in a non-synaptic manner. In contrast, cLHRH-II-positive axon profiles are more often found juxtaposed to unlabeled nerve endings, indicating that cLHRH-II release might be differently regulated.

In view of the regulation of LHRH release, local glia have been expected to play a crucial role (Ma, Berg-von der Emde, Rage, Wetsel, & Ojeda, 1997). Our ultrastructural data show that cLHRH-II as well as cLHRH-I ir axons are often found in close apposition to glial cell bodies, indicating that they may play some regulatory function.

In conclusion, the present data clearly demonstrate the neuroanatomic segregation of both gonadotropin-releasing hormone systems. The regulation of LHRH secretion and the secretion mechanisms themselves are unknown, but the present data suggest the involvement of glial-neuronal interactions.

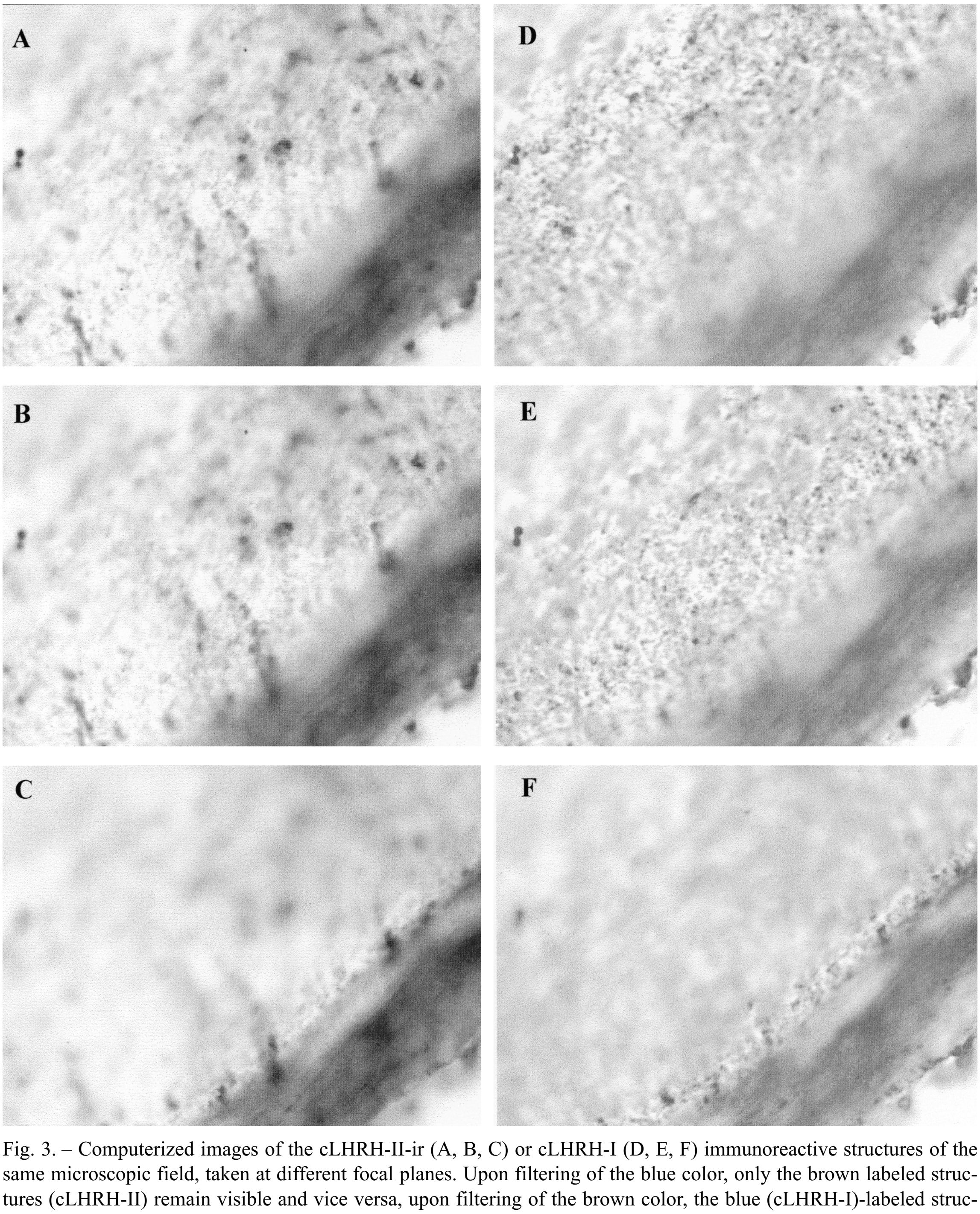

Fig. 3. – Computerized images of the cLHRH-II-ir (A, B, C) or cLHRH-I (D, E, F) immunoreactive structures of the same microscopic field, taken at different focal planes. Upon filtering of the blue color, only the brown labeled structures (cLHRH-II) remain visible and vice versa, upon filtering of the brown color, the blue (cLHRH-I)-labeled structures are left. Comparison of both sequences of images clearly indicates that cLHRH-I and cLHRH-II are present in separate fibers in the ME.

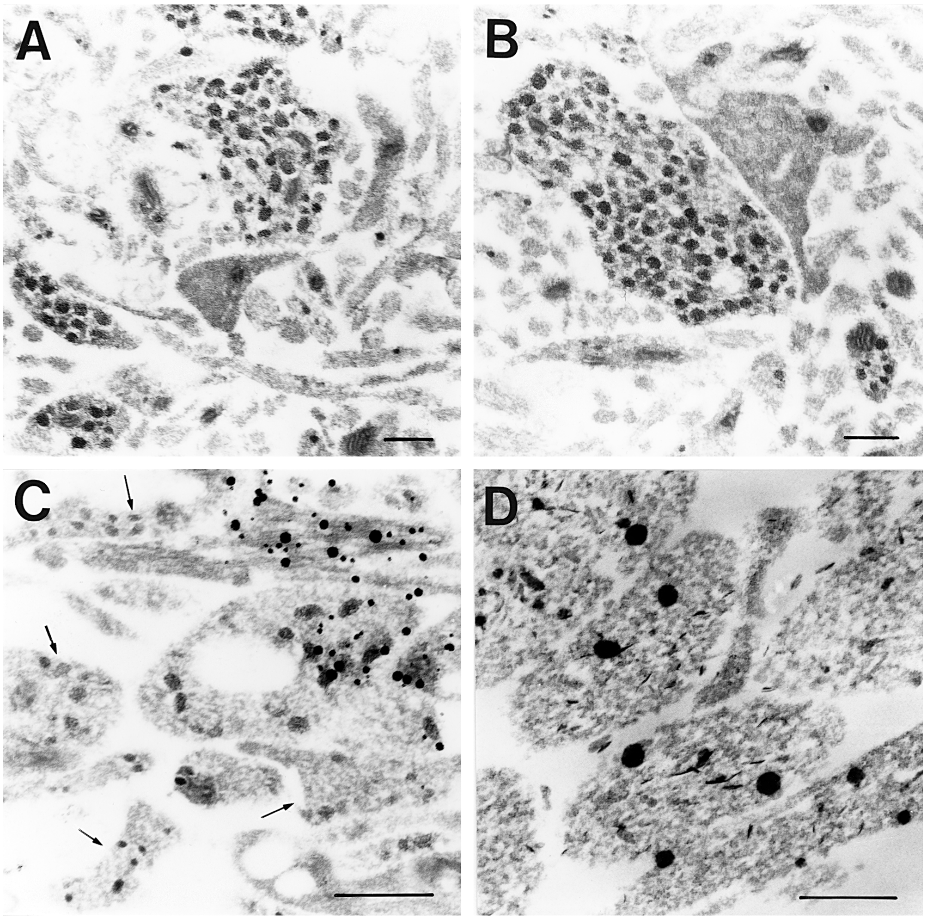

Fig. 4. – Electron micrographs demonstrating the results from a double staining for cLHRH-I and –II in the median eminence (ME) of the quail. A & B : DAB-labeled cLHRH-II-ir axons containing many secretory vesicles ; C : cLHRH-I (silver-gold label) and cLHRH-II (DAB labeled, indicated by arrows) are present in distinct fiber terminals of the ME ; D : high power micrograph of immunogold-stained cLHRH-I fibers in the ME (scale bars are 25 nm).

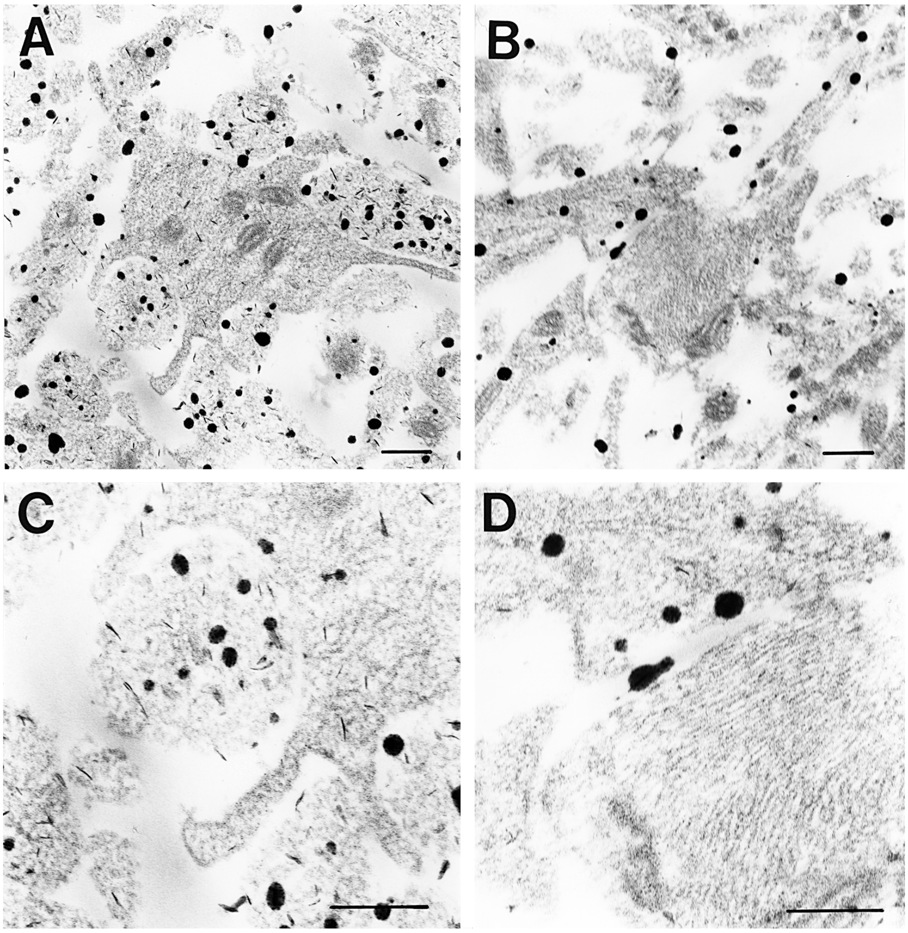

Fig. 5. – Electron micrographs demonstrating cLHRH-I (immunogold-labeled) axons in close apposition to glial cells in the median eminence (ME) of the quail. C & D are enlargements of A & B (scale bars are 25 nm).

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REFERENCES

CONTIJOCH, A.M., C. GONZALEZ, H.N. SINGH, S. MALAMED, S. TRONCOSO & J.-P. ADVIS (1992). Dopaminergic regulation of luteinizing hormone-releasing hormone release at the median eminence level: Immunocytochemical and physiological evidence in hens. *Neuroendocrinology*, 55: 290-300.

CONTIJOCH, A.M., S. MALAMED, J.K. MCDONALD & J.-P. ADVIS (1993a). Neuropeptide Y regulation of LHRH release in the median eminence: Immunocytochemical and physiological evidence in hens. *Neuroendocrinology*, 57: 135-145.

CONTIJOCH, A.M., S. MALAMED, D.K. SARKAR & J.-P. ADVIS (1993b). β-Endorphin regulation of LHRH release at the median eminence level: Immunocytochemical and physiological evidence in hens. *Neuroendocrinology*, 57: 365-373.

D'HONDT, E., M. EELEN, L.R. BERGHMAN & F. VANDESANDE,(2000a). Colocalization of cLHRH-I and arginine-vasotocin in the chicken hypothalamus. *Brain Research*, 856: 55-67.

KAWAKAMI, S.L., K. HIRUNAGI, H. TSUKAMURA, & K.I. MAEDA (1998). Evidence for terminal regulation of GnRH release by excitatory amino acids in the median eminence in female rats a dual immunoelectron microscopic study. *Endocrinology*, 139: 1458-1461.

KING, J.A. & R.P.MILLAR (1995). Evolutionary aspects of gonadotropin-releasing hormone and its receptor. *Cellular and Molecular Neurobiology*, 15: 5-24.

KULJIS, R.O. & J.-P. ADVIS (1989). Immunocytochemical and physiological evidence of a synapse between dopamine-and luteinizing hormone-releasing hormone-containing neurons in the ewe median eminence. *Endocrinology*, 124: 1579-1581.

MA, Y.J., K. BERG-VON DER EMDE, F. RAGE, W.C. WETSEL & S.R. OJEDA (1997). Hypothalamic astrocytes respond to transforming growth factor-a with the secretion of neuroactive substances that stimulate the release of luteinizing hormone-releasing hormone. *Endocrinology*, 138: 19-25.

MIKAMI, S.-I., S. YAMADA, Y. HASEGAWA & K. MIYAMOTO (1988). Localization of avian LHRH-immunoreactive neurons in the hypothalamus of the domestic fowl, *Gallus domesticus* and the Japanese quail, *Coturnix coturnix*. *Cell and Tissue Research*, 251: 51-58.

MILLAM, J.R., P.L. FARIS, O.M. YOUNGREN, M.E. EL HALAWANI & B.K. HARTMAN (1993). Immunohistochemical localization of chicken gonadotropin- releasing hormones I and II (cGnRH I and II) in turkey hen brain. *Journal of Comparative Neurology*, 333: 68-82.

MOONS, L., M. CAMBRÉ, S. MARIVOET, T.F.C. BATTEN, J.-J. VANDERHAEGHEN, F. OLLEVIER & F. VANDESANDE (1988). Peptidergic innervation of the adrenocorticotropic hormone (ACTH)- and growth hormone (GH)-producing cells in the pars distalis of the sea bass (Dicentrarchus labrax). *General and Comparative Endocrinology*, 72: 171-180.

VAN GILS, J., P. ABSIL, L. GRAUWELS, L. MOONS, F. VANDESANDE & J. BALTHAZART (1993). Distribution of luteinizing hormone-releasing hormones I and II (LHRH-I and LHRH-II) in the quail and chicken brain as demonstrated with antibodies directed against synthetic peptides. *Journal of Comparative Neurology*, 334: 304-323.

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Life history, habitat use and dispersal of a dune wolf spider (*Pardosa monticola* (Clerck, 1757) Lycosidae, Araneae) in the Flemish coastal dunes (Belgium)

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ABSTRACT. *Pardosa monticola* (Araneae, Lycosidae) is a rare spider in Flanders. It is restricted to thermophilic mesotrophic (dune and heath) grasslands. Its life cycle and its habitat preference in the coastal dunes were analysed by interpreting data of more than 200 year-round pitfall-samplings. Viable populations are found in short dune grasslands (grazed by rabbits) and in mown young dune slacks. The life cycle is mixed annual-biannual and hibernation takes place in the juvenile or sub-adult instars. In short grasslands, the species overwinters in the rough neighbouring vegetation, in dune slacks, in litter accumulations. In the latter, the species survives submerging during winter inundation.

Dispersal between suitable habitats can occur by male terrestrial movements via xerophylic habitats and dense grassland vegetation. Aeronautic dispersal is a rare phenomenon in the first instars that takes place only in periods of food shortage. Although a low proportion of the population exhibits this behaviour, this kind of dispersal can be of great importance for gene exchange between distant or strongly isolated populations. The implications and the importance of these data are discussed in relation to contemporary nature management.

KEY WORDS: *Pardosa monticola*, coastal dunes, life history, dispersal, habitat.

INTRODUCTION

In Flanders and in the rest of the Atlantic biogeographical region coastal dunes form a unique biological and geomorphological landscape. Because of the presence of several biotic and abiotic gradients (vegetation succession, sand dynamics, hydrology, lime richness and microclimatological conditions), they represent a high biological diversity in animals and plants (PROVOOST & HOFFMANN, 1996). Contrary to higher plants, the typical arthropod communities are characteristic for sandy and thermophilic habitats such as Marram dunes, grey dunes and short grazed dune-pastures (DESENDER et al., 1991; KOEHLER et al., 1995; BONTE, 1997; BONTE & DE KNIJF, 1997). These habitats are typical of subclimax situations under grazing regimes and/or continuous eolian dynamics (DE RAEVE, 1989).

First of all, the recent expansion of the human population along the coast (tourism) resulted in a significant reduction of the formerly non-urbanised dune surface and hence in a strong fragmentation of the dune entities (VERMEERSCH, 1986). Since fragmentation, sand stabilisation and the retreat of the former agro-pastoral land use enhance vegetation succession to massive dune scrubs and woodland, thermophilic habitats (grey dunes, short grazed dune grasslands) have been strongly isolated on a (sub)regional scale. This fragmentation process is a rather recent phenomenon, which started in the fifties.

Further, predatory arthropods of coastal habitats are probably under constant environmental pressure as a result of the sometimes-extreme climatological conditions and related trophic problems, such as food deprivation from lack of suitable prey under hot, dry circumstances (BONTE et al., 2000a). In addition to this, dynamic eolic processes may destroy potentially optimal habitats. Moreover, fluctuations in grazing intensity by both

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domestic and semi-natural grazers (rabbits) may influence vegetation patterns, important for their survival and juvenile development (Bonte et al., 2000a,b).

In addition to the recent habitat fragmentation, these severe climatological conditions and dynamic vegetation processes can result in a high turn-over rate within the arthropod populations, resulting in fairly large amounts of unoccupied but suitable habitat remnants.

There is a general consensus that spiders Araneae are good ecological indicators (Maelfait & Baert, 1988; Rushton, 1988; Speight, 1986; Maelfait et al., 1989; MAelfait & Hendrickx, 1998). Blandin (1986) defined a special case of bio-indication in which the absence or presence of a species and, in the latter case, its abundance are the bio-indicators. The indicator species concept is, however, problematic because there is no consensus on what the indicator is supposed to indicate (Simberloff, 1997). In monitoring or habitat evaluation using spiders as indicators, the absence of typical species (stenotopic species) is often indicative for low habitat qualities, i.e. vegetation structure. Whether the absence of the species is the result of the low global ecosystem quality has so far never been questioned. Habitats may be intrinsically suitable but unoccupied due to severe isolation, edge, surface and matrix quality effects.

Although conservation and restoration of thermophilic mesophytic grassland habitats is one of the primordial aims of contemporary (floristically based) dune-management (Provoost & Hoffmann, 1996), the absence of typical arthropod species is generally explained by low habitat quality (Maelfait & Baert, 1996; Bonte et al., 1998) and by the local turnover phenomena (Baert & Desender, 1993; Desender, 1996). Whether these factors lead to dynamic, patchily distributed populations is not yet investigated. If so, arthropod populations of these habitats are organised within the several dune-entities as meta-populations. The maintenance of these meta-structured populations is dependant on both the suitability of the habitats and the species-specific dispersal possibilities between the several remnants (Hanski, 1999). While capture – recapture techniques can be used for butterflies (see e.g. Hill et al., 1996; Mousson et al., 1999), they cannot be used for the determination of dispersal of spiders, because of the small size of the juvenile and adult individuals. In order to study spider dispersal, data of pitfall trapping for terrestrial dispersal (Bonte et al., 2000) should be used, while laboratory experiments are necessary for the determination of the species' specific ballooning capability (dispersal via air currents). Ballooning has not been studied thoroughly because of the difficulty of estimating effective dispersal by field- or laboratory experiments (Foelix, 1996, Duffey, 1998). This distant dispersal is probably the determining factor in inter-population exchange of individuals and, consequently, in gene flow.

Within the framework of this study, the distribution, dispersal and life history of the wolf spider *Pardosa monticola* (Clerck, 1757) have been investigated. This wolf spider is a widespread species in Europe and Asia (Alderweireldt & Maelfait, 1990). In Europe it is typical for short grazed and oligotrophic pastures and heathlands (Wiebes & Den Hollander, 1974; Alderweireldt & Maelfait, 1990); in the Flemish and Dutch coastal dunes, the species is dominant in rabbit-grazed pastures (Van der Aart, 1975; Maelfait et al., 1989). *Pardosa monticola* is also listed on the Red list of spiders from Flanders (Maelfait et al., 1998). Apparently restricted to thermophilic short-grazed dune grasslands, its habitat-binding and multi-habitat use have been studied in order to detect potential migration barriers between the grassland remnants. Bonte et al. (2000a,b) discussed the seasonal migration of several stenotopic grey-dune species and of *Pardosa monticola* via gradient pitfall trapping. The habitat use of *P. monticola* has been studied during the winter-period in both inundating and permanently dry grassland habitats. The data obtained on habitat use, terrestrial migration and hibernation habitat could be used to optimise an 'arthropod-friendly'-dune management.

MATERIAL AND METHOD

Data collection

Habitat use, terrestrial dispersal and life history

From the seventies onwards, spiders have been collected in all possible dune habitats in the Flemish coastal dunes by means of pitfall traps (Hublé, 1975; Hublé, 1976; Hublé & Maelfait, 1981; Baert & Desender, 1993; Maelfait, 1993; Bonte & Hendrickx, 1997; Bonte et al., 1999; Bonte, unpub.data; Maelfait, unpub. data; Vanbiervliet, unpub. data). These data from more than 220 pitfalls during more than 30 year-round sampling campaigns, concern more than 130,000 identified adult individuals. Sixty five percent of these traps were placed in dune grasslands, grey and blond dunes.

Within this data-set, we selected all data concerning *Pardosa monticola,* from 61 pitfalls in which the species was present and where data were available on the vegetation composition around the pitfalls. The vegetation composition was studied by means of the 'fast-Londo'-scale, so only the coverage of the dominant plant species was taken into account in the analysis.

Although population densities can undergo year-to-year fluctuations (Baert & Desender, 1993), we assume that a total analysis of these data in relation to the different habitat types results in a good description of the habitat of adult *Pardosa monticola* by comparing total annual catches between the discerned habitats. Apart from the total abundance, we also investigated the differences in the ratio of males/females between the different habitats. A dominant male activity registered from the pitfalls indicates a higher abundance of the latter. While juvenile terrestrial activity is a patchily restricted phenomenon related to feeding and searching for suitable hibernation habitats (BONTE et al, 2000b), male activity can be interpreted as the only terrestrial activity developed outside the native population in searching for suitable mating partners in other suitable habitat patches (MAELFAIT & BAERT, 1975).

In addition to this data collection, a quadrat sampling (30x30 cm^2) was performed to estimate winter densities in a mesophytic dune grassland and a young dune slack in De Panne during 1995-1997. Thirty replicas were taken in respectively the short grazed grassland; the rough grassland border and the litter beneath *Salix repens*-shrubs, the young dune slack before and after a long winter inundation. Periodic hand collection was carried out in the mesophytic grassland of the Westhoek-reserve in De Panne in order to reconstruct the life cycle from field data by measurement of the cephalothorax width of juveniles and adult individuals with a measurement ocular (cf. TOFT, 1976).

Laboratory experiment for aeronautic behaviour

Spider dispersal occurs not only via terrestrial migration: an even more important way for distant migration in spiders is aeronautic dispersal (DECAE, 1987, FOELIX, 1996). In order to estimate the proportion of potential aeronauts in *P. monticola,* we conducted laboratory experiments in a test chamber as designed by LEGEL & VAN WINGERDEN (1980). The temperature within the test chamber was 30°C, the wind velocity 0.25 m/s and the relative air humidity was 40%. Individuals displaying tiptoe-behaviour (i.e. stretching of the legs, followed by rising the abdomen and the production of silk threads) were considered to be ready for aeronautic behaviour. Juveniles from five females with cocoons from three different populations (two in the Westhoek-reserve, De Panne, and one from Ter Yde, Oostduinkerke) were reared under standard laboratory conditions (20°C, $\underline{+}$60 % RH). The juveniles were fed with eight *Drosophila* flies per week. After each moult, the individuals were tested in a well-fed condition (8 flies/week) and a starving condition (no prey for one week). Since the total number of females per sampling place was too small to analyse differences within populations, data from the three populations were pooled in this preliminary assessment of the ballooning capacity.

Data analysis

The reconstruction of the life history of *P. monticola* (seasonal growth) was performed by measuring the cephalothorax width of the caught juvenile and adult individuals from one dune grassland. When these measures are plotted against the period in which they were caught, the life-history pattern becomes visible (TOFT, 1976). Since the measurements of the cephalothorax overlap, it is difficult to disentangle the different juvenile instars or the adult cohorts. The latter can be deduced by the analyses of the frequency diagram, based on the cephalothorax measurements of the adult individuals. Since the different cohorts are visible in different unimodal distributions (SEGERS, 1989; SEGERS & MAELFAIT, 1990, BONTE & MAELFAIT, 1998), the different distributions were disentangled by the application of the program Mixture 1.0 (VAN DONGEN et al., 1999), which was originally designed for the analysis of Fluctuating Asymmetry data. Different models (combinations of different normal – unimodal-distributions) can be tested against each other by the application of a bootstrapping procedure. These data enabled us to reconstruct the expected summated distribution, via z-statistics, which were compared with the observed frequencies by χ^2-goodness of fit tests (JERROLD, 1996).

By using Euclidean similarity dendrograms and nonmetric multi-dimensional scaling ordination (MDS: KRUSKAL & WISH, 1978) we were able to classify the pitfall data into several habitat-groups and hence to study the different determining vegetation characteristics. Multivariate analysis by applying MDS enables us to study non-linearly or non-normally distributed biological data. Because the ordination is based on different iteration algorithms, both a stress-factor and a significance level are listed. The stress is a measure of deviation from monotonicallity and the dissimilarity (distances) in the original and reduced ordination. A high stress-factor indicates an ambiguous ordination, a low one represents an ordination that is a good reflection of reality (CLARCKE & AINSWORTH, 1993).

An important advantage of this methodology is the possibility to calculate a stress-factor (an indication of the ordination stability) and hence the ordination significance via a randomised Monte-Carlo permutation test.

Plant species composition, spider abundance and sex-ratio differences within the clustered habitat types were analysed by one-way ANOVAs and Scheffé post hoc tests.

Independent t-tests were used for the analysis of quadrat densities between the different hibernation habitats. Both differences in occupancy between the several habitat classes and ballooning proportions between the tested different instars and the feeding regimes were analysed by applying sequential Chi-square tests for the comparison of proportions. Bonferroni corrections were used for the elimination of multiple testing errors. The different analyses were performed with the Statistica 5.0, Primer 3.1 and the PC-ord 3.03 software.

RESULTS

Life cycle

The life cycle of *Pardosa monticola* can be derived from Fig. 1. In the Flemish coastal dunes, adulthood is reached in the period May-June, which is also the mating season. Shortly after, the males die. Females live till September and from June till August-September, they

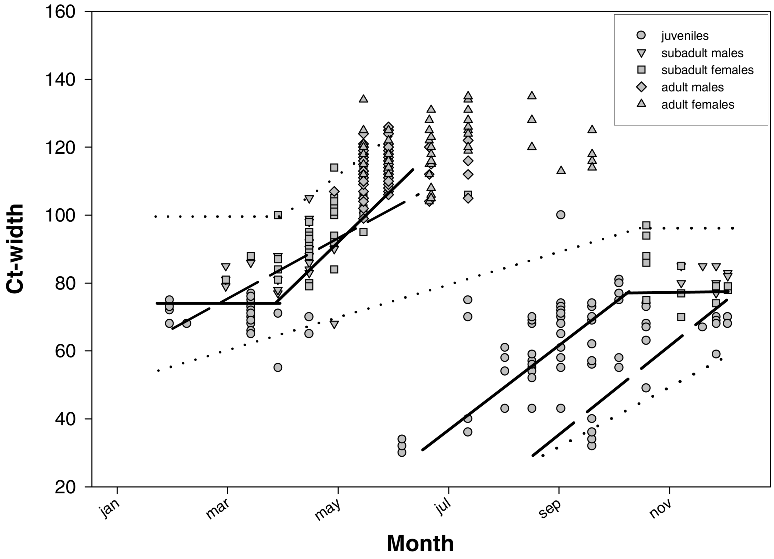

Fig. 1. – Seasonal growth of *Pardosa monticola* in a dune grassland in the Flemish coastal dunes (Full line: cohort I; long dashed line: cohort IIa; dotted line: cohort IIb).

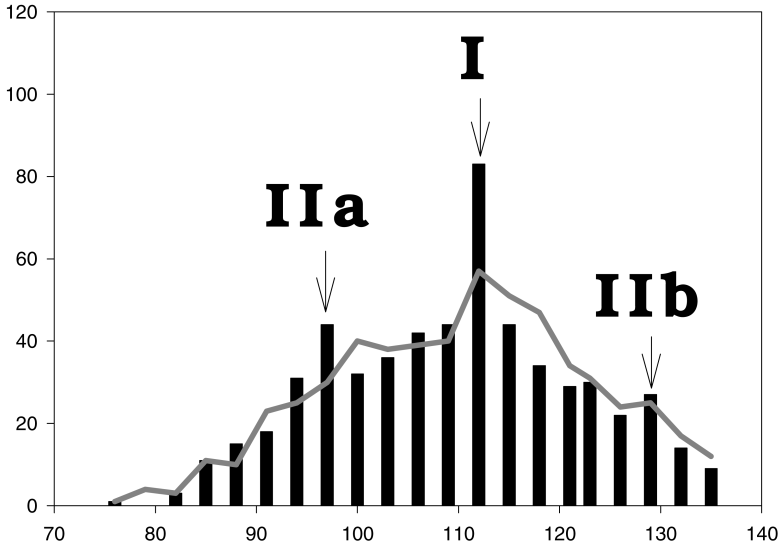

Fig. 2. – Cephalothorax width frequency diagram (bars) with the expected summated normal distribution (Red line).

produce several broods (two?). This results in two periods with early juvenile instars: June-July and September. Juveniles of the first brood hibernate as large juveniles and as sub-adults, as opposed to those of the second brood, which hibernate as smaller juveniles. This life cycle pattern results in two or three cohorts, which can be deduced from the cephalothorax width diagram from adult males measurements (Fig. 2): the trimodal distribution is characterised by the lowest log-likehood (Table 1) and is significantly different from a bi- and unimodal distribution (Bootstrapping, 100 permutations, $p<0.05$). The hypothesis that the calculated estimated distribution does not fit the observed pattern should be accepted for the unimodal ($\chi^2_{0.05,20} = 31.41$; $\chi^2 = 212.93$; χ^2-goodness of fit-test) and the bimodal model ($\chi^2_{0.05,20} = 31.41$; $\chi^2 = 75.57$, χ^2-goodness of fit-test). The trimodal distribution should be accepted at the 0.05-level ($\chi^2_{0.01,20} = 37.65$; $\chi^2 = 36.68$, χ^2-goodness of fit-test). The hypothesis should, however, been rejected at 0.01-level because of a higher number of observations at the distribution means in comparison with the expected model (Fig. 2).

As a result, the adult population of *P. monticola* can be divided into three cohorts with proportions of 48.8% of cohort I, 38.8% of cohort IIa and 12.3% of cohort IIb. So, the first-brood spiders will reach adulthood in the next spring (annual life cycle: cohort I). The majority of the individuals of the second brood will also reach adulthood in one year (cohort IIa), while a minor part will become mature after one more hibernation (cohort IIb);

TABLE 1

Results of the mixture-analysis for the separation of different mixed unimodal distributions within the cephalothorax-width frequency data (567 measurements)

Tested model	Normal distribution number	Mean cephalothorax width of the different distributions	Variance	Proportion of the data-set belonging to the distribution	Log-likehood
Unimodal	1	111.16	18.77	1.000	-1638.95
Bimodal	1	97.10	7.85	0.372	-1630.49
	2	118.57	9.98	0.628	
Trimodal	1	97.03	7.23	0.388	-1623.77
	2	111.78	5.44	0.488	
	3	130.75	1.85	0.123	

they will overwinter a second time and become adult in their second spring (biannual life cycle). This differentiation in seasonal growth is reflected in the cephalothorax-width variation of the adult spiders.

Habitat use, terrestrial and aerial dispersal

Habitat preference of the adult P. monticola

The similarity dendrogram indicates the presence of *Pardosa monticola* in six different habitat types (Fig. 3): grey dunes, blond dunes, shrub edges, tall grasslands (both wet and dry), short grasslands and young dune slacks. Each type is characterised by a typical floristic composition (Table 2). The grey dunes are characterised by a moderate coverage of bare sand and open mosses (mainly *Tortula ruralis ruraliformis*) and the blond dunes by a high amount of bare sand and *Ammophila arenaria*. Shrub species (*Hippophae rhamnoides, Ligustrum vulgare, Salix repens*) and *Calamagrostis epigejos* are typical for the stations situated along the shrub borders. *Avenula pubescens* is abundant in the two mesophilic grasslands. The rabbit-grazed pastures are covered with typically mesophylic herbs (*Galium verum, Helianthemum nummularium, Potentilla neumanniana* and *Thymus pulegioides*) and open mosses (mainly *Hypnum cupressiforme*). The tall grasslands on the other hand are characterised by a dense sward consisting of *Calamagrostis epigejos, Arrhenaterium elatius* and *Rosa pimpinellifolia*. Finally a large amount of bare sand and the presence of freatic plant species (*Carex trinervis, C. flacca* and *Salix repens*) are typical for the young dune slack. The sampling stations situated in the young dune slacks are characterised by nearly annual inundations, because of their low height above the freatic water-level. The other habitats are typically xerophilic (Schaminée et al., 1996).

The syntaxonomical classification according to Schaminée et al. (1995, 1996, 1997) is listed in Table 2.

The MDS-ordination confirms this dendrogram clustering (Fig. 4). The stress-factor is moderate (0.129) and the ordination in two axes is significantly stable (Monte Carlo-permutation test: 99 runs; p=0.01). Pearson correlation results of the vegetation characteristics with the two axes are listed in Table 3. The differentiation along the first axis can be interpreted as the variation in moss and herb coverage. The second axis represents the gradient from open, bare sandy habitats to well-vegetated habitats.

In proportion to the total number of analysed traps within a habitat type, the amount of occupied traps is significantly higher in the short grasslands and the young dune slacks (χ^2-test; p<0.001; χ^2=12.94) than in the shrub edges, tall grasslands and blond dunes. A pair-wise comparison of the occupancy proportion did not reveal any differences between these groups (χ^2-test; χ^2<3.00; p>0.05). This indicates a higher occupancy rate in short grasslands and dune slacks.

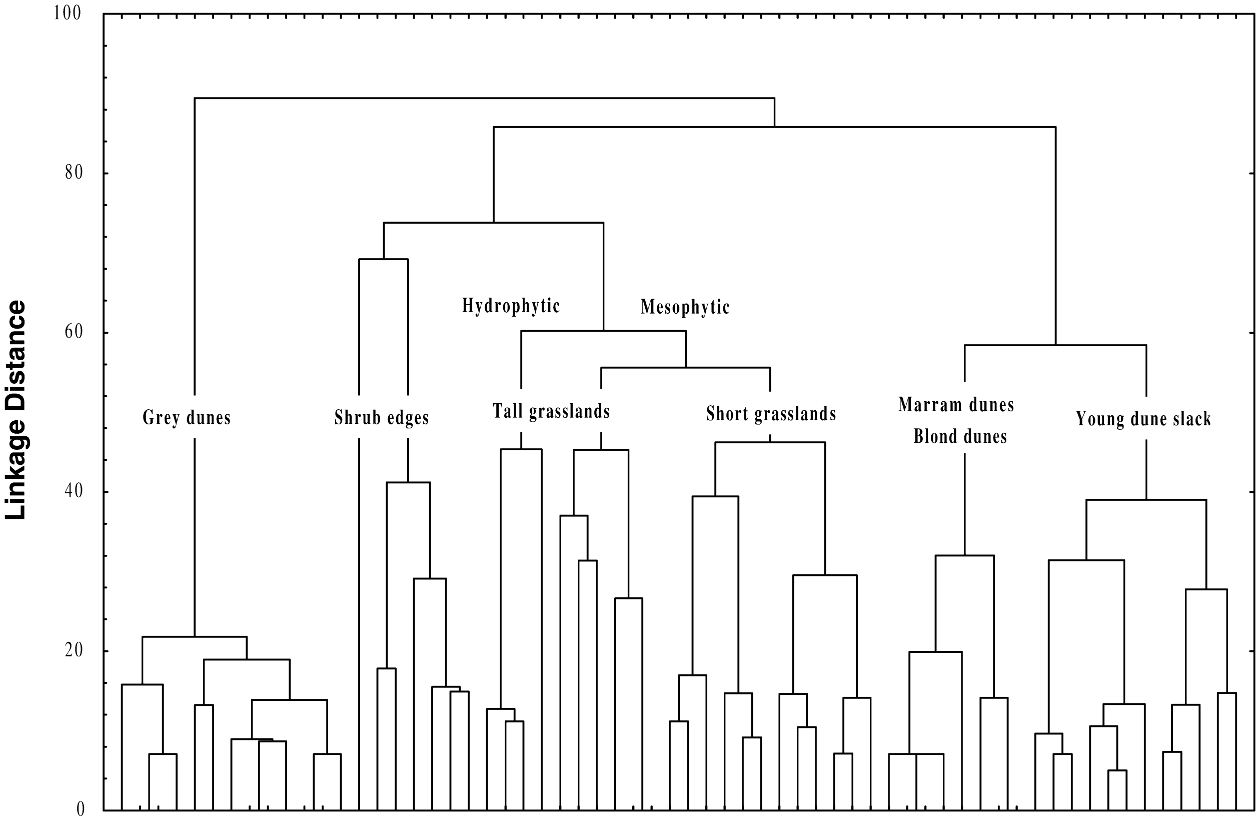

Fig 3. – Bray Curtis similarity dendrogram of the vegetation composition around the pitfall traps with *P. monticola*.

TABLE 2

Plant species composition, vegetation typology, number of traps of the distinct habitat types of *Pardosa monticola* in the Flemish coastal dunes. Marked coverages per plant species (incl. coverage bare sand and non overgrown -open- moss) do not differ between the respective habitats (one way ANOVA, post hoc Scheffé-test, p>0.01)

	Grey dunes	**Shrub edges**	**Tall grassland**	**Short grassland**	**Blond dunes**	**Young dune slack**
Vegetation typology (SCHAMMINÉE et al., 1995, 1996 & 1997)	*Tortulo-Koelerion*	*Trifolio-Geranietea sanguinei*	*Arrhenatheretum elatioris*	*Polygalo-Koelerion*	*Ammophilion arenariae*	*Parnassio-Juncetumatri-capillia*
Total number of traps in type	28	28	36	24	35	15
Total number of traps with *P. monticola*	10	7	9	18	6	12
Mean coverage:						
Bare sand	15.76	2.4	0	5.41	80.5	37.72
Open moss	77.15	12.14	13.5	28.75	5.75	10.9
Ammophila arenaria	0	0	0	0	10	0
Arrhenaterium elatius	0	15.71	10	0	0	2.72
Avenula pubescens	0	7.85	38	23.75	0	1.36
Calamagrostis epigejos	0	36.42	15	0	1	4.54
Carex arenaria	3.23**	1.75**	0.6*	7.08	0	2.45***
Carex flacca	0	0	0	1.35	0	15.72
Carex trinervis	0	0	1.5	0.08	1.75	9.54
Festuca rubra	1.53	0	1.4	5.41	0.75	0
Galium verum	0	0.71	5.5	9.16	0	0
Helianthemum nummelarium	0	0	0	7.08	0	0
Hippophae rhamnoides	0	33.14	0.5	0	0	3.63
Ligustrum vulgare	0	10	0	0	0	0
Poa pratensis	1.15*	2.14*	2.5*	8.75	0	0.45
Potentila neumanniana	0	0	0	7.5	0	0
Potentila reptans	0	0	0	2.08	0	0
Rosa pimpinellifolia	0	0	18	0	0	0
Salix repens	0	20.71	5.5	0.16	1	11.18
Thymus pulegioides	0	0	1	1.2	0	0

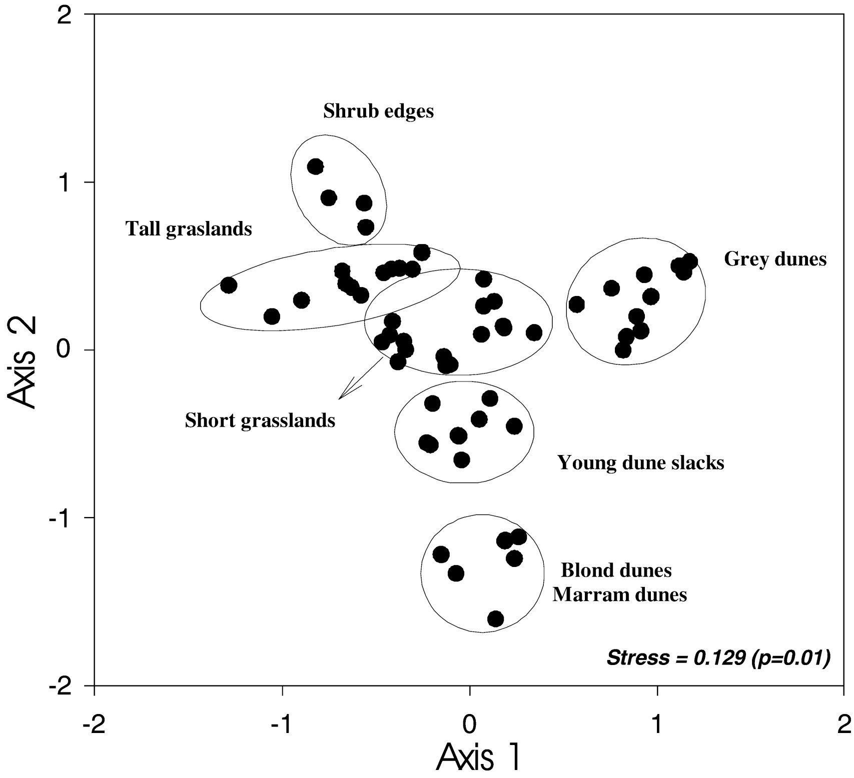

Fig. 4. – MDS-ordination of the pitfall traps containing *P. monticola*, based on the vegetation composition. Typology cfr. Bray-Curtis analysis (Fig. 2, Table 1).

TABLE 3

Pearson correlations of the identified plant species (incl. coverage bare sand and non overgrown –open-moss) with the two axes of the MDS-ordination

	Axis 1		**Axis 2**	
Coverage of:	r	p	r	p
Bare sand	0.218	0.09	-0.939	**< 0.001**
Open moss	**0.846**	**< 0.001**	**0.367**	**0.004**
Ammophila arenaria	-0.053	0.685	**-0.465**	**< 0.001**
Arrhenatherium elatius	**-0.513**	**< 0.001**	**0.389**	**0.002**
Avenula pubescens	**-0.685**	**< 0.001**	**0.339**	**0.007**
Calamagrostis epigejos	**0.570**	**< 0.001**	**0.467**	**< 0.001**
Carex arenaria	0.210	0.104	0.228	0.077
Carex flacca	-0.040	0.760	-0.179	0.166
Carex trinervis	-0.073	0.574	-0.172	0.183
Festuca rubra	0.125	0.337	0.116	0.372
Galium verum	**-0.398**	**0.001**	0.193	0.136
Helianthemum nummelarium	-0.148	0.255	-0.002	0.986
Hippophae rhamnoides	**-0.366**	**0.004**	**0.390**	**0.002**
Ligustrum vulgare	-0.023	0.857	0.126	0.331
Poa pratensis	-0.141	0.276	0.286	0.025
Potentila neumanniana	0.030	0.816	0.075	0.562
Potentila reptans	0.089	0.493	0.043	0.737
Rosa pimpinellifolia	-0.229	0.075	0.216	0.094
Salix repens	**-0.415**	**0.001**	0.243	0.059
Thymus pulegioides	-0.082	0.526	0.178	0170

The superpositioning of the total number of individuals caught per pitfall (Fig. 5) visualises the dominant abundance of the species in the short-grazed dune grasslands and in the young dune slacks. This observation is confirmed by the one-way ANOVA-analysis ($F_{1,5}$ = 6.94; p<0.001: Table 4): annual abundances are significantly (Post-hoc Scheffé-test, p<0.01) larger in these habitat types. The numbers do not differ between the other occupied habitats (grey dunes, tall grasslands, shrub edges and blond dunes; Post-hoc Scheffé-test, p>0.01).

TABLE 4

Mean abundance and sex-ration per pitfall trap within the six distinguished habitat types. Same letter codes in the 'Post-hoc difference' column indicate no significant difference (Post-hoc Scheffé-tests, p>0.01)

Habitat type	**Post-hoc difference**	**Mean abundance *P. monticola* /trap**	**Mean sex-ration females: males/trap**
Blond dunes	A	1.256	0.000
Tall grassland	A	23.000	0.132
Young dune slack	B	96.583	0.385
Short grassland	B	10.917	0.361
Grey dunes	A	13.384	0.118
Shrub edges	A	3.421	0.000

Sex-ratio in the different occupied habitats

The sex-ratio differences within *P. monticola* between the different habitats show an analogue pattern for the species abundance. The proportion mm/ff are plotted on the MDS-ordination in Fig. 5 (sex-rations > 10 are plotted as equal values). Since the proportion ff/mm is well correlated with the total numbers per trap (Pearson correlation, r=0.72; p<0.001), habitats sharing a low abundance are characterised by a high proportion of males. This observation is confirmed by the variance analysis of this proportion between the different habitat types (one-way ANOVA, $F_{1,5}$=14,63, p<0.001). Post hoc Scheffé-tests reveal significant differences (p<0.01) between young dune slacks, short grasslands and the other occupied habitats (Table 4). The higher proportion of males in the marginal habitats suggests male dispersal via these habitats without the establishment of viable populations.

Hibernation in rabbit-grazed dune pastures and young dune slacks (Table 5)

Density estimates during the winter in both short vegetation (rabbit-grazed pasture and mown dune slack) and in higher vegetation reveal a significant difference between the rabbit-grazed and the rough dune grassland (independent t-test, p<0.001). In the dune slack however, mean densities do not differ between the mown and unmown vegetation. Although the mown parts were inundated dur-

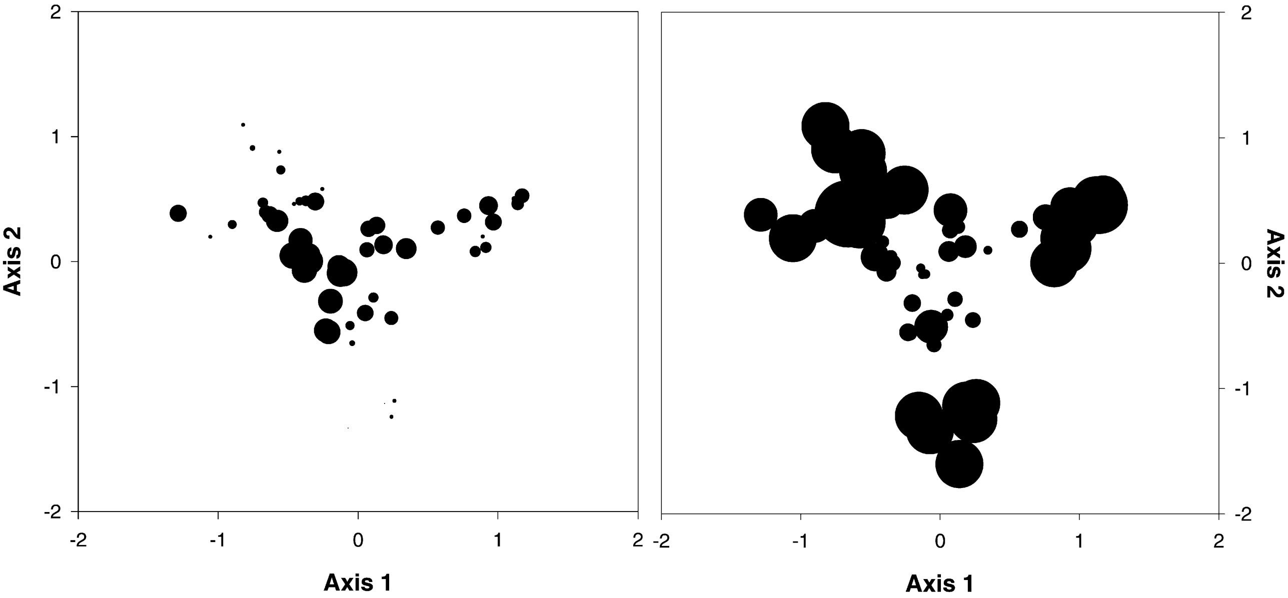

Fig. 5. – Superpositioning of the abundance (left) and sex-ratio proportion males:females (right) on the MDS-plot (Fig. 3).

TABLE 5

Mean densities and 95% confidence intervals of overwintering *Pardosa monticola*, based on 30 replica's of 30x30 cm^2 in different vegetation in a mesophytic grassland and an young dune slack. Densities in vegetation marked with * are significantly different (dependent t-test, p<0.001)

Habitat	Vegetation	Mean density	Conf. int.
Mesophytic grassland:	Tall vegetation (border)*	0.56	0.27
	Short vegetation *	0.00	0.00
Young dune slack:	Litter under Salix repens	0.40	0.17
	Slack: litter before inundation	0.56	0.23
	Slack: litter after inundation	0.46	0.17

ing two months, the mean densities remained the same before and after the inundation (independent t-test, p>0.05). Since no individuals were trapped in pitfalls during this period, we may conclude that *P. monticola* stayed in the inundated litter and did not move to higher and dry habitats.

Aerial behaviour under laboratory conditions

Aerial behaviour of spiderlings of *P. monticola* was only observed in the second, third and fourth instar (Table 6). When the spiderlings were well fed with *D. melanogaster*, no tiptoe behaviour was observed. However, when starved, tiptoe behaviour was shown in 7.1 % of instar II and in 10.5 % of instar III of the tested individuals. This proportion was significantly higher than in the well-fed individuals (instar II: dependent χ^2-test; χ^2=6.33; p<0.05; instar III: dependent χ^2-test; χ^2=4.14; p<0.05). In general, the proportions of ballooning spiderlings within instar II and III did not show any differences (χ^2-test; χ^2=3.02, p=0.22).

TABLE 6

Total tested and ballooning individuals per instar after one week starving

Instar	Total tested individuals	Total individuals showing tiptoe behaviour
II	64	4
III	59	6
IV	45	0
V	38	0

This means that under food shortage, the proportion of potential aeronauts (based on the population structure in the field – proportion in instar X ∗ proportion of potential aeronauts in instar X) reaches peaks in July (1.25-4.15 %) and August-September (0-1.47 %) (Table 7). Using the data of RICHTER (1970), this proportion increases to 12.07±5.82 % in July, to 3.54±1.71 % in August and to 5.95±2.87% in September.

TABLE 7

Estimated proportion of aeronautic juveniles in a general *Pardosa monticola* population of the Flemish coastal dunes

Instar-month	**Proportion potential aeronauts in the population**	**Estimated proportion (%) of aeronauts (this study)**	**Estimated proportion (%) of aeronauts (data Richter, 1970)**
I-6	0	0	0
II-6	0	0	0
I-7	0.45	4.14	12.07±5.82
II-7	0.2	1.28	5.31±2.56
I-8	0.13	0.81	3.54±1.71
II-8	0.13	0.53	3.54±1.71
I-9	0.22	1.47	5.95±2.87
II-9	0	0	0
I-10	0	0	0
II-10	0	0	0

DISCUSSION

Although only based on measurements from one population, the mixed annual-biannual life cycle of *Pardosa monticola* that we observed seems to be typical for the genus *Pardosa* species in NW-Europe (DEN HOLLANDER, 1971; ALDERWEIRELDT & MAELFAIT, 1988; SEGERS, 1989; BONTE & MAELFAIT, 1998). In general, adult spiders of *P. monticola* are present from May till October. Mating takes place in May-June and the adult males disappear from the population in July. Females with cocoons are present from June till the end of September; this is also the period during which spiderlings hatch. The greater amount of observations than expected around the mean of the observed cephalothorax-width measurements probably indicates a rather synchronised hatching period in June and in the late summer. If the hatching period was continuous during the summer, the cephalothorax width of the adult males would have been characterised by a higher amount of variance around the mean instead of the observed leptokurtic distribution. A consequence of this life cycle pattern is the hibernation of the species in a juvenile life-stage.

Large populations with both males and females are present in two habitat types: short grazed dune grasslands and young dune slacks with a low sedge (*Carex flacca* and *C. trinervis*) and Creeping willow (*Salix repens*) vegetation. Our data suggest that the species does not hibernate in open grassland situations, but in the litter of the shrub layer, where winter temperatures are less extreme (DE BACKER, 1963, BARKMAN & STOUTJESDIJK, 1987). The winter-density estimates confirm these findings, since quadrat densities of juveniles are significantly larger in the shrub litter than in the rabbit-grazed pastures. In the young dune slacks, however, hibernation takes places in the *Salix repens* litter, which is still present as a result of the late mowing regime for the conservation of late-summer flowering plants such as *Parnassia palustris.* Although no data are present about the species' cold resistance, KIRCHNER (1973) found that the supercooling points of species with analogue habitat preferences were intrinsically comparable, and for grassland species lie between –10°C and –4°C during the winter period. The temperature in short grazed dune-pasture grasslands will decrease to –5°C during severe frost (air temperature of –5.4), while the temperature in the litter will never be less than –0.8°C (ANTHEUNIS, 1969 and BONTE, unpub.data). As a consequence these 'thermophile' habitats are unsuitable for the species' survival during the winter period. Analogue multi-habitat use has also been demonstrated by EDGAR (1970: *Pardosa lugubris*; Araneae), DENNIS et al. (1994: *Tachyporus hypnorum*; Coleoptera, Staphylinidae and *Demetrias atricapillus*; Coleoptera, Carabidae), DELETTRE et al. (1998: Diptera, Empidoidea) and BONTE et al. (2000a): *Typhochrestus digitatus, Pelecopsis nemoralis*: Araneae) in grass- and woodlands.

Apparently the species is able to withstand long periods of winter inundations since densities are hardly affected after the inundation period. The species' inundation tolerance is remarkable and may also explain its presence in saltmarshes around Mont Saint Michel (France; FOUILLET, 1988). In our country *Pardosa monticola* is absent from this habitat but replaced by its sister-species *P. purbeckensis* (ALDERWEIRELDT & MAELFAIT, 1990; HENDRICKX & MAELFAIT, 1998), which is also characterised by a high inundation tolerance resulting from the presence of hydrophobic hairs on its abdomen. As opposed to the latter, however, *P. monticola* is generally a species typical of dry habitats. Although the spiders' population densities are not affected by winter inundations (in contrast to different butterfly species: LEJEUNE et al., 1955; BERRY et al., 1996 and other spider species: DECLEER 1988), submerging of the habitat during the winter can have a marked impact on the species long-term survival and fitness (JOY & PULLIN, 1997): it will significantly decrease the population's viability. These long-term effects should consequently be studied in order to estimate the global effects of the winter inundation.

In the adult stage, *Pardosa monticola* migrates only via terrestrial movement. Terrestrial migration may occur in two ways: dispersal for the colonisation of new habitat remnants and seasonal dispersal between the hibernation sites and the adult mating and feeding habitat, as discussed above. Our study indicates that mainly male individuals leave their optimal reproduction habitats for the foundation of other suitable habitat remnants. This terrestrial dispersal seems only to occur via open xerophylic habitats (grey and blond dunes) and higher grassland or dwarf-shrub vegetation (*Arrhenatheretum elatioris* grasslands, with or without *Rosa pimpinellifola* dwarf shrubs). The catches in shrub borders may indicate both dispersal along shrub edges and withdrawal into this habitat-type for hibernation.

In contrast to some other Lycosid species (GREENSTONE et al*.,* 1985, MILLER , 1984; BLANDENIER & FÜRST, 1998; BONTE et al, 1998; DUFFEY, 1998), aerial dispersal of *Pardosa monticola* in the field has never been described. Our laboratory experiments, however, indicate that a small proportion of the population does show pre-ballooning behaviour. In comparison with the results of RICHTER (1970) (ballooning proportions of 26.55 ± 12.81 % of species of the second instar - cephalothorax length of 0.8-1 mm), our study showed a low proportion of ballooning individuals. This may indicate that aerial dispersal differs from population to population and has as a consequence been submitted to natural selection. (SUTCLIFFE et al., 1997; HILL et al., 1999). We should, however, be careful in making the comparison because it is not known whether the testing conditions are similar in both studies: temperature and air humidity in both the testing chambers were the same, but nothing is known about Richter's feeding and breeding conditions during the experiment.

As RICHTER (1970) and GREENSTONE et al. *(*1985) discussed, only the first instars are able to balloon due to their low body mass. In our experiment however, the species only showed tiptoe-behaviour when they were starved. This is in agreement with the findings of VAN WINGERDEN (1980a, b) and WEYMAN & JEPON (1994) who investigated Erigonid spiders in the laboratory and in field situations and observed higher take-off rates when food was deprived. In our case this means that the species will probably only disperse via ballooning when food availability is limited as a result of meteorological conditions or high densities of other predators. The food of the early instars mostly consists of larger Collembola of the genus *Entomobria* and *Isotoma*. In dry and hot weather conditions, these species will migrate into the soil (into the F-layer, which consists of fragmented plant material) and become unavailable for the predator (BONTE & VAN EUVERSWYN, unpub. data). Since these meteorological conditions, which in turn enhance aerial dispersal (VUGHTS & VAN WINGERDEN, 1976), occur during the juvenile period (BONTE et al., 1998), ballooning is probably a regularly occurring phenomenon. This hypothesis, however, needs further field research.

As stated by THOMAS (1996), aerial migration is only effective over relatively short distances (up to 3.5-4 km), while terrestrial dispersal is effective on an even smaller scale. These findings would imply that the species should easily be capable of moving between suitable habitat remnants in 'open' dune landscapes via male wandering. Cursorial dispersal via male movement in shrubby dune landscapes is impossible because of the unsuitable migration matrix. On a small scale, however, exchange of individuals between isolated populations should be possible via ballooning. The chance, however, of effective exchange of individuals within these metapopulations will depend on (1) the distance and the patch surface, determining the chance of colonisation and (2) the intrinsic dispersal rate of the source population (influenced by external stimuli such as food deprivation - possibly as a consequence of population densities and weather conditions), which may differ between different populations.

Exchange of individuals between distant populations from remote dune entities, separated by unsuitable urbanised or polder areas, is probably impossible. As a consequence gene flow between fragmented dune entities is inhibited and probably only occurs within the metapopulations from one dune entity.

Implications for conservation

Since the presence of *P. monticola* is affected by the presence of suitable habitats and corridors (although concrete data are needed on this topic), which are both influenced by local sand- and vegetation dynamics, the species can be used as an indicator for the follow up and evaluation of the contemporary management and the quality of the dune-ecosystem. The maintenance of the species by conservation and restoration of the suitable habitats and by the connection of the fragmented dune entities via suitable dispersal matrices, is of primary importance: extensive grazing in the dune will both create suitable habitats for adults and connect the grassland remnants without eliminating all the hibernation habitats. The maintenance of the species in the young dune slacks is impossible without machined restoration of the habitat. Natural formation of the habitat will soon burn out because of the high amount of dune fragmentation and sand stabilisation, which as a consequence impede sand dynamics.

Population interchange between the different isolated dune entities will probably only occur via migration along coastal Marram dunes. The restoration and conservation of these narrow corridors should be encouraged, especially at the seaside of the larger coastal communities.

REFERENCES

ALDERWEIRELDT, M. & J.-P. MAELFAIT (1988). Life cycle, habitat choice and distribution of *Pardosa amentata* (Clerck, 1757) in Belgium (Araneae, Lycosidae). *Bulletin de la Société scientifique de Bretagne: Comptes rendus du Xème*

Colloque Européen d'Arachnologie, 59 (N° hors série 1): 7-15.

Alderweireldt, M. & Maelfait, J.-P. (1990). Catalogus van de spinnen van België. Deel VII. Lycosidae. *Studiedocumenten van het KBIN*, 61: 92 pp.

Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat. *Oikos*, 71: 355-366.

Anteunis, A. (1956). Biosociologische studie van de Belgische zeeduinen. Verband tussen de plantengroei en de mollusken-fauna. *Verhandelingen van de Koninklijke Academie voor Wetenschappen, Letteren en Schone Kunsten. Klasse der Wetenschappen,* nr. 54: 193 pp.

Baert, L. & K. Desender (1993). De Spinnenfauna van het militair domein te Lombardsijde (Araneae). *Nwsbr. Belg. Arachnol. Ver.*, 8(1): 15-20.

Barkman, J.J. & P. Stoutjesdijk (1987). *Microklimaat, vegetatie en fauna*. Pudoc Wageningen, 223 pp.

Berry, A.Q., F. Gale, J.L. Daniels & W. Allmark, W. (1996). *Fenn's and Whixall Mosses*. Clwyd County Council, Mold.

Blandin, P. (1986). Bioindicateurs et diagnostic des systèmes écologiques. *Bull. Ecol.*, 17: 215-307.

Blandenier, G. & P.A. Fürst (1998) Ballooning spiders caught by a suction trap in an agricultural landscape in Switzerland In: P.A. Selden (1998) (ed.). *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: 177-185.

Bonte, D. (1997). Het voorkomen van *Hyles euphorbiae, Aricia agestis, Hipparchia semele* en *Issoria lathonia* in het duingebied van de Vlaamse Westkust in 1996 (*Lepidoptera*). *Phegia*, 25 (1):1-5.

Bonte, D. & G. De Knijf (1997). Occurrence and habitat preference of grasshoppers (*Saltatoria*) in the Flemish coastal dunes. *Biol. Jb. Dodonea*, 65: 109-110.

Bonte D. & F. Hendrickx (1997). Aanvullende gegevens omtrent de spinnenfauna van enkele duingebieden aan de Belgische Westkust. *Nwsbr. Belg. Arachnol. Ver.*, 12 (2): 33-43.

Bonte D. & J.-P. Maelfait (1998). De levenscyclus van enkele spinnen uit de duinen. *Nwsbr. Belg. Arachnol. Ver.*, 13 (1): 1-14.

Bonte, D., M. Hoffmann & J.-P. Maelfait (1999). Monitoring van het begrazingsbeheer in de Belgische kustduinen aan de hand van spinnen. *Nieuwsbr. Belg. Arachnol. Ver.*, 14 (1): 24-36.

Bonte, D., J.-P. Maelfait & M. Hoffmann (1998). Aeronautisch actieve spinnen in een duingebied te Oostduinkerke. *Nieuwsbr. Belg. Arachnol. Ver.*, 13 (3): 77-85.

Bonte, D., M. Hoffmann & Maelfait, J.-P. (2000a). Seasonal and diurnal migration patterns of the spider fauna of coastal grey dunes. *Ekologia* (Bratislava), 19/4 suppl.: 5-16.

Bonte, D., J.-P. Maelfait & M. Hoffmann (2000b). The impact of intensive cattle grazing on the spider communities *Araneae* in a mesophytic dune grassland. *J. coastal. Conserv.,* 6 (2): 135-144.

Clarke, K.R. & M. Ainsworth (1993). A method of linking multivariate community structure to environmental variables. *Mar. Ecol. Prog. Ser.*, 92: 205-219.

De Backer, S.M. (1963). Etudes microclimatiques. II. Dunes littorales – Oostduinkerke août 1951 et juillet-août 1952. *K.M.I. België, Publicaties*, serie A, nr 39, 24 pp.

De Raeve, F. (1989a). Sand dune vegetation and management dynamics. In: van der Meulen, F., Jungerius, P.D. & Visser, J.H. (red). *Perspectives in coastal dune management*. Academic publishing, Den Haag: 99-110.

Decae, A.E. (1987). Dispersal: ballooning and other mechanisms. In: Nentwig W. (ed) (1987). *Ecophysiology of spiders*. Springer Verlag, Berlin, 448 pp.

Decleer, K. (1998). Temporary inundation as a determining factor for the spider communities of marshland habitats. In: Haupt, J. (ed). *Comptes Rendus du XIème Colloque d'Arachnologie*, Berlin, 1998: 161-167.

Declerq E. & G. De Moor (1996). Geomorfologie van de Vlaamse kust. In: Provoost, S. & M. Hoffmann (eds.) (1996). *Ecosysteemvisie voor de Vlaamse Kust*. Universiteit Gent en Instituut voor Natuurbehoud (Brussel), in opdracht van de Vlaamse Gemeenschap (Afdeling Natuur): 48-86.

Delettre, Y.R., N. Morvan, P. Tréhen & P. Grootaert (1998). Local biodiversity and multi-habitat use in empidoid flies (Insecta: Diptera, Empidoidea). *Biodiversity and Conservation*, 7: 9-25.

Den Hollander, J. (1971). Life histories of species of the *Pardosa pullata* group, a study of ten populations in the Netherlands (Aranaea, Lycosidae). *Tijdschrift Voor Entomologie*, 114 (8): 255-280.

Dennis, P., M.B. Thomas & N.W. Sotherton (1994). Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators*. J. Appl. Ecol.*, 31: 361-370.

Desender K. (1996). Diversity and dynamics of coastal dune carabids. *Ann. Zool. Fennici*, 33: 65-75.

Desender, K. & H. Turin (1989). Loss of habitats and change in the composition of the ground- and tigre beetle fauna in four West European countries since 1950 (Coleoptera, Carabidae, Cicindelidae). *Biol. Conserv*., 48: 277-294.

Desender, K., J.-P. Maelfait & L. Baert (1991). Monitoring Carabid beetles in Belgian Coastal dunes. *Proceedings of the 4th ECE/XII.SIEEC*,Gödöllö: 153-158.

Duffey, E. Aerial dispersal in spiders. In: P.A Selden (1998) (ed.). *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: 187-191.

Edgar, W.D. (1970). The life cycle, abundance and seasonal movement of the wolf spider Lycosa lugubris in Central Scotland. *J. Animal. Ecol.*, 40: 303-322.

Foelix, R.F. (1996). *Biology of spiders*. Oxford University Press, Georg Thieme Verlag, 330 pp.

Fouillet, Ph. (1988). Les Araneides des schorres de la baie du Mont Saint Michel: distibution and rélations avec les facteurs mésologiques. *Bulletin de la Société scientifique de Bretagne: Comptes rendus du Xème Colloque Européen d'Arachnologie*, 59 (N° hors série 1): 65-86.

Greenstone, M.H., C.E. Morgan, A.-L. Hultsch (1985). Ballooning methodology: equations for estimating masses of sticky-trapped spiders. *J. Archnol.*, 13: 225-230.

Hanski, I. (1999). *Metapopulation Ecology*. Oxford University Press Inc., New York.

Hendrickx, F., J.-P. Maelfait, W. Muylaert & M. Hoffmann (1998). Spider distribution along the tidal River Scheldt

(Belgium). In: P.A SELDEN (1998) (ed.). *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: 265-291.

HILL, J.K., C.D. THOMAS & O.T. LEWIS (1996). Effects of habitat patch size and isolation on dispersal by *Hesperia comma* butterflies: implications for metapopulation structure. *J. Animal Ecol.*, 65: 725-735.

HILL, J.K., C.D. THOMAS & O.T. LEWIS (1999). Flight morphology in fragmented populations of a rare butterfly, *Hesperia comma*. *Biol. Conserv.*, 87: 227-283.

HUBLÉ J. (1975). Arachnofauna van strooisel onder duinstruweel van de Belgische Westkust (soortenlijst). *Biol. Jb. Dodonea*, 43: 146-150.

HUBLÉ J. (1976). Bodemspinnen van duinmoeras en helmduinen in het staatsnatuurreservaat 'De Westhoek' (Soortenlijst). *Biol. Jb. Dodonea*, 44: 226-230.

HUBLÉ J. & J.-P. MAELFAIT (1981). Analysis of the spider fauna from a north and a south-facing slope of a coastal dune (Belgium). *Faun.-Ökol. Mitt.*, 5: 175-189.

JERROLD, H.Z. (1996). *Biostatistical analysis*. Prentice Hall International Editions.

JOY, J. & S. PULLIN (1997). The effect of flooding on the survival and behaviour of overwintering Large Heath Butterfly *Coenonympha tullia* Larvae. *Biol. Conserv.*, 82: 61-66.

KIRCHNER, W. (1973). Ecological aspects of cold resistance in spiders (a comparative study). In: WIESER, W. (1973) (ed). *Effects of Temperature on Ectotherm organisms*. Springer Verlag Berlin: 271-279.

KOEHLER H., E. MUNDERLOH & S. FOFMANN (1995). Soil microarthropods (Acari, Collembola) from beach and dune: characteristics and ecosystem context. *Journal of Coastal Conservation*, 1: 77-86.

KRUSKAL, J.B. & M. WISH (1978). *Multi-dimensional scaling*. Sage Publications, Beverly Hills.

LEGEL, G.J. & W.K.R.E. VAN WINGERDEN (1980). Experiments on the influence of food and crowding on the aeronautic dispersal of *Erigone atrica* (White, 1852) (Araneae, Linyphiidae). In: GRUBER, J. (ed.), 8. *Internationaler Arachnologen Kongress Wien 1980*. Verhandulingen, Eggerman, Vienna: 97-102.

LEJEUNE, R..R., W.H. FELL & D.P. BURBIDGE (1955). The effect of flooding on development and survival of the larch sawfly *Pristiphora erichsonii* (Tenthrenidae). *Ecology*, 36: 63-70.

MAELFAIT J.-P. (1993). Spinnen en natuurontwikkeling in het duinengebied 'Home Theunis' te Oostduinkerke. *Duinen*, 4: 146-154.

MAELFAIT, J.-P. & L. BAERT (1975). Les araignées sont-elles de bons indicateurs écologiques? *Bull. Soc. sci. Bret*, 59 h.s. 1: 155-160.

MAELFAIT J.-P. & L. BAERT (1987). Het gebruik van spinnen bij ecologische indicatie. *Nwsbr. Belg. Arachnol. Ver.*, 6: 24-27.

MAELFAIT, J.-P., M. ALDERWEIRELDT, K. DESENDER, & L. BAERT. (1989). Lycosid spiders of the Belgian Coast. *Bull. Annls. Soc. r. belge Ent.*, 125: 327-332.

MAELFAIT J.-P., BAERT L. & K. DESENDER (1996). Nature conservation management in coastal dunes and spiders. *Proceedings of the 16th European colloquium of arachnology*. Siedlce, Poland: 221-236.

MAELFAIT J.-P., L. BAERT. & K. DESENDER (1998). Effects of groundwater catchment and grassland management on the spider fauna of the dune nature reserve 'De Westhoek' (Belgium). In: P.A. SELDEN (1998) (ed.), *Proc. 17th Europ. Coll. Arachn.*: 221-236.

MAELFAIT, J.-P., L. BAERT, M. ALDERWEIRELDT & M. JANSSENS (1998). A red list for the spiders of Flanders. *Bull. K. Belg. Inst. Natuurwet., Entomologie*, 68: 131-142.

MAELFAIT, J.-P. & F. HENDRICKX (1998). Spiders as bio-indicators of anthropogenic stress in natural and semi-natural habitats in Flanders (Belgium): some recent developments. *Proceedings of the 17th European Colloqium of Arachnology*, Edinburgh 1997: pp. 293-300.

MILLER, G.L. (1984). Ballooning in *Geolycosa turricola* (Treat) and *Geolycosa patellonigra* Wallace: high dispersal frequencies in stable habitats. *Can. J. Zool.*, 62: 2110-2111.

MOUSSON, L., G. NÈVE & M. BAGUETTE (1999). Metapopulation structure and conservation of the cranberry fritillary *Boloria aquilonaris* (Lepidoptera: Nymphalidae) in Belgium. *Biol. Conserv.*, 87: 285-293.

PROVOOST, S. & M. HOFFMANN (eds.) (1996). *Ecosysteemvisie voor de Vlaamse Kust*. Universiteit Gent en Instituut voor Natuurbehoud (Brussel), in opdracht van de Vlaamse Gemeenschap (Afdeling Natuur), 3 parts.

RICHTER C.J. (1970). Aerial dispersal in relation to habitat in eight wolf spider species (*Pardosa*, Araneae, Lycosidae). *Oecologia*, 5: 200-214.

RUSHTON, S.P. 1988. The effect of Scrub Management Regimes on the Spider Fauna of Chalck Grassland, Castor Hanglands National Nature Reserve, Cambridgeshire, UK. *Biol. Conserv.*, 46:169-182.

SCHAMINÉE, J.H.J., A.H.F. STORTELDER & E.J. WEEDA (1995). *De vegetatie van Nederland. Deel 2. Plantengemeenschappen van waters, moerassen en natte heide*. Opulus pres, Upssala-leiden.

SCHAMINÉE, J.H.J., A.H.F. STORTELDER & E.J. WEEDA (1996). *De vegetatie van Nederland. Deel 3. Plantengemeenschappen van graslanden, zomen en droge heiden*. Opulus pres, Upssala-leiden.

SCHAMINÉE, J.H.J., A.H.F. STORTELDER & E.J. WEEDA (1997). *De vegetatie van Nederland. Deel 4. Plantengemeenschappen van pioniers- en kustvegetaties*. Opulus pres, Upssala-leiden.

SEGERS, H. (1989). De levenscyclus van *Pardosa lugubris* (Walckenaer, 1802) in het Zoniënbos (Araneae, Lycosidae). *Nwsbr. Belg. Arachnol. Ver.*, 12: 5-14.

SEGERS, H. & J.-P. MAELFAIT (1990). Field and laboratory observations on the life cycle of *Coelotes terrestris* and *Coelotes inermis* (Araneae, Agelenidae). *Bull. Soc. d'Arachnol.*, 1: 314-324.

SIMBERLOFF, D. (1998). Flagships, umbrellas and keystones: is single-species management passé in the landscape era. *Biol. Conserv.*, 83 (3): 247-257.

SPEIGHT, M.C.D. (1986). Criteria for the selection of insects to be used as bio-indicators in nature conservation research. *Proceedings of the third European Congress of Entomology,* Amsterdam: 485-488.

SUTCLIFFE, O.L., THOMAS, C.D. & D. PEGGIE (1997). Area-dependent migration by ringlet butterflies generates a mixture of patchy population and metapopulation attributes. *Oecologia*, 109: 229-234.

THOMAS C.F.G. (1996). Modelling aerial dispersal of Linyphiid spiders. *Asp.of Appl. Biol.*, 46: 217-222.

TOFT S. (1976). Life-histories of spiders in a Danish beech wood. *Natura Jutlandica*, 19: 6-39.

VAN DER AART, P.J.M. (1975). D*e verspreiding van wolfspinnen in een duingebied, geanalyseerd met behulp van multivariate technieken*. PhD-thesis, Leiden.

VAN DONGEN, S., L. LENS & G. MOLENBERGHS (1999). Mixture analysis of asymmetry: modelling directional asymmetry, antisymmetry and heterogeneity in fluctuating asymmetry. *Ecol. Lett*., 2: 387-396.

VAN WINGERDEN W.K.R.E. & H.F. VUGHTS (1974). Factors influencing aeronautic behaviour of spiders. *Bull. Br. Arachnol. Soc.*, 3 (1): 6-10.

VAN WINGERDEN W.K.R.E. (1980a). Aeronautic dispersal of immatures of two Linyphiid spider species (Araneae, Linyphiidae). *Proc. 8th. Int. Congress of Arachnology*. 1980, Vienna. Verlag H. Egerman, Vienna: 91-96.

VAN WINGERDEN W.K.R.E. (1980b). Experiments on the influence of food and crowding on the aeronautic dispersal of *Erigone arctica* (White, 1852) (Araneae, Linyphiidae). In: GRÜBER J., (ed.). *Proc. 8th. Int.Congress of Arachnology*. 1980, Vienna. Verlag H. Egerman: 92-102.

VERMEERSCH, C. (1986). De teloorgang van de Belgische kust. *Ruimtelijke planning*, 15, II E.2.f. Van Loghum Slaterus, Antwerpen, 37 pp.

VLIJM L. & A. KESSLER-GESCHIERE (1967). The phenology and habitat of *Pardosa monticola, P. nigriceps* and *P. pullata* (Aranaea, Lycosidae). *J. Anim. Ecol.*, 36: 31-56.

VUGHTS H.F. & W.K.R.E. VAN WINGERDEN (1976). Meteorological aspects of aeronautic behaviour of spiders. *Oikos*, 27: 433-444.

WEYMAN G.S. & P.C. JEPSON (1994). The effect of food supply on the colonisation of barlet by aerially dispersing spiders (Araneae). *Oecologia*, 100: 386-390.

WIEBES, J.T. & J. DEN HOLLANDER (1974). Nederlandse wolfspinnen (Lycosidae en Pisauridae). *Wetenschappelijke mededelingen KNNV*, 23 pp.

WONNACOT & WONNACOT (1990). *Introductionary statistics*. John Wiley & Sons, New York.

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Biogéographie et Ecologie historique du bouquetin de Nubie en Egypte

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RÉSUMÉ. La Biogéographie et Ecologie historique est un champ de recherche nécessitant la compilation des informations relatives à la présence d'un animal dans un pays ou une région en vue de retracer l'évolution de son aire de répartition au cours d'une assez longue période de temps. Il est présenté ici une Biogéographie et Ecologie historique du bouquetin de Nubie en Egypte de 1800 à nos jours. Trois cartes montrant la localisation de cet animal dans le Sinaï et le Désert Oriental sont dressées, pour le XIX^e siècle, la première moitié du XX^e siècle, et la deuxième moitié du XX^e siècle. Au terme de cette étude, il s'avère que la chasse effectuée par l'homme est la principale cause de la disparition de ce capriné dans certaines parties de l'Egypte.

MOTS CLÉS: Bouquetin de Nubie, *Capra ibex nubiana*, Egypte, Ecologie historique, Biogéographie.

Historical ecology and biogeography of the Nubian Ibex in Egypt

ABSTRACT. Historical ecology and biogeography is a field of research that necessitates the compilation of data in relation to the presence of animals, in a country or in a specific region, in order to retrace their distribution over a long period of time. This paper presents the historical ecology and biogeography of the Nubian Ibex in Egypt from 1800 up to today. Three maps showing the location of this animal in the Sinai and the Eastern Desert are established: the XIXth century, the first half of the XXth century, and the second half of the XXth century. It appears that man's hunting principally caused the disappearance of this caprinae from some part of its Egyptian area.

KEY WORDS: Nubian ibex, *Capra ibex nubiana*, Egypt, Historical ecology, Biogeography.

INTRODUCTION

La Biogéographie et Ecologie historique est un champ de recherche interdisciplinaire dont le principal promoteur est Grout de Beaufort (1988), à l'origine de travaux ultérieurs (Manlius, 1996, 1998, 2000a, 2000b, 2000c; Manlius & Gautier, 1999). Il nécessite l'analyse d'une importante bibliographie sur un animal dans une zone géographique d'étude en vue de compiler les informations relatives à sa présence dans celle-ci, et aboutit à l'établissement de carte montrant l'évolution de la distribution de ses populations au cours du temps. Des travaux approchants (Uerpmann, 1987) ou similaires (Kinzelbach, 1991) ont été réalisés, mais ils n'appréhendent pas l'aspect évolutif au cours du temps, où, s'ils le font, les résultats pèchent par manque de précision et ne sont pas obtenus à l'issue d'une enquête transversale effectuée avec d'autres disciplines.

L'Egypte est un pays idéal pour les études de Biogéographie et Ecologie historique car il est possible d'y suivre sur une assez longue période de temps l'évolution de la distribution des populations d'animaux. En effet, elle fut très tôt peuplée par l'homme, et par conséquent les représentations rupestres et les ossements d'animaux consommés par les peuples préhistoriques qui l'habitaient s'y trouvent en quantité. Le delta et la vallée du Nil furent ensuite le siège de la civilisation pharaonique, qui laissa des représentations animales fidèles. L'Egypte fut enfin parcourue par des voyageurs ou des scientifiques rapportant des informations sur sa faune.

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Un panoramique de l'évolution de la distribution des populations égyptiennes d'une vingtaine de grands mammifères terrestres et sauvages à déjà été réalisé (MANLIUS, 1996), dont le bouquetin de Nubie, *Capra ibex nubiana* F. Cuvier, 1825. Cet herbivore, habitant les steppes, les semi-déserts ou les déserts de montagnes rocheuses accidentées jusqu'à 2000 m d'altitude, et dont le mâle porte de grandes cornes recourbées en arrière en forme d'arc de cercle (HALTENORTH & DILLER, 1985), est susceptible d'être identifié sans trop d'ambiguïtés dans le bestiaire iconographique et les écrits des voyageurs en Egypte.

MATÉRIEL ET MÉTHODES

La consultation de documents écrits est réalisée dans les grandes bibliothèques parisiennes. Malgré la relativement grande quantité d'informations dont dispose l'Egypte pour les périodes correspondant à la Préhistoire, à l'époque pharaonique, à l'Antiquité et au Moyen Age, très peu désignent avec précision une région. Seules peut-être les figurations pariétales permettraient-elles de le faire mais elles sont difficilement datables et assez peu nombreuses. En revanche, il existe une grande quantité de données très précises pour les XIX^{e} et XX^{e} siècles. Par conséquent, seuls ces deux siècles seront étudiés.

La première carte (Fig. 1) aidera le lecteur à situer les observations. Les trois dernières cartes (Figs 2 à 4) présentent les recherches et recouvrent les périodes suivantes: de 1800 à 1900, de 1900 à 1950, et de 1950 à 2000. En ce qui concerne le texte, il faut préciser que les notes misent entre guillemets sont de la main de l'auteur cité.

RÉSULTATS

Présence en Egypte antérieurement à 1800

Les populations africaines de bouquetins de Nubie descendraient d'ancêtres originaires d'Asie ayant franchi l'isthme de Suez (BODENHEIMER, 1958: 167; TCHERNOV, 1988: 213). Elles semblent avoir été uniquement cantonnées à l'est du Nil (FLOWER, 1932: 435; KOCK, 1971: 34). Une telle distribution pourrait s'expliquer par le fait que le bouquetin de Nubie, n'aimant pas à nager (COUTURIER, 1962: 1135 à 1138), n'aurait jamais tenté de franchir un fleuve aussi large et animé d'aussi forts courants que le Nil; fleuve qui, par ailleurs, était à l'époque infesté de crocodiles. Quand bien même l'aurait-il franchi, il n'aurait sans doute pu gagner les falaises de la dépression de Qattara ou le djébel Uweinat car cet animal est connu pour ne pas pouvoir traverser les plaines désertiques (CUVIER & GEOFFROY SAINT-HILAIRE, 1825: livraison 50), habitat qu'il ne cherche d'ailleurs pas à fréquenter (MUZZOLINI, 1987: 131). Il se serait donc contenté d'étendre son aire de répartition le long des montagnes de la mer Rouge jusqu'en Abyssinie. Dans cette optique, le bouquetin d'Ethiopie, *Capra ibex walie* Rüppell, 1835, endémique aux montagnes de Semien (YALDEN et al., 1984: 147), constituerait la relique d'une ancienne distribution plus étendue des actuels bouquetins égyptiens et soudanais (CLUTTON-BROCK, 1987: 59). Le fait que le bouquetin d'Ethiopie fut présent "de mémoire d'homme" dans le Gojam et au sud du lac Tana (COUTURIER, 1962: 850), c'est-à-dire au sud des montagnes de Semien, irait dans le sens de cette hypothèse.

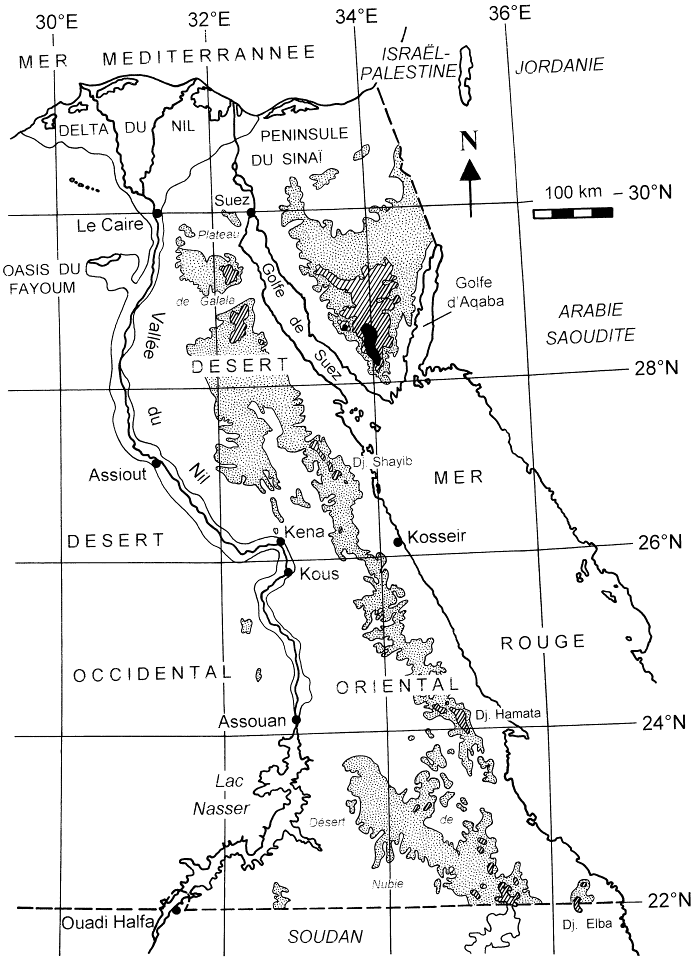

Fig. 1. – Carte topographique et toponymique du Désert Oriental et du Sinaï. En pointillé, altitudes comprises entre 500 et 1000 m; en hachuré, altitudes comprises entre 1000 et 1500 m; en noir, altitudes comprises entre 1500 m et 2637 m.

De ce qui précède, nous pouvons appréhender que le bouquetin de Nubie fut très probablement présent dans la totalité du Sinaï et du Désert Oriental à l'époque préhistorique. En effet, de nombreuses gravures préhistoriques ou décors de poteries le représentent (ROTHENBERG, 1979: 94; OSBORN & OSBORNOVÁ, 1998: 181 à 183), mais l'inventaire archéozoologique se réduit à une seule mention certaine dans un site néolithique du Sud-Sinaï (UERPMANN, 1987: 119-120). Cette carence est sans doute due au fait que peu de sites susceptibles de contenir ses restes ont été fouillés dans le Sinaï et dans le Désert Oriental (GAUTIER, comm. pers.). Dans le Désert Occidental, aucune représentation ni aucun reste osseux attribués avec certitude au bouquetin de Nubie n'ont été recensés (COUTURIER, 1962: 565, 589; KOCK, 1971: 34).

Quant à la période pharaonique, bien que l'on ait jamais mis à jour de momies de bouquetins de Nubie, ce dernier orne fréquemment les bas-reliefs ou les peintures des premières dynasties (GAILLARD, 1912: 10). Il fait partie de la faune de chasse et des animaux offerts en sacrifice aux dieux (BUXTON et al., 1895). Pour ce dernier but, des bouquetins étaient élevés en captivité mais, contrairement aux idées reçues, l'espèce ne fut pas l'objet d'une tentative de domestication (GAUTIER, 1999: 306). L'inventaire archéozoologique se réduit à quelques restes dans le temple de Satet à Eléphantine et datant des V^{e} et VI^{e} dynasties (BOESSNECK & VON DEN DRIESCH, 1982: 65-66, 87, fig. 22).

Pour la période s'étalant entre celle de l'Egypte pharaonique et le XIX^{e} siècle il y a peu ou prou de documents. THÉVENOT (1665: 313) rapporte avoir vu en 1658 sur des montagnes proches de la côte occidentale du Sinaï et situées un peu au nord d'El Gharandal, un animal qui n'est pas une gazelle mais "qui tient du chevreuil et du daim". Peu après, GONZALES (1977: 34, 379-380) signale qu'en 1665-66 le désert de la Thébaïde, c'est-à-dire le Désert Oriental au niveau de Thèbes, est "si plein" de bouquetins que l'on peut les voir "par paires ou par troupeaux".

Les quelques renseignements qui précèdent ne permettent pas d'évaluer l'impact de l'homme sur la distribution du bouquetin de Nubie.

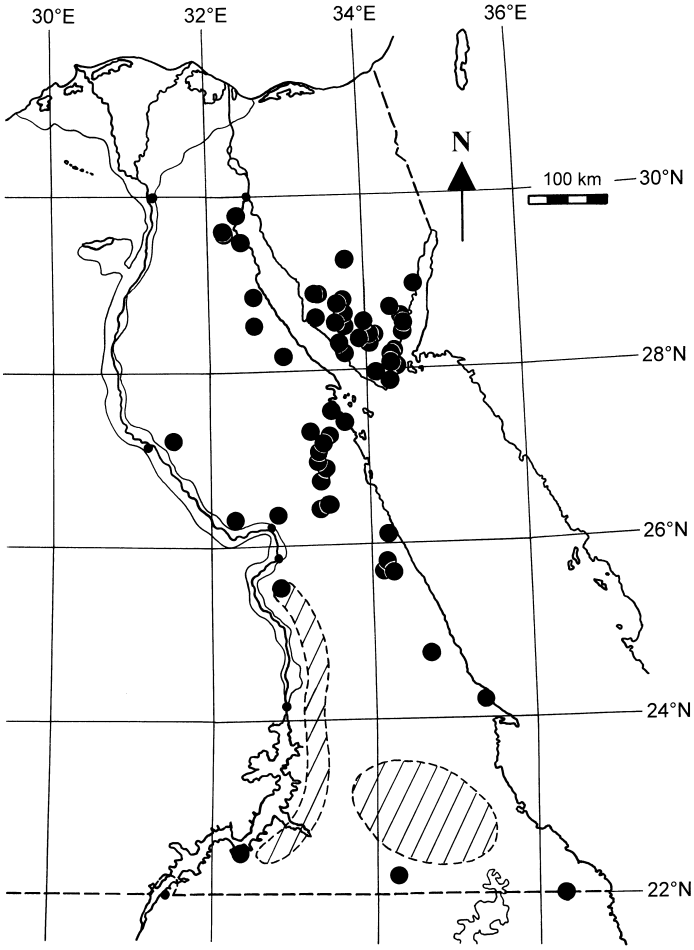

Fig. 2. – Localités égyptiennes où la présence du bouquetins de Nubie est attestée entre 1800 et 1900. Les petits ronds noirs indiquent l'emplacement des villes et les gros ronds noirs désignent des sites où la présence du bouquetin de Nubie est attestée. Les hachurés obliques correspondent à de vastes régions ne désignant pas spécifiquement un site mais où cette présence est également attestée.

Présence en Egypte postérieurement à 1800

De 1800 à 1900 (Fig. 2)

Selon OSBORN & HELMY (1980: 520, 522), les voyageurs du XIX^{e} siècle en Egypte rapportent que l'on rencontre le bouquetin de Nubie sur les falaises à pic surplombant la rive est du Nil, sur tous les plateaux ou montagnes du Désert Oriental, ainsi que dans la péninsule du Sinaï. Cette affirmation va être confirmée par l'énumération des témoignages qui vont suivre.

Péninsule du Sinaï

BURCKHARDT (1822b) voyageant au Sinaï en 1816, aperçoit un bouquetin dans l'oued Moladge (p. 526) et ses accompagnants observent des individus près du djébel Umm Shomar (p. 590). HEMPRICH & EHRENBERG (1830) indiquent la présence du bouquetin en 1823 sur le djébel Musa (le Mont Sinaï), entre les oueds Hebran et Islah, et près de Tor. RÜPPELL (1829: 187) le situe en 1826 sur les massifs montagneux compris entre l'oued Feiran, le monastère de Sainte-Catherine sur le djébel Musa, et la baie de Sharm El-Sheikh. BARTLETT (1848: 66) confirme l'existence du bouquetin sur ce dernier djébel, où il découvre une paire de cornes. OUMANETZ (1850: 218) prétend qu'en 1842-43 l'on rencontre habituellement sur le djébel Horeb (c'est-à-dire le djébel Musa) des "moutons sauvages", et OUSPENSKY (1856: 275) écrit qu'en 1845 l'on rencontre souvent le "chamois" sur le djébel Banat et le plateau de Zebir, selon les dires des Bédouins. Il est probable, comme le pense VOLKOFF (1972: 197), que ces deux auteurs ont voulu parler du bouquetin.

LOTTIN DE LAVAL (1855-1859: 264) aperçut en 1850 un bouquetin poursuivi par une panthère à Nuweiba. BREHM (1855) signale l'existence du bouquetin en 1851 dans les oueds Hebran (p. 330), Sulaf (p. 340-341) et El Rharakit (p. 344-345). PALMER (1871) rapporte la présence d'un mâle et de sa famille en 1868 dans une cour du monastère de Sainte-Catherine (p. 63); en 1869, il cite un animal abattu près de l'oued Feiran (p. 157) et voit de nombreuses traces dans l'oued Geba (p. 213), ainsi qu'une harde au sommet du djébel Umm Shomar (p. 248-249) et une autre traversant l'oued Saal (p. 257). En 1898, selon A. Kœnig, le bouquetin serait présent sur les djébels Baba, El-Hamra et Serbal, ainsi que dans les oueds Aleyat et Shellal, et près de Nabq (NIETHAMMER, 1964). HUME (1906), explorant la pointe sud-est de la péninsule en 1898-99, rapporte la présence d'une femelle sur le Tellat Gimal et observe un mâle et plusieurs femelles sur les pentes du djébel Sheikh El Arab (p. 48), où le bouquetin serait abondant (p. 49); il découvre un squelette dans un affluent de l'oued Nasb (p. 51, 112), oued où J. MARRIOTT abat neuf individus (p. 54), et examine des traces qui lui font penser que les bouquetins sont très nombreux dans l'oued Umm Shoka (p. 62); il aperçoit ensuite une harde de sept individus sur le djébel Genaui (p. 71) et une autre de dix dans l'oued Kid (p. 73); enfin, il découvre trois paires de cornes dans l'oued Ethmiemat (p. 75), et estime que le bouquetin est présent en grand nombre dans les oueds Umm Adawi (p. 82) et Aad (p. 83). BARRON (1907), explorant cette fois-ci la pointe sud-ouest du Sinaï, toujours en 1898-99, le dit être abondant dans l'oued Satakh, un affluent de l'oued Akhdar, où une harde de dix individus fut aperçue sur les pentes des collines environnantes (p. 61), et découvre de très nombreuses traces dans l'oued Geba (p. 81).

Désert Oriental

BURCKHARDT (1822a: 22), voyageant en 1813 le long du Nil, cite la présence du bouquetin à l'est d'Assiout et l'estime être présent en faible nombre entre Assouan et El-Diwan. HEMPRICH & EHRENBERG (1830) l'indiquent en 1823 sur des montagnes près de Kosseir, sur le djébel Gharib et près de Kena. WILKINSON (1832) l'observe en 1823 au nord de l'oued Hommath, situé au sud-ouest de Suez (p. 32), ainsi que sur le djébel Umm Tinassib, situé dans le sud du plateau de Galala (p. 38), et le dit provenir de l'oued séparant les djébels Abu Dukhan et Qattar (p. 49-50). Ce même auteur (WILKINSON, 1835: 228) l'indique également près de Thèbes.

LINANT DE BELLEFONDS (1854), prospectant dans l'extrême sud-est de l'Egypte en 1831, relate la présence de "capricornes" sur le djébel Elba (p. 122) et généralise cette présence aux montagnes situées au sud de Kosseir (p. 131). Il est en partie confirmé par FITZINGER (1855: 250, 252) qui précise que le bouquetin vit en Nubie égyptienne. HEUGLIN (1861b: 311) le localise sur les montagnes situées entre le Golfe de Suez et le Nil et l'indique (HEUGLIN, 1861a: 16) se trouver "en nombreuses familles" le long des côtes, confirmé par FIGARI (1864: 262) qui précise que le bouquetin est plus abondant sur les versants des montagnes de la mer Rouge inclinés vers la côte que sur ceux inclinés vers la Vallée. COLSTON (1886: 531) aperçoit "de près deux capricornes" en 1874 à proximité de l'oued Daffeti. HEUGLIN (1877: 126) le dit être présent en 1875 sur les montagnes situées entre Suez et Bérénice ainsi que dans le désert de Korosko. SCHWEINFURTH (1925) le signale en 1865 sur les djébels Abu Tiyur et "Ssubah" (ce dernier correspond à un prolongement de la chaîne du djébel El-Siba'i), situés au sud de Kosseir (p. 44), et entre 1876 et 1878 près du Dayr Al Qiddis Bulus (le monastère de Saint-Paul), situé dans le sud du plateau de Galala (p. 95). Le bouquetin est indiqué de 1863 à 1869 aux alentours de Kosseir (KLUNZINGER, 1878a: 246) et, au sud de cette ville, sur le djébel Abu Tiyur et près du bir Hindusi (KLUNZINGER, 1878b: 67). RIEBECK (1881: 47), au cours d'un voyage effectué en 1881 entre Le Caire et les rivages de la mer Rouge situés à la limite nord du plateau de Galala, voit six bouquetins dans l'oued El Abyad et croit en l'existence d'autres animaux dans "l'oued Naqud" (c'est-à-dire l'oued No'oz). FLOYER (1887), explorant le centre du Désert Oriental en 1886, rapporte que le bouquetin est abondant dans l'oued Qattar (p. 671), très présent sur le djébel du même nom, d'où il descend pour s'abreuver aux trous d'eau situés en contrebas tel le bir Qattar (p. 675), avoir vu cinq individus dans l'oued Mellaha (p. 676), découvert des crottes dans l'oued Rwashid (p. 678), et aperçu une petite harde sur la rive sud de l'oued Abu Duq (p. 680). WYLDE (1888: 215) l'indique d'ailleurs présent depuis l'extrême sud égyptien jusqu'à son extrême nord à Abu Darag, non loin de Suez. FLOWER (1932: 436) relate les observations d'un Anglais employé à la construction du chemin de fer reliant Louksor à Assouan lors de la dernière décennie du XIX^{e} siècle, et d'après lequel le bouquetin descendait boire jusque dans le fleuve avant que l'achèvement de la ligne de chemin de fer n'isolât les rives orientales du Nil des montagnes où il vivait. FLOYER, retournant dans le Désert Oriental en 1891, rapporte avoir chassé un vieux mâle dans l'oued Lehama (1893a: 14), qu'H. PRETYMAN participa à une partie de chasse au bouquetin sur le djébel Qattar (1893a: 25; 1893b: 423) et qu'un animal fut abattu par H. MANSUR sur le djébel Zabara (1893a: 27; 1893b: 425). G. SCHWEINFURTH, dans une lettre à J. ANDERSON le 22 février 1893, écrit: "Mr ALLEN [...] chasse l'ibex juste à l'opposé de Nagi Hamada, près de Farchout" (ANDERSON & DE WINTON, 1902: 333). LANGKAVEL (1894: 155) indique que le bouquetin est présent sur le djébel Abu Dukhan et cite E.N. BUXTON qui le situe durant l'hiver 1892-93 sur une montagne près des ruines de Myos Hormos. BARRON & HUME (1902), explorant en 1897-98 le centre du Désert Oriental, le disent beaucoup fréquenter le bir Hedeba (p. 18-19), être abondant sur le djébel Abu Harba (p. 25) et dans l'oued Umm Diqal (p. 38), fréquenter assidûment les environs des djébels Abu Harba, Ri'El-Garra et El Gidami, les Arabes indiquant par ailleurs comme "meilleure localité" le djébel Gharib (p. 106).

De 1900 à 1950 (Fig. 3)

Péninsule du Sinaï

Deux individus furent pris sur le djébel El Rabba en 1905 (OSBORN & HELMY, 1980: 518). BALL (1916: 5) explorant en 1913 et 1914 la moitié ouest de la partie centrale de la péninsule, signale un couple de bouquetins dans le district du djébel El Tih. ALLEN (1915 : 14) découvre un nouveau-né dans l'oued Feiran en 1914 et MÜLLER (1916) cite le djébel Tarbush et l'oued Hebran. FLOWER (1932 : 446) indique que deux mâles furent tués en 1918 sur le djébel Serbal. BEADNELL (1927), en 1923 pour le nord de la péninsule, rapporte qu'une chasse au bouquetin s'est déroulée sur le djébel El Raha "il y a dix ans" [donc en 1913] (p. 84) et qu'un prospecteur nommé NOTESTEIN observa deux animaux sur le Shushet El Maghara "il y a quelques années" [donc vers 1920] (p. 91). En 1924, BEADNELL (1927) effectue les observations suivantes au centre de la péninsule : il voit deux bouquetins sur le djébel Umm Afruth (p. 118), trois autres dans l'oued Ghilm (p. 143-144), des traces fraîches sur le djébel Mikeimin (p. 148), certifie la présence de cet animal à Ain El Furtaga (p. 149), rapporte qu'au moins un individu fut tué non loin de la côte près de Nuweiba (p. 154), et enfin, en vit six dans l'oued Umm Musma (p. 158) et trois sur le djébel Tarbush (p. 170). JARVIS (1931 : 208-209) indique que des femelles se rencontrent sur le djébel Yelleg (Nord-Sinaï) et vit un grand mâle sur le djébel Tarbush (Sud-Sinaï).

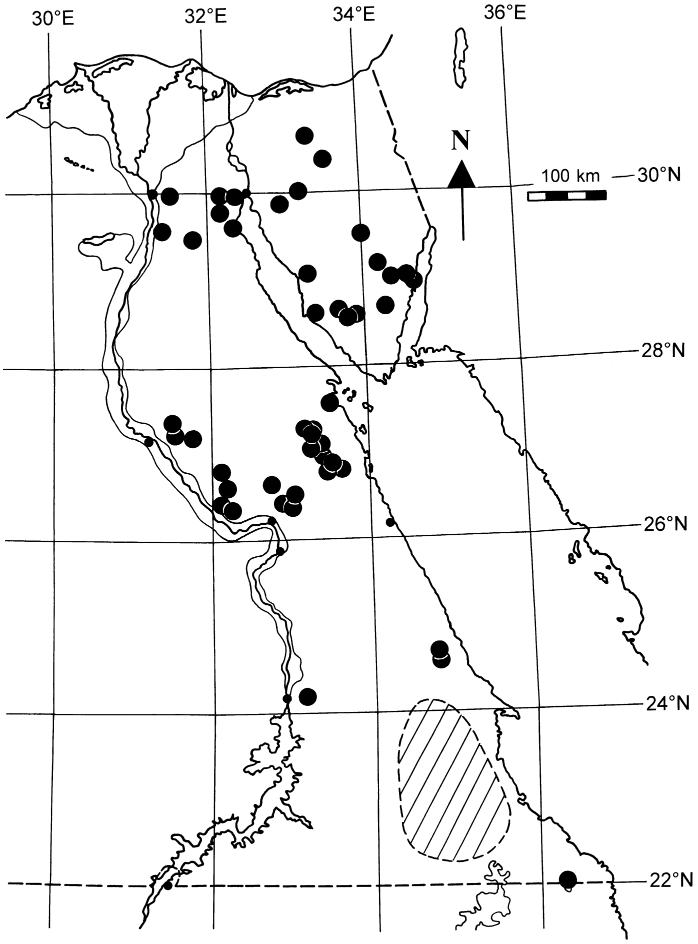

Fig. 3. – Localités égyptiennes où la présence du bouquetins de Nubie est attestée entre 1900 et 1950. Pour l'explication des symboles utilisés, voir la figure 2.

Deux individus furent observés près du bir Nukhul (MURRAY, 1935 : 121) et RUSSELL (1949a : 5 ; 1949b : 101) indique l'existence de bouquetins sur les djébels Serbal et Tarbush.

Désert Oriental

MAC ALISTER (1900 : 548), dans les tout premiers jours de l'année 1900, constate que les bouquetins sont nombreux dans la région globalement comprise entre les oueds Sikait et Nugrus. H.J.L. BEADNELL (1927) écrit : "Je suis à peu près sûr que les ibex se rencontrent dans les oueds entre Assiout et Kena, et ils sont souvent tués par les Bédouins dans l'oued Sheitun, selon leurs propres dires" (ANDERSON & DE WINTON, 1902 : 333). FLOWER (1932 : 446) signale d'ailleurs un mâle abattu dans cet oued en 1905, ainsi qu'une femelle provenant de la région d'Assouan pensionnaire au Jardin Zoologique de Giza en 1912. W.F. HUME rapporte à S.S. FLOWER qu'aux environs d' "Undisi" (c'est-à-dire le djébel Umm Disi) : "Les ibex sont évidemment abondants, à en juger par les traces laissées près des points d'eau" (ANDERSON & DE WINTON, 1902 : 333). BALL (1912 : 24), explorant entre 1905 et 1908 le sud-est de l'Egypte au sud de Bérénice, reconnaît que les bouquetins n'y ont "jamais été vus avec certitude, bien que leurs cornes et leurs tanières furent souvent découverts dans les montagnes" de cette région. Durant la première décennie du XX^{e} siècle, RUSSELL (1949b : 102) précise que le bouquetin se trouvait encore en grand nombre dans le désert à l'est d'Assiout, et cite plus précisément (RUSSELL, 1949a : 5-6) les oueds Qena, El Asyuti, Habib, Sheitun et Qasab. RUSSELL (1949b) cite également le djébel Elba (p. 112) ainsi que le bir Sheitun (p. 110), où il calcula (RUSSELL, 1949a : 7) vers 1920 qu'une centaine d'animaux y furent capturés en l'espace d'un été par des chasseurs commerciaux. En effet, après la Première Guerre mondiale ce puits, constituant parfois le seul point d'eau disponible sur des centaines de kilomètres, devint l'endroit favori pour tirer les bouquetins (OSBORN & HELMY, 1980 : 520). FLOWER (1932 : 436-437) cite G.W. MURRAY qui écrit le 3 avril 1920 que les traces et les crottes de bouquetins sont rares sur les grandes montagnes, excepté au centre du Désert Oriental sur le presque inaccessible djébel Shayib, où au dessus de 1200 m il voit des crottes fraîches "dans tous les coins et recoins", ce qui l'autorise à penser qu'en cet endroit les bouquetins doivent être très nombreux, bien qu'il avoue n'en avoir vu aucun. Pour DOLLMAN & BURLACE (1935 : 272), le bouquetin serait toujours présent à proximité immédiate du Caire.

SADEK (1926) le dit plutôt abondant sur les djébels Akheider, Ataqa et Kahaliya, au sud-ouest de Suez (p. 23), ainsi que dans l'extrême nord du plateau de Galala en surplomb de l'oued Ghuweibba

(p. 14). Russell (1949b: 118) relate que vers les années 1900 le prince Kemal El Dine créa une réserve de chasse pour les bouquetins dans l'oued Rishrash, situé à environ 80 km au sud-est du Caire, réserve qui devint en 1932 un sanctuaire pour ces animaux. La même année, Russell (1949b: 120) put y observer une cinquantaine d'animaux venant ensemble se désaltérer et se nourrir en un point de distribution. Flower (1932: 436) indique l'existence du bouquetin dans les collines près du Caire et de Suez et rapporte avoir vu deux individus capturés dans la région d'El-Saff (à environ 50 km au sud du Caire), mais précise que la plupart des spécimens proviennent des provinces d'Assiout, de Girga et de Kena. Owen (1937: 159) le signale sur le djébel Elba. Russell (1951) dénonce le massacre des bouquetins des oueds Qena et El Asyuti par des chasseurs commerciaux durant la Seconde Guerre mondiale. Tregenza explore le centre du Désert Oriental en 1949 et écrit deux livres sur le sujet. Dans le premier (Tregenza, 1955), il relate qu'en 1946 un bouquetin fut tué et consommé sur le djébel Qattar (p. 180-181) et qu'en 1947 l'espèce était présente dans l'oued Mellaha (p. 92). Ses autres observations relatives au bouquetin se rapportent toutes à l'année 1949. Celles effectuées sur les djébels sont les suivantes: présence de bouquetins sur le djébel Umm Gidri (p. 71); un individu entendu dans les carrières du Mont Claudianus (p. 124); des tanières (p. 126-127), un cadavre près d'un trou d'eau (p. 134), un mâle et deux femelles (p. 135) puis deux autres individus (p. 136) vus sur les pentes du djébel Abu Dukhan; enfin, un individu (p. 158) et une harde constituée d'un mâle et de trois femelles (p. 160) vus sur les pentes du djébel Abu Harba. Les observations relatives aux oueds sont les suivantes: une paire de cornes trouvée dans l'oued El Merkh (p. 20); une autre, d'un mâle, dans l'oued Abu Shehat (p. 33); des bouquetins viendraient boire à un puits dans l'oued Mitgal (p. 58); des tanières existent dans l'oued Umm Balad, alors que le bouquetin descendrait dans les oueds Abu Ma'amel, Umm Sidri et El Atrash (p. 129); enfin, des individus viendraient boire à un trou d'eau dans l'oued Nagat (p. 175). Dans le second livre (Tregenza, 1958), l'auteur relate qu'en 1947 l'espèce étaient présente dans l'oued Showak (p. 89). Ses autres observations relatives au bouquetin se rapportent toutes à l'année 1949. Il l'indique sur le djébel Shayib car de l'urine y fut découverte par deux fois (p. 105, 119), un squelette de juvénile (p. 108) puis un cadavre y furent trouvés (p. 132), et il vit près du sommet deux femelles (p. 121-122), puis deux autres individus dont un mâle (p. 124), et en redescendant aperçu encore deux femelles (p. 135). Il vit encore un mâle sur les pentes du djébel Abu Abid (p. 125-126), un cadavre dans l'oued Abu Erin (p. 128), et décrit une chasse effectuée sur le djébel Barud (p. 150, 152).

De 1950 à 2000 (Fig. 4)

Péninsule du Sinaï

Couturier (1958: 17-18) indique la présence du bouquetin sur les contreforts des djébels Musa et Katharina (le Mont Sainte-Catherine) et De Beaux (1956: 179) en 1955 à Ayun Musa (les Sources de Moïse). Harrison (1968: 331, 333) cite une peau de mâle non datée provenant du djébel El Rabba.

Rothenberg (1979: 192) estime que le bouquetin est abondant dans les montagnes situées autour du monastère de Sainte-Catherine. Baharav & Meiboom (1981: 91) évaluent entre 1977 et 1979 la population de bouquetins du Sinaï à quelque 300 individus. Pour le nord de la péninsule, ils désignent seulement trois djébels (Maghara, Yelleg et Halal) occupés par une cinquantaine d'individus (p. 92). Pour le centre, par contre, ils citent d'ouest en est les djébels El Raha, Sumar, El-Igma, El-Sha'ira, les pentes des oueds Watir et Zalaqah, et la région d'Eilat (p. 93-94). Pour le sud, enfin, ils totalisent plus de 200 individus, soit environ 70% de la population du Sinaï, répartis sur les djébels Achmar, Baab, Freha, Gunna, Sabbagh, Katharina, Serbal, Thebt et Umm Shomar; dans les oueds

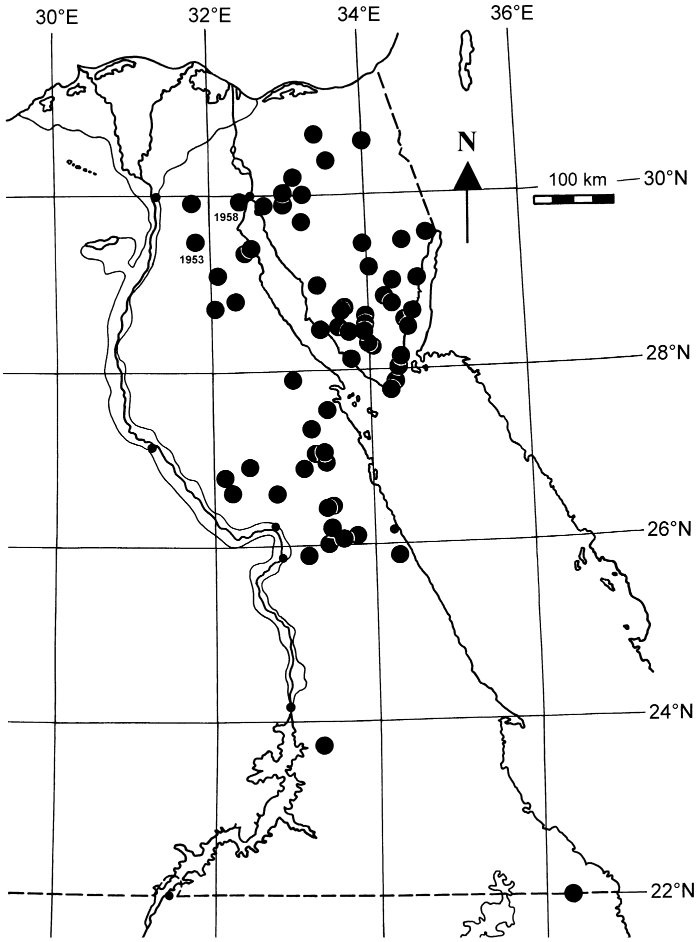

Fig. 4. – Localités égyptiennes où la présence du bouquetins de Nubie est attestée entre 1950 et 2000. Pour l'explication des symboles utilisés, voir la figure 2.

Kid, Nasb et Saal, et dans les environs de la baie de Sharm El-Sheikh (p. 93, 96). Selon Saleh & Basuony (1998: 570), en cette dernière décennie du XX^e siècle, le bouquetin serait présent dans les localités suivantes: le bir El Giddi, le col de Mitla, les plateaux El Tih et El-Igma, l'Umm Bigma, les djébel Araba et Serbal, les oueds Akhdar, Hebran, Mahr, Nasb et Islah, l'oued Kid et ses affluents, la région du djébel Katharina, quelques oueds à l'ouest de Nabq, la Ras Muhammed, les montagnes à l'ouest et au sud-ouest de Dahab, l'oued El Gahlib et ses affluents, la zone protégée d'Abu Galum, l'oued Watir et ses affluents, et pour finir, la région de Ras El Naqb.

Désert Oriental

Tregenza (1958: 163) rapporte l'existence de tanières de bouquetins en 1951 dans l'oued Semna. Fontaine (1954: 66) écrit que les pistes reliant les sources d'Ain Barda entre elles ou aux falaises nord du plateau de Galala "sont parsemées d'excréments de chèvres, d'ânes, de chameaux et même de bouquetins, indices d'une fréquentation assez coutumière". Daumas (1960: 42) indique en 1955 que les bouquetins s'abreuvent parfois dans une vasque située à la naissance de l'oued Nagat. Selon Ralli (1954), l'espèce était répandue tout le long des montagnes de la mer Rouge depuis le djébel Elba jusqu'à Suez (p. 44) avant que la réserve de Rishrash et ses cent cinquante bouquetins ne disparaisse (p. 45). C'est-à-dire avant la révolution de 1953, date à partir de laquelle la réserve fut fermée et la population de bouquetins résidente exterminée (Schomber, 1963: 124). De la même façon, Bourgoin & Dandelot (1955: 88) faisaient remonter son aire de répartition depuis le sud des montagnes de la mer Rouge jusqu'au djébel Ataqa, c'est-à-dire non loin de Suez. Si Couturier (1958: 17-18) confirme pour ce djébel, il précise cependant que la Deuxième Guerre israéloarabe de 1956 à dû avoir pour conséquence une réduction de sa population de bouquetins. Hoogstraal (1964) le certifie exister en 1954 sur le djébel Elba. Osborn & Helmy (1980: 518) citent une peau d'immature en provenance de l'oued El Ghuzz examinée en 1964, un individu provenant de l'oued Rawd'Aid en 1965, et des cornes et des crânes en provenance du djébel Abu Harba et du bir Umm Hibal. Ils aperçurent un individu sur le djébel El Kutamiya en 1964, un autre près du bir Mellaha en 1965, et une petite harde et des individus isolés en plusieurs occasions près du bir Qiseib entre 1964 et 1967. Enfin, ils relevèrent des traces dans l'oued Abu Sanduq en 1964.

Osborn & Helmy (1980: 521) le disent fréquenter les sommets montagneux les plus inaccessibles du centre du Désert Oriental, c'est-à-dire entre approximativement le sud du 28°N et le nord du 26°N. Ils soulignent que les hommes de la tribu des Bicharins ramènent régulièrement de la région du djébel Elba des cornes pour alimenter les bazars d'Assouan: ce qui signifie que sur ce djébel vit une population de bouquetin suffisamment importante. Hobbs (1989: 80), de 1982 à 1984 et en 1986, l'indique très présent dans le centre du Désert Oriental, plus précisément sur le territoire des Ma'azas, délimité au nord par le sud du plateau de Galala, et au sud par la route reliant Kous à Kosseir. Selon cet auteur, il existerait entre 200 et 300 bouquetins sur le djébel Qattar, peut-être la moitié de ce nombre sur le djébel Shayib, et peut-être un millier dans le sud du plateau de Galala; par ailleurs, d'importantes populations occuperaient les environs du djébel Dara et du bir Sheitun (p. 97). Toujours selon cet auteur, l'animal vivrait également dans la région du bir Umm Laseifa (p. 80), près du djébel El Gidami et du bir Muwayh, ainsi que dans les oueds Atalla, Umm Hadd (p. 33) et "Adayd": dans ce dernier, situé dans le sud du plateau de Galala (nous l'assimilons à l'oued El Abeid car c'est le seul de la région à avoir un nom approchant), un individu fut tué (p. 42-43) et un mâle capturé (planches de photographies entre les p. 48 et 49); enfin, un bouquetin est observé sur le djébel Dhibaah, d'autres sont signalés dans l'oued Sheitun en 1986, un individu est vu dans l'oued Umm Ruutha (p. 95), un autre sur le djébel Mi'tiq, et un dernier à El Heita (p. 96).

DISCUSSION

Evolution des populations de bouquetin de Nubie en Egypte depuis le début du XIX^e siècle

De 1800 à 1900

Entre les XVIII^e et XIX^e siècles, les informations sont plus nombreuses et se font plus précises. Certains auteurs soulignent déjà que la chasse est la cause principale de la diminution du nombre de bouquetins en Egypte (Burckhardt, 1822b: 571). Toutefois, durant la totalité du XIX^e siècle, l'animal est encore commun et fréquent dans le Sinaï (Burckhardt, 1822b: 571), particulièrement dans le sud (Barron, 1907: 92; Hume, 1906: 112), ainsi que dans la portion centrale (Barron & Hume, 1902: 108) et septentrionale (Floyer, 1893b: 430) du Désert Oriental. En effet, la chasse n'avait encore qu'une incidence relative sur le sort de l'espèce car les chasseurs étaient peu nombreux et leurs armes primitives (Russell, 1949a: 6; 1949b: 102). A ce sujet, De Pardieu (1851: 203-204) relate une tentative de chasse pittoresque tournant au ridicule effectuée en 1849 au Sinaï par des indigènes utilisant des fusils à mèche totalement inadaptés à un gibier – des gazelles – se déplaçant avec célérité. Encore à l'orée du XX^e siècle, le bouquetin était assez fréquent au Sinaï (Carruthers, 1915: 23, 26-27) et très fréquent dans le Désert Oriental (Russell, 1949a: 6; 1949b: 102-103).

La carte de la Fig. 2 montre une distribution dans le sud de la péninsule et dans la totalité du Désert Oriental, y compris aux abords du Nil. Une présence du bouquetin dans le nord et le centre du Sinaï est plus que probable mais la vacuité de témoignages ne permet pas de l'affirmer.

De 1900 à 1950

Bien que moins nombreux qu'au siècle précédent car très chassés par les indigènes et leurs chiens, les bouquetins ont maintenu un effectif conséquent en Egypte jusqu'à la Première Guerre mondiale (ALLEN, 1915: 14). Mais après celle-ci, chaque Arabe du Proche-Orient entra en possession d'au moins une arme à feu moderne et d'une provision illimitée de cartouches, ce qui rendit possible un massacre qui ne put prendre fin qu'après l'épuisement des munitions et la détérioration des armes à feu par manque d'entretien (JARVIS, 1931: 202). Au Sinaï comme dans le Désert Oriental, le bouquetin était tué pour sa viande (OSBORN & HELMY, 1980: 520), sa peau et ses cornes (HARPER, 1945: 621). Par ailleurs, les européens continuaient toujours de le tirer pour le sport (BAHARAV & MEIBOOM, 1981: 96) ou par désœuvrement (on le tirait à partir de bateaux mouillant sur le Nil), si bien qu'il devint très vite excessivement rare dans tous les districts faciles d'accès (FLOWER, 1932: 436).

Le bouquetin fut si exagérément chassé qu'il aurait faillit disparaître du Sinaï en 1924 si des mesures aussi draconiennes qu'efficaces n'avaient été prises par JARVIS (1935: 16), le gouverneur de la péninsule. Ce dernier interdit sa chasse durant cinq années d'affilée, plaça des gardes sur les six plus importantes chaînes de montagnes, prohiba la vente de sa viande et confisqua toutes les armes à feu et les munitions. Après quoi, l'interdiction de chasser le bouquetin fut étendue à toute l'Egypte par une décision du Département des Frontières datée du 6 mai 1930 (HARPER, 1945: 621). Bien que souffrant de nombreuses tentatives d'infraction, ces lois eurent le mérite de ralentir suffisamment l'hémorragie des populations de bouquetins qui s'était accélérée à l'issue du premier conflit armé mondial pour leur permettre d'inverser la tendance et de se reconstituer partout où cela était possible. Un effet inattendu de la passion cynégétique de l'homme fut la reconversion de la réserve de chasse de l'oued Rishrash. Créée en 1900 par le prince Kemal El Din, elle fut mutée en 1932 en un sanctuaire pour bouquetins (RUSSELL, 1949a: 8; 1949b: 118), sanctuaire qui permit le maintien d'un noyau de population stable dans le nord du Désert Oriental.

Les variations du climat n'eurent qu'une incidence secondaire sur le devenir de la faune sauvage. Il est vrai que lorsque RUSSELL (1949a: 6) mentionne l'apparition d'une série de cinq années sèches consécutives survenues au début du XX^{e} siècle dans le centre du Désert Oriental, il annonce ensuite la destruction résultante d'une grande partie du couvert végétal et l'importante diminution du gibier associé. Cependant, il ne fait pas de doutes qu'avec le retour des pluies ce dernier se reconstitue à l'identique si la pression de chasse n'existe pas.

La carte de la Fig. 3 montre une distribution globalement similaire à celle de la figure précédente. Seul le Sinaï présente d'importants changements car le bouquetin est cette fois-ci répertorié dans sa moitié nord alors qu'il ne l'est plus dans sa pointe sud. Ce vide soudain survenant dans le sud de la péninsule est dû à la rareté des témoignages et ne correspond absolument pas à la chute qu'eurent à subir les effectifs des populations de bouquetins durant le premier quart du XX^{e} siècle. Cette chute fut annulée par une remontée au cours du second quart de ce siècle, mais les fluctuations de distribution des populations n'ont pu transparaître sur la carte car celle-ci recouvre une trop longue période de temps (un demi siècle). Un plus grand nombre d'observations ont été réalisées le long du Nil et, pour le reste du Désert Oriental, une présence importante se révèle dans le nord et se confirme dans le centre. Bien que nous ne disposions que de très peu de témoignages concernant l'extrême sud de ce désert, l'existence de populations de bouquetins y est attestée (BALL, 1912: 24).

De 1950 à 2000

Les effectifs du bouquetin diminuèrent au Sinaï durant les années 1950 du fait, d'une part, d'une chasse incessante menée par les Bédouins (WASSIF & HOOGSTRAAL, 1953: 73), chasse d'autant plus efficace qu'elle s'effectuait à l'aide d'armes à feu modernes issues des stocks de la Deuxième Guerre mondiale (TALBOT, 1960: 267), et du fait, d'autre part, des conflits armées avec Israël, en particulier la Deuxième Guerre israélo-arabe de 1956 (COUTURIER, 1958: 17-18). Si bien qu'après la Troisième Guerre israélo-arabe (Guerre des Six Jours) et l'occupation de la péninsule par l'armée israélienne en 1967, l'espèce était au bord de l'extinction (BAHARAV & MEIBOOM, 1981: 96). Ce fut, selon ces derniers auteurs, l'application stricte de lois de protection de la nature édictées sur des bases scientifiques par les autorités israéliennes, qui sauvèrent le bouquetin. L'application de ces lois aurait porté ses fruits car à la fin des années 1970, ROTHENBERG (1979) constatait une remontée de ses effectifs dans le sud de la péninsule (p. 95) et relatait qu'autour du monastère de Sainte-Catherine les bouquetins acceptaient à la présence de l'homme et se laissaient approcher à quelques mètres seulement, preuve indirecte qu'ils n'étaient donc plus chassés (p. 192). Lorsqu'en 1982 l'Egypte recouvra sa souveraineté sur la totalité du Sinaï, les lois de protection furent cette fois-ci appliquées de façon efficace, et permirent au bouquetin d'être à nouveau commun dans les collines du nord et trouvé en grand nombre au centre et dans les hautes montagnes du sud (SALEH & BASUONY, 1998: 570).

A la chasse traditionnelle des Bédouins du Désert Oriental (HOBBS, 1989: 96) s'ajouta, peu après la Seconde Guerre mondiale, celles de riches particuliers poursuivant le bouquetin à l'aide de jeeps (TALBOT, 1960: 267). Mais les forces armées égyptiennes furent également responsables de la régression des populations de cet animal dans certaines parties de ce désert. En effet, les soldats patrouillant aux frontières après la Deuxième Guerre Mondiale, et qui avaient normalement pour mission de faire respecter les lois de conservation de la faune et de la flore, tiraient parfois les animaux sauvages qu'ils apercevaient (TALBOT, 1960: 266). Par ailleurs, les derniers conflits armés avec Israël dans le Sinaï, qui se sont étagés entre 1956 et 1973 et qui eurent pour théâtre d'opération le Sinaï, eurent un effet indirect sur les populations de bouquetins du nord du Désert Oriental en ce sens que les stations de gardes frontières venus renforcer les oueds Abu Sanduq et Qiseib, dans le nord du plateau de Galala, seraient cause de la disparition de leurs troupes de bouquetins indigènes (OSBORN & HELMY, 1980: 521). Le fait que la présence militaire soit beaucoup moins importante dans le centre du Désert Oriental et que les populations civiles soient animées du souci de protéger leur patrimoine naturel (HOBBS, 1989: 107 à 109) font que les effectifs du bouquetin ont pu jusqu'à présent s'y maintenir à un niveau satisfaisant.

La carte de la Fig. 4 montre une distribution dans la totalité du Sinaï et dans le centre du Désert Oriental. Elle met en évidence une forte régression dans le nord de ce désert (les deux chiffres figurant sur la carte correspondent aux années présumées de disparition de deux populations de bouquetins dans cette région), due à une présence militaire accrue. Elle met également en relief une quasi disparition le long du Nil, due sans doute à une plus grande fréquentation par l'homme des déserts bordant la Vallée. Le manque de données pour le Désert de Nubie ne permet pas d'évaluer l'évolution de l'aire de répartition de ses populations de bouquetins.

CONCLUSIONS

Les principaux ouvrages susceptibles d'apporter des informations sur la présence du bouquetin en Egypte depuis 1800 ont été consultés, mais il est très probable que d'autres, secondaires, existent sans que nous ayons pu en prendre connaissance. Par ailleurs, il est évident que toutes les populations égyptiennes de cet animal n'ont pu être observées. Par conséquent, les cartes montrant l'évolution de leur distribution ne donneront qu'une vision partielle de la réalité; il suffit, pour s'en convaincre, de considérer la quasi absence de points pour les montagnes de la Nubie égyptienne, alors que cette région constitue un écosystème convenant tout à fait à l'épanouissement d'importantes populations de bouquetins. De plus, ces cartes manquent de finesse dans le sens où elles recouvrent des périodes de temps trop longues (un siècle ou un demi-siècle) pour permettre de déceler l'évolution d'aires de répartition ne portant que sur quelques décennies. Ainsi, les points qui correspondent uniquement à une présence au début d'une période sont tout de même comptés comme portant sur toute la période. Les points flanqués des dates 1953 et 1958 sur la carte de la Fig. 4, dates présumées de la disparition du bouquetin dans les régions qu'ils désignent, illustrent tout à fait ce genre de problème. Enfin, il faut souligner que les points sur les cartes correspondent à des indications de présence et n'informent en rien sur les densités de populations.

Il a cependant été possible de déduire certaines informations de l'examen des cartes. Ainsi, nous pouvons constater qu'en dépit d'une désaffection récente le long de la rive est du Nil et dans le nord du Désert Oriental, d'importantes populations de bouquetins subsistent encore au centre de ce désert ainsi que dans la totalité du Sinaï. Cette évolution de la distribution des populations peut être mise en parallèle avec la fréquentation humaine, qui s'est récemment accrue dans les deux premières régions alors qu'elle restait stable ou très réglementée dans les deux dernières. En effet, depuis la disparition en Egypte durant la première moitié du XX^{e} siècle du léopard, principal prédateur naturel du bouquetin (MANLIUS, 1996: 115-116), le déclin de ce capriné dans le pays doit être entièrement imputable à l'homme (HOATH, 2000: 27). Cependant, il apparaît que des mesures de protection efficaces, telle celle appliquée au Sinaï au début du XX^{e} siècle, permettent un repeuplement somme toute rapide; ce qui va dans le sens des prédictions de TALBOT (1960: 269), qui pensait que si la protection du bouquetin était sérieusement entreprise ses effectifs augmenteraient de nouveau.

L'Egypte a clairement affiché sa volonté politique de préserver sa faune et sa flore en adhérant aux grandes organisations et conventions internationales pour la protection de l'environnement (ALESCO, CITES, IUCN, UNESCO, WHC). Il ressort des réflexions menées sur ce thème que la menace la plus invoquée pesant sur la faune mammalienne des pays arabes d'Afrique et du Proche-Orient est la destruction de son habitat (GHABBOUR, 1997: 143 à 150). Une plus grande information et une sensibilisation des populations humaines vivant loin des espaces naturels semblent constituer la parade la plus efficace à cette menace (GHABBOUR, 1997: 153). C'est dans les grandes villes, en effet, que les décideurs, des citadins éloignés des espaces sauvages, statuent sur le plan d'occupation des sols.

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BIBLIOGRAPHIE

ALLEN, G.M. (1915). Mammals obtained by the Phillips Palestine Expedition. *Bull. Mus. Comp. Zool.*, 59: 3-14.

ANDERSON, J. & W.E. DE WINTON (1902). *Zoology of Egypt. Vol. 2: Mammalia*. Rees, London (374 pp).

BAHARAV, D. & U. MEIBOOM (1981). The status of the Nubian ibex *Capra ibex nubiana* in the Sinai Desert. *Biol. Conserv.*, 20: 91-97.

Ball, J. (1912). *The geography and geology of South-Eastern Egypt*. Government Press, Cairo (394 pp).

Ball, J. (1916). *The geography and geology of West-Central Sinai.* Government Press, Cairo (219 pp).

Barron, T. (1907). *The topography and geology of the Peninsula of Sinai (western portion).* National Printing Department, Cairo (241 pp).

Barron, T. & W.F. Hume (1902). *The topography and geology of the Eastern Desert of Egypt (central portion)*. National Printing Department, Cairo (331 pp).

Bartlett, W.H. (1848). *Forty days in the desert, on the track of the Israelites. A journey from Cairo, by Wadi Feiran, to Mount Sinai and Petra*. Hall & Co, London (206 pp).

Beadnell, H.J.L. (1927). *The Wilderness of Sinaï. A record of two years' recent exploration.* Arnold & Co, London (180 pp).

Bodenheimer, F.S. (1958). The present taxonomic status of the terrestrial mammals of Palestine. *Bull. Res. Counc. Israel*, 7B : 165-190.

Boesnneck, J. & A. von den Driesch (1982). Studien an subfossilen Tierknochen aus Ägypten. *Münchner Ägyptologische Studien*, 40.

Bourgoin, P. & P. Dandelot (1955). *Animaux de chasse d'Afrique*. La Toison d'Or, Paris (255 pp).

Brehm, A.E. (1855). *Reiseskizzen aus Nord-Ost-Afrika oder den unter egyptischer Herrschaft stehenden Ländern Egypten, Nubien, Sennahr, Rosseeres und Kordofahn gesammelt auf seinen in den Jahren 1847 bis 1852 unternommenen Reisen. Vol. 3.* Mauke, Jena (358 pp).

Burckhardt, J.L. (1822a). *Travels in Nubia*. Murray, London (498 pp).

Burckhardt, J.L. (1822b). *Travels in Syria and the Holy Land*. Murray, London (668 pp).

Buxton, H.M.B., C.E.B. Buxton & T.B. Buxton (1895). *On Either Side of the Red Sea*. Stanford, London (163 pp).

Carruthers, D. (1915). The Near East. In : *The Big Game of Asia and North America.* Carruthers, D. et al. (Eds). The London and Counties Press Association, London : 9-35.

Clutton-Brock, J. (1987). *A natural history of domesticated animals*. Cambridge University Press, London (208 pp).

Colston, R.E. (1886). Journal d'un voyage du Caire à Kéneh, Bérénice et Berber, et retour par le désert de Korosko. *Bull. Soc. Khéd. Geogr.*, 9 : 489-568.

Couturier, M.A.J. (1958). Statut actuel des représentants de genre *Capra* dans le bassin méditerranéen. In : *Extrait des comptes rendus de la 7ème réunion technique de l'UICN.* UICN (Ed). Hayez, Bruxelles : 12-19.

Couturier, M.A.J. (1962). *Le Bouquetin des Alpes*. Chez l'auteur, Grenoble (1564 pp).

Cuvier, F. & E. Geoffroy Saint-Hilaire (1825). *Histoire Naturelle des Mammifères. Vol. 4. T. 6.* Berlin, Paris (non paginé).

Daumas, J. (1960). Le Gebel Qattar. *Bull. Soc. d'études historiques et géographiques de l'isthme de Suez*, 6 : 39-47.

De Beaux, O. (1956). Posizione sistematica degli stambecchi e capre selvatiche viventi (*Capra* Linneo 1758) e loro distribuzione geografica. *Atti Accad. ligure sci. lett.*, 12 : 123-228.

De Pardieu, C. (1851). *Excursion en Orient. L'Egypte, le Mont Sinaï, L'Arabie, La Palestine, La Syrie, le Liban.* Garnier Frères, Paris (400 pp).

Dollman, G. & J.B. Burlace (1935). *Rowland Ward's Records of Big Game. African and Asiatic Sections*. Rowland Ward Publication, London (408 pp).

Figari, A. (1864). *Studii scientifici sull'Egitto e sue adiacenze compressa la Penisola dell'Arabia Petrea. T. 1.* Giusti, Lucca (300 pp).

Fitzinger, L.J. (1855). Bericht an die kaiserlichen Akademie der Wissenschaften über die von dem Herrn Consulatsverweser Dr. Theodor v. Heuglin für die kaiserliche Menagerie zu Schönbrunn mitgebrachten lebenden Thiere. *Sitz.ber. Kais. Akad. Wiss. Wien, Math.-nat.wiss. Cl.*, 17 : 242-253.

Flower, S.S. (1932). Notes on the Recent Mammals of Egypt with a list of the species recorded from that Kingdom. *Proc. Zool. Soc. London*, 1 : 369-450.

Floyer, E.A. (1887). Notes on a sketch map of two routes in the Eastern Desert of Egypt. *Proc. Royal Geog. Soc.*, 9 : 659-681.

Floyer, E.A. (1893a). *Etude sur le Nord-Etbaï, entre le Nil et la mer Rouge.* Imprimerie Nationale, Le Caire (193 pp).

Floyer, E.A. (1893b). Further Routes in the Eastern Desert of Egypt. *Geogr. J.*, 1 : 408-431.

Fontaine, A.L. (1954). Exploration dans l'ouadi Arabah. Aïn Barda : ses vestiges d'habitats anciens. *Bull. Soc. d'études historiques et géographiques de l'isthme de Suez*, 5 : 59-88.

Gaillard, C. (1912). Les tâtonnements des égyptiens de l'Ancien Empire à la recherche des animaux à domestiquer. *Revue d'Ethnographie et de Sociologie*, 11-12 : 1-20.

Gautier, A. (1999). Fauna, domesticated. In : *Encyclopedia of the Archaeology of Ancient Egypt*. Bard, K.A. & S.B. Shubert (Eds). Routledge, London/New York : 300-306.

Ghabbour, S.I. (1997). Threats to Biodiversity in Arab Countries. In : *Reviews in Ecology : Desert Conservation and Development*. Barakat H.N. & A.K. Hegazy (Eds). Metropole Press, Cairo : 129-157.

Gonzales, A. (1977). *Voyage en Egypte du Père Antonius Gonzales. T. 1.* IFAO, Le Caire (392 pp).

Grout de Beaufort, F. (1988). *Ecologie historique du loup Canis lupus L. 1758 en France*. Thèse de doctorat. d'Etat, Université de Rennes I.

Haltenorth, T. & H. Diller (1985). *Mammifères d'Afrique et de Madagascar*. Delachaux et Niestlé, Neuchâtel (397 pp).

Harper, F. (1945). Extinct and Vanishing Mammals of the Old World. *American Comm. for Int. Wild Life Protection*, special publication 12 (850 pp).

Harrison, D.L. (1968). *The Mammals of Arabia. Vol. 2: Carnivora, Artiodactyla, Hyracoidea.* Benn, London (381 pp).

Hemprich, F.G. & C.G. Ehrenberg (1830). *Symbolae physicae seu icones et descriptiones mammalium quae ex itinere per Africam borealem et Asiam occidentalem.* Decas secunda. Berolini ex officina academia (non paginé).

Heuglin, T. von (1861a). Forschungen über die Fauna des Rothen Meeres und der Somali Küste. *Petermann's Mittheilungen der Geographie*, 7 : 11-32.

Heuglin, T. von (1861b). Einige Bemerkungen über die Wirbelthiere des nördlichen Ägyptens und des Peträischen

Arabiens. *Petermann's Mittheilungen der Geographie*, 7: 310-312.

HEUGLIN, T. von (1877). *Reise in Nordost-Afrika. Schilderungen aus dem Gebiete der Beni Amer und Habab, nebst zoologischen Skizzen und einem Fürher für Jagdreisende. T. 2.* Westermann, Braunschweig (304 pp).

HOATH, R. (2000). *Wild Sinai.* American University in Cairo Press, Cairo (52 pp).

HOBBS, J.J. (1989). *Bedouin Life in the Egyptian Wilderness.* University of Texas Press, Austin (165 pp).

HOOGSTRAAL, H. (1964). A brief review of the contemporary land mammals of Egypt (including Sinai). 3. Carnivora, Hyracoidea, Perissodactyla, and Artiodactyla. *J. Egypt. Publ. Health Assn.*, 39: 205-239.

HUME, W.F. (1906). *The topography and geology of the Peninsula of Sinai (south-eastern portion)*. National printing Department, Cairo (280 pp).

JARVIS, C.S. (1931). *Yesterday and to-day in Sinai*. Blackwood & Sons, Edinburgh/London (312 pp).

JARVIS, C.S. (1935). Sinai. *Journal Soc. Preserv. Fauna Emp.*, 25: 16.

KINZELBACH, R. (1991). Distribution of Selected Large Vertebrates and Their Decline in Historical Times. In: *Tübinger Atlas des Vorderen Orient.* TAVO (Ed). Reichert, Wiesbaden: A, VI, 13.

KLUNZINGER, C.B. (1878a). *Upper Egypt: its people and its products.* Scribner, Armstrong & Co, New York (408 pp).

KLUNZINGER, C.B. (1878b). Zur Wirbeltierfauna im und am Rothen Mer. *Zeitsch. Gesell. Erdkunde*, 13: 61-96.

KOCK, D. (1971). Zur Verbreitung von Mähnenschaf und Steinbock im Nilgebiet. Ein Beitrag zur Zoogeographie Nordost-Afrikas. *Säugetierkdl. Mitt.*, 19: 28-39.

LANGKAVEL, B. (1894). Kleinere Mitteilungen. *Capra beden* am Gebel Dukhan. *Der Zool. Garten*, 35: 155-156.

LOTTIN DE LAVAL, M. (1855-1859). *Voyage dans la péninsule Arabique du Sinaï et l'Egypte moyenne.* Gide & Co, Paris (355 pp).

LINANT DE BELLEFONDS, L.M.A. (1854). *L'Etbaye, pays habité par les Arabes Bicharieh. Géographie, ethnologie, mines d'or.* Bertrand, Paris (176 pp).

MAC ALISTER, D.A. (1900). The Emerald Mines of Northern Etbai. *Geogr. J.*, 16: 537-549.

MANLIUS, N. (1996). *Biogéographie et Ecologie historique de quelques grands mammifères terrestres et sauvages en Egypte, depuis le Pléistocène final jusqu'à nos jours*. Thèse de doctorat de troisième cycle en Zoologie-Ecologie historique du Muséum national d'histoire naturelle de Paris (364 pp).

MANLIUS, N. (1998). L'ours brun en Egypte. *Ecologie*, 29: 565-581.

MANLIUS, N. (2000a). Biogéographie et Ecologie historique de l'hippopotame en Egypte. *Belg. J. Zool.*, 130: 59-66.

MANLIUS, N. (2000b). Did the Arabian Oryx live in Egypt during pharaonic times? *Mammal Rev.*, 30: 65-72.

MANLIUS, N. (2000c). Historical ecology and biogeography of the Addax in Egypt. *Isr. J. Zool.*, 46: 261-271.

MANLIUS, N. & A. GAUTIER (1999). Le sanglier en Egypte. *C. R. Acad. Sci. Paris, Sér. III, Science de la vie/Life Science*, 322: 573-577.

MÜLLER, C. (1916). Am Sinai. *Deuts. Jagërzeitung*, 67: 533-536.

MURRAY, G.W. (1935). *Sons of Ishmael*. Routledge & Sons, London (344 pp).

MUZZOLINI, A. (1987). Les premiers moutons sahariens d'après les figurations rupestres. *ArchœoZoologia*, 1: 129-148.

NIETHAMMER, G. (1964). *Alexander Kœnig's Reisen am Nil.* Alexander Kœnig Stiftung, Bonn.

OSBORN, D.J. & I. HELMY (1980). The contemporary Land Mammals of Egypt (Including Sinai). *Fieldiana Zool.*, special number 5 (579 pp).

OSBORN, D.J. & J. OSBORNOVÁ (1998). *The Mammals of Ancient Egypt*. Aris & Phillips, Warminster (213 pp).

OUMANETZ, A. (1850). *Voyage au Sinaï avec l'adjonction de fragments sur l'Egypte et la Terre Sainte. Première partie.* Imprimerie du III^{ème} département de la chancellerie de S.M.I, Saint-Pétersbourg.

OUSPENSKY, P. (1856). *Premier voyage au monastère du Sinaï, en 1845, de l'Archimandrite Porphyre Ouspensky, Première partie*. Imprimerie de l'Académie impériale des Sciences, Saint-Pétersbourg.

OWEN, T.R.H. (1937). The Red Sea ibex. *Sudan notes record*, 20: 159-165.

PALMER, E.H. (1871). *The Desert of the Exodus: journeys on foot in the wilderness of the forty years' wanderings. Vol. 1.* Deighton, Bell & Co, Cambridge/Bell & Daldy, London (280 pp).

RALLI, A.M. (1954). La Chasse en Egypte. In: F. EDMOND-BLANC ed., *Le grand livre de la faune africaine et de sa chasse. T. 2: Chasse*. Union Européenne d'Editions, Monaco, Paris, Bruxelles, Genève, Zurich: p. 44-49.

RIEBECK, E. (1881). Tagebuch einer Reise von Kairo nach den Gebirgen am Rothen Meer. *Mitth. Vereins f. Erdkde*: 40-50.

ROTHENBERG, B. (1979). *Le Sinaï*. Kümmerly & Frey-Vilo, Paris (239 pp).

RÜPPELL, E. (1829). *Reisen in Nubien, Kordofan und dem peträischen Arabien.* Wilmans, Franckfurt am Main (388 pp).

RUSSELL, T. (1949a). Desert fauna. *Bull. Zool. Soc. Egypt*, 8: 5-8.

RUSSELL, T. (1949b). *Egyptian service, 1902-1946.* Murray, London (294 pp).

RUSSELL, T. (1951). The fauna of the Egyptian deserts. *Bull. Zool. Soc. Egypt*, 9: 19-21.

SADEK, H. (1926). *The Geography and Geology of the District between Gebel' Atâqa and El-Galâla El-Baharîya. (Gulf of Suez)*. Government Press, Cairo (120 pp).

SALEH, M.A. & M.I. BASUONY (1998). A contribution to the mammalogy of the Sinai Peninsula. *Mammalia*, 62: 557-575.

SCHOMBER, H.W. (1963). Wild life in the Sudan. Part IV. *Afr. Wildlife*, 17: 117-124.

SCHWEINFURTH, G. (1925). *Afrikanisches Skizzenbuch.* Deutsche Buch-Gemeinschaft, Berlin (312 pp).

TALBOT, L.M. (1960). A look at threatened species: a report on some animals of the middle east and southern Asia which are threatened with extermination. *Oryx*, 5: 153-293.

TCHERNOV, E. (1988). The biogeographical history of the southern Levant. In: *The zoogeography of Israel*. YOM-TOV, Y. &

E. Tchernov (Eds). Junk, Dordrecht/Boston/Lancaster: 159-250.

Thévenot, J. (1665). *Relation d'un voyage fait au Levant, dans laquelle il est curieusement traité, etc.* Jolly, Paris (576 pp).

Tregenza, L.A. (1955). *The Red Sea Mountains of Egypt*. Oxford University Press, London (247 pp).

Tregenza, L.A. (1958). *Egyptian Years.* Oxford University Press, London (198 pp).

Uerpmann, H.P. (1987). *The Ancient Distribution of Ungulate Mammals in the Middle East*. Reichert, Wiesbaden (173 pp).

U.S. Board on Geographic Names (1959). *Egypt, Official Standard Names*. Office of Geography of Department of the Interior, Washington (415 pp).

Volkoff, O.V. (1972). *Voyageurs russes en Egypte*. IFAO, Le Caire (387 pp).

Wassif, K. & H. Hoogstraal (1953). The Mammals of South Sinai. *Proc. Egypt. Acad. Sci.*, 9: 63-79.

Wilkinson, J.G. (1832). Notes on a part of the Eastern Desert of Upper Egypt. *J. R. Geogr. Soc.*, 2: 28-60.

Wilkinson, J.G. (1835). *Topography of Thebes, and general view of Egypt.* Murray, London (595 pp).

Wylde, A.B. (1888). *'83 to '87 in the Soudan*. "2", London.

Yalden, D.W., M.J. Largen & D. Kock (1984). Catalogue of the Mammals of Ethiopia. Vol. 5: Artiodactyla. *Monitore zool. Ital.*, 4: 67-221.

ANNEXE

Gazette des localités égyptiennes mentionnées

Les coordonnées ont été obtenues à l'aide de l'U.S. Board on Geographic Names (1959). Quelques unes, non trouvées ou mal indiquées dans cet ouvrage, ont due être calculées. Les noms des grandes villes sont écrits en français. Mais il n'a pas été possible de trouver une traduction dans cette langue des noms de toutes les petites villes ou agglomérations, des djébels, des oueds, des puits (birs) ou des lieux-dits; par conséquent, les noms de ces derniers seront écrits en anglais. Dans le cas des oueds particulièrement longs, les coordonnées ponctuelles désignent soit une de leur extrémité, soit leur centre.

Localité	Province	Lat. N	Long. E
Abu Darag (Daraj)	SUEZ	29 29	32 27
Abu Galum	SINAI	28 38	34 35
Abu Sha'r	BAHR EL AHMAR	27 22	33 45
Ain Barda	BAHR EL AHMAR	29 06	32 04
Ain El Furtaga (Ayn Al Furtajah)	SINAI	29 03	34 33
Assiout	ASSIOUT	27 11	31 11
Assouan	ASSOUAN	24 05	32 53
Ayun Musa (Uyun Musa)	SINAI	29 52	32 39
Baie de Sharm El-Sheikh (Ash Shaykh)	SINAI	27 51	34 17
Bérénice (Mina'Baranis)	BAHR EL AHMAR	23 55	35 28
Bir El Giddi (Al Jidy)	SINAI	30 13	33 03
Bir Hedeba	BAHR EL AHMAR	Près du djébel Umm Disi	
Bir Hindusi	BAHR EL AHMAR	25 49	34 11
Bir Mellaha (Milahah)	BAHR EL AHMAR	27 34	33 27
Bir Muwayh (Al Muwayh)	BAHR EL AHMAR	26 03	33 26
Bir Nukhul (Nakhl)	SINAI	29 03	33 15
Bir Qattar	BAHR EL AHMAR	27 05	33 17
Bir Qiseib (Qusayb)	BAHR EL AHMAR	29 24	32 29
Bir Sheitun (Shaytun)	BAHR EL AHMAR	26 48	32 07
Bir Umm Hibal	ASSOUAN	23 42	33 14
Bir Umm Laseifa (Abu Lusayfah)	BAHR EL AHMAR	26 54	32 27
(Le) Caire	LE CAIRE	30 03	31 15
Col de Mitla	SINAI	30 02	32 58
Dahab (Dhahab)	SINAI	28 29	34 32
Dayr Al Qiddis Bulus	BAHR EL AHMAR	28 51	32 33
Djébel Abu Abid	BAHR EL AHMAR	26 58	33 27
Djébel Abu Dukhan	BAHR EL AHMAR	27 13	33 16
Djébel Abu Harba (Abu Harbah)	BAHR EL AHMAR	27 17	33 13
Djébel Abu Tiyur (Abu Tuyur)	BAHR EL AHMAR	25 43	34 16
Djébel Achmar	SINAI	28 32	33 58
Djébel Akheider (Ukhaydir)	BAHR EL AHMAR	29 44	32 11
Djébel Araba (Arabah)	SINAI	28 23	33 26
Djébel Ataqa (Ataqah)	SUEZ	29 55	32 20
Djébel Baab	SINAI	28 34	33 56
Djébel Baba	SINAI	29 16	33 43
Djébel Banat	SINAI	28 45	33 38
Djébel Barud	BAHR EL AHMAR	26 47	33 39
Djébel Dara (Darah)	BAHR EL AHMAR	27 54	33 00
Djébel Dhibaah (Dibbah, Dabbagh)	BAHR EL AHMAR	Près de l'oued Dhibaah	
Djébel Elba	BAHR EL AHMAR	22 11	36 21
Djébel El Gidami (Al Jidami)	BAHR EL AHMAR	26 25	33 24
Djébel El-Hamra	SINAI	28 35	34 30
Djébel El-Igma (Al Ajmah)	SINAI	29 12	34 02
Djébel El Kutamiya (Al Kutamiyah)	SUEZ	29 56	31 49

Localité	Province	Lat. N	Long. E
Djébel El Rabba (Ar Rabbah)	SINAI	30 01	33 11
Djébel El Raha (Ar Rahah)	SINAI	29 53	32 57
Djébel El-Sha’ira (Ash Sha’irah)	SINAI	29 31	34 29
Djébel El-Siba’i	BAHR EL AHMAR	25 43	34 09
Djébel El Tih	SINAI	29 30	34 00
Djébel Freha	SINAI	28 35	33 58
Djébel Genaui	SINAI	28 20	34 08
Djébel Gharib	BAHR EL AHMAR	28 07	32 54
Djébel Gunna (Junnah)	SINAI	28 52	34 15
Djébel Halal (Hilal)	SINAI	30 37	34 01
Djébel Hamata (Hamatah)	BAHR EL AHMAR	24 12	35 00
Djébel Horeb	*voir djébel Musa*		
Djébel Kahaliya (Kahaliyah)	BAHR EL AHMAR	29 56	32 10
Djébel Katharina (Katrinah)	SINAI	28 31	33 57
Djébel Maghara (Magharah)	SINAI	30 42	33 23
Djébel Mikeimin (Mukaymin)	SINAI	29 02	34 31
Djébel Mi’tiq (Mu’tiq)	BAHR EL AHMAR	26 07	33 44
Djébel Musa	SINAI	28 32	33 59
Djébel Qattar	BAHR EL AHMAR	27 05	33 22
Djébel Ri’El-Garra (Ri’Al Jarrah)	BAHR EL AHMAR	26 26	33 27
Djébel Sabbagh	SINAI	28 12	34 04
Djébel Serbal (Sirbal)	SINAI	28 39	33 39
Djébel Shayib (Sha’ib Al Banat)	BAHR EL AHMAR	26 59	33 29
Djébel Sheikh El Arab (Shaykh Al Arab)	SINAI	28 24	34 02
Djébel Sumar	SINAI	29 39	33 10
Djébel Tarbush	SINAI	28 36	33 50
Djébel Thebt (Thabt)	SINAI	28 16	34 01
Djébel Umm Afruth	SINAI	29 10	34 15
Djébel Umm Disi	BAHR EL AHMAR	27 02	33 15
Djébel Umm Gidri (Umm Jubari)	BAHR EL AHMAR	26 58	33 36
Djébel Umm Shomar (Umm Shawmar)	SINAI	28 22	33 55
Djébel Umm Tinassib	BAHR EL AHMAR	28 30	32 34
Djébel Uweinat (Al Uwaynat)	OUADI EL GEDID	21 54	24 58
Djébel Yelleg (Yi’Allaq, Yu’Alliq)	SINAI	30 22	33 31
Djébel Zabara (Zabarah)	BAHR EL AHMAR	24 45	34 42

Localité	Province	Lat. N	Long. E
Eilat	*ETAT D’ISRAËL*	29 34	34 57
El-Diwan (Ad Diwan)	ASSOUAN	22 44	32 12
El Gharandal	SINAI	29 15	32 55
El Heita (Al Haytah)	BAHR EL AHMAR	26 37	32 46
El-Saff	GIZEH	29 34	31 17
Farchout	KENA	26 03	32 09
Girga (Jirja)	SOHAG	26 20	31 53
Ile d’Eléphantine	ASSOUAN	24 05	32 53
Kena	KENA	26 10	32 43
Korosko	ASSOUAN	22 36	32 20
Kosseir	BAHR EL AHMAR	26 06	34 17
Kous	KENA	25 55	32 45
Louksor	KENA	25 41	32 39
Monastère de Sainte-Catherine	SINAI	28 31	33 57
Monastère de Saint-Paul	*voir Dayr Al Qiddis Bulus*		
Mont Claudianus	BAHR EL AHMAR	26 48	33 29
Mont Sainte-Catherine	*voir djébel Katharina*		
Mont Sinaï	*voir djébel Musa*		
Myos Hormos	*voir Abu Sha’r*		
Nabq (Nebk)	SINAI	28 04	34 25
Nagi Hamada (Naj’ Hammadi)	KENA	26 09	32 10
Nuweiba (Nuwaybi)	SINAI	28 58	34 39
Ouadi Halfa	*SOUDAN*	21 56	31 20
Oued Aad	SINAI	27 59	34 12
Oued Abu Duq	BAHR EL AHMAR	26 45	33 22
Oued Abu Erin	BAHR EL AHMAR	Près du djébel Shayib	
Oued Abu Ma’amel	BAHR EL AHMAR	27 14	33 17
Oued Abu Sanduq (Abu Sunduq)	BAHR EL AHMAR	29 25	32 31
Oued Abu Shehat (Shihat)	BAHR EL AHMAR	26 33	33 04
Oued Akhdar (El Akhdar)	SINAI	28 42	33 41
Oued Aleyat	SINAI	28 41	33 41
Oued Atalla (Ata Allah)	BAHR EL AHMAR	26 03	33 36
Oued Daffeti	BAHR EL AHMAR	22 13	34 11
Oued Dhibaah (Dibbah, Dabbagh)	BAHR EL AHMAR	25 53	34 14
Oued El Abeid	BAHR EL AHMAR	28 44	32 05
Oued El Abyad	BAHR EL AHMAR	29 38	32 13
Oued El Asyuti	BAHR EL AHMAR	27 10	31 16
Oued El Atrash	BAHR EL AHMAR	26 39	32 46
Oued El Ghalib	SINAI	28 34	34 28
Oued El Ghuzz	BAHR EL AHMAR	26 52	33 08
Oued El Merkh (Al Markh)	BAHR EL AHMAR	26 21	33 03
Oued El Rharakit (El Rharageh)	SINAI	28 53	33 24
Oued Ethmiemat	SINAI	28 25	34 24
Oued Feiran (Firan, Fayran)	SINAI	28 40	33 25

Localité	Province	Lat. N	Long. E
Oued Geba (Jeeba)	SINAI	28 36	33 36
Oued Ghilm (Ghalim)	SINAI	29 00	34 22
Oued Ghuweibba (Ghuwaybah)	BAHR EL AHMAR	29 36	32 20
Oued Habib (Habeibat, Hubaybat)	BAHR EL AHMAR	27 20	31 30
Oued Hebran (Hebron, Hibron)	SINAI	28 31	33 42
Oued Hommath (Hammad)	BAHR EL AHMAR	29 45	32 24
Oued Islah	SINAI	28 08	33 43
Oued Kid	SINAI	28 07	34 25
Oued Lehama (Lehema, Lahmi)	BAHR EL AHMAR	24 13	35 25
Oued Mahr (Mir)	SINAI	28 28	33 45
Oued Mellaha (Milahah)	BAHR EL AHMAR	27 34	33 33
Oued Mitgal	BAHR EL AHMAR	26 48	33 27
Oued Moladge (Malhaq)	SINAI	28 10	34 19
Oued Nagat (Naggaat)	BAHR EL AHMAR	27 04	33 18
Oued Nasb	SINAI	28 35	34 28
Oued No'oz (Nu'z)	BAHR EL AHMAR	29 35	32 14
Oued Nugrus (Nuqrus)	BAHR EL AHMAR	24 35	34 49
Oued Qasab	BAHR EL AHMAR	26 19	32 02
Oued Qattar	BAHR EL AHMAR	27 05	33 17
Oued Qena (Qina)	KENA	26 12	32 44
Oued Qiseib (Qusayb)	BAHR EL AHMAR	29 26	32 30
Oued Rawd'Aid	BAHR EL AHMAR	25 54	33 10
Oued Rishrash	BAHR EL AHMAR	29 29	31 16
Oued Rwashid	BAHR EL AHMAR	26 58	33 23
Oued Saal (Sa'l)	SINAI	28 46	34 21
Oued Satakh	SINAI	Près de l'oued Akhdar	

Localité	Province	Lat. N	Long. E
Oued Semna	BAHR EL AHMAR	26 27	33 27
Oued Sheitun (Shaytun)	BAHR EL AHMAR	26 34	32 12
Oued Shellal	SINAI	28 56	33 18
Oued Showak	BAHR EL AHMAR	27 01	33 26
Oued Sikait (Sukayt)	BAHR EL AHMAR	24 40	34 48
Oued Sulaf	SINAI	28 42	33 41
Oued Umm Adawi	SINAI	28 04	34 26
Oued Umm Balad	BAHR EL AHMAR	27 09	33 18
Oued Umm Diqal	BAHR EL AHMAR	Près du Mont Claudianus	
Oued Umm Hadd	BAHR EL AHMAR	26 13	33 23
Oued Umm Musma	SINAI	~ 28 40	~ 34 18
Oued Umm Sidri (Umm Sidr)	BAHR EL AHMAR	27 17	33 20
Oued Umm Shoka	SINAI	28 32	34 27
Oued Umm Ruutha	BAHR EL AHMAR	32 20	28 47
Oued Watir	SINAI	29 01	34 40
Oued Zalaqah	SINAI	29 00	34 18
Plateau de Zebir (Zabir)	SINAI	28 47	33 40
Plateau El-Igma	*voir djébel El-Igma*		
Plateau El Tih	*voir djébel El Tih*		
Ras El Naqb	SINAI	29 36	34 51
Ras Muhammed (Muhammad)	SINAI	27 44	34 15
Shushet El Maghara (Al Magharah)	SINAI	30 38	33 23
Sources de Moïse	*voir Ayun Musa*		
Suez	SUEZ	29 58	32 33
Tellat Gimal	SINAI	28 20	34 03
Thèbes	KENA	25 43	32 39
Tor (At Tur)	SINAI	28 14	33 37
Umm Bigma (Umm Bugma)	SINAI	28 59	33 21

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Limb joint kinematics during vertical climbing and level running in a specialist climber: *Gekko gecko* Linneus, 1758 (Lacertilia: Gekkonidae)

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ABSTRACT. Previous studies revealed that, despite clear morphological adaptations for climbing, performance and gait characteristics are barely affected when the specialist climbing lizard *Gekko gecko* is forced to run on its non-preferred level substrate. The present study focuses on the detailed joint kinematics of front and hind limbs to investigate whether this lizard modulates its limb movements while running on its non-preferred substrate. The intra-limb (fore and hind limbs) kinematic patterns were determined at three different speeds in *G. gecko* when climbing and running horizontally. Additionally, three-dimensional angles were determined at lift-off and at touch-down for both the fore and hind limbs over a wide range of running and climbing speeds. Generally, the intra-limb movement patterns used during level running are similar to those used when climbing. Moreover, the joint angles at lift-off and touch-down also show a high similarity for climbing and level running. There are some differences in joint angles: during climbing the shoulder and the elbow tend to be more extended at lift-off and touch-down compared to level running, and when the hind foot touches the substrate both the hip and the knee show a greater extension on level surface whereas the ankle is more extended during climbing. These differences can be grouped into two categories: the differences in the hip, ankle and wrist are likely to be related to the observed change in the posture and gait between climbing and level running. The changes in the shoulder, the elbow and the knee angles when *G. gecko* runs over-ground are likely to be the result of differences in the biomechanical constraints encountered during climbing and level-running.

KEY WORDS: *Gekko gecko*, kinematics, locomotion, climbing, level running

INTRODUCTION

In nature, lizards have to perform in a complex, three-dimensional environment. From field observations, some species appear to be restricted to horizontal surfaces or to substrates with a relatively low degree of inclination (e.g. ground dwelling geckoes such as *Eublepharis macularius*), whereas others can move seemingly effortlessly on even very steep inclines (AUTUMN et al., 2000). Given that the mechanical demands for climbing differ largely from those for level running (part of the climbing effort is used to counter the altered effects of gravity; e.g. ZAAF et al., 1999), adaptations or specialisations that allow maximal performance on inclined substrates are expected (BAUER et al., 1996; ZAAF et al., 1999). Results of some experimental studies, in which typically ground dwelling species are induced to run up-hill, indicate that running on an incline does confront these animals with serious physical constraints. Not only are the metabolic costs considerably higher (e.g. FARLEY & EMSHWILLER, 1996), also the running performance decreases with incline (e.g. FARLEY, 1997; VAN DAMME et al., 1997; IRSCHICK & JAYNE, 1998; JAYNE & ELLIS, 1998; JAYNE & IRSCHICK, 1999; VANHOOYDONCK et al., 2000).

It is often assumed that specialisation for extreme habitat types (e.g. vertical walls) constrains performance in other habitats due to the conflicting demands imposed on the system (LEVINS, 1968). Yet HUEY & HERTZ (1982), could not detect significant negative effects of incline on performance in small ground dwelling agamid lizards. Similarly, in the specialised climbing lizard *Gekko gecko*, no effect of incline on performance was observed (ZAAF, 2000). Whereas one might argue that the case of the agamid lizard is just an example of the 'jack of all trades is the master of none' paradigm (LEVINS, 1968; HUEY & HERTZ, 1984), in the case of highly specialised climbers

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such as *G. gecko* this is definitely not true. Apart from the premised features obviously favouring climbing (such as adhesive toe pads, short legs, flattened body shape and posture, appropriate gait, Pianka & Pianka, 1976; Jaksic et al., 1980; Cartmill, 1985; Pounds, 1988; Sinervo & Losos, 1991; Garland & Losos, 1994; Miles, 1994; Zaaf et al., 2001), Zaaf et al. (1999) even found subtle functional shifts in the musculature, which could be related to the preferred substrate orientation. Yet, despite these morphological differences, neither the performance nor the gait seem to change markedly when this species is forced to run on its non-preferred (horizontal) substrate (Zaaf, 2000; Zaaf et al., 2001).

These rather unexpected results for *G. gecko* might be explained in two ways. Firstly, adaptations needed to climb vertical structures might not detrimentally affect performance on the horizontal. In this way, high climbing performance does not impede good performance on a level surface (see also Vanhooydonck & Van Damme, 2001). Secondly, specimens might compensate or accommodate behaviourally for reduced running performance as a result of their adaptations for climbing. In the latter case altered locomotor behaviour should likely be reflected in the spatio-temporal aspects of gait (stride frequencies and lengths, step lengths, duty factors, floating phases). However, as mentioned above, these variables in their relation with speed are largely unaffected by changes in substrate inclination. Despite this, the intra-leg movements used to produce the unchanged foot fall pattern might still differ between substrates (i.e. alternative combinations of joint rotations for similar linear leg displacements), thus reflecting behavioural accommodation.

Moreover, such changes of the intra-leg kinematics, if present, can be expected to be different for the fore and hind limbs. During vertical climbing, tension from the fore limbs is needed to avoid backward tumbling, thus assisting the hind limbs in generating propulsion. During level locomotion of many species, however, the hind limbs are considered as the predominant propulsive element (Snyder, 1952; Reilly & Delancey, 1997a,b). At high speeds, the fore limbs often do not contribute to locomotion at all (Snyder, 1952, 1962; Irschick & Jayne, 1999). If this functional shift occurs in *G. gecko*, the fore limb kinematics are likely to change with substrate orientation in a manner differing from that of the hind limbs.

In this paper we investigate whether, and if so how, accommodation of the locomotor behaviour occurs when *G. gecko* is forced to run on its non-preferred (horizontal) substrate orientation. Therefore, we quantify and compare the three-dimensional joint angles at touch-down and lift-off over a range of speeds. Moreover, the patterns of these angles are compared at three different speeds for running and climbing. Given the potential shift in limb pair function and dominance, this is done for fore and hind limb separately.

MATERIAL AND METHODS

Three specimens of *Gekko gecko* were used in this study. All individuals had similar snout-vent lengths (Table 1). The animals were obtained from a commercial dealer and housed in separate terraria (60 x 100 x 40 cm) on a 12:12h light dark cycle. Ambient temperature varied from 26°C during daytime to 20°C at night. A heating lamp provided a basking place at a higher temperature (40°C). The animals were provided with food (crickets, mealworms, and grasshoppers) and water ad libitum.

TABLE 1

Morphometrical characterisation of the three *Gekko gecko* specimens used in this study.

	snout-vent length (cm)	**mass (g)**	**fore limb length (cm)**	**hind limb length (cm)**
specimen 1	13.03	57.92	2.97	3.91
specimen 2	13.29	61.78	3.45	4.52
specimen 3	12.36	40.01	3.30	3.90
mean ± S.D.	12.89 ± 0.48	53.24 ± 11.62	3.24 ± 0.25	4.11 ± 0.36

For the experiments, a track was constructed consisting of two removable wooden boxes at each end of a glass-tunnel (140 x 20 x 15 cm) fixed on a wooden support. The tunnel was large enough to permit free limb and body movements and its floor was covered with a cork-film. To study climbing, the tunnel was placed vertically. The animals were put in the box at the bottom of the tunnel and induced to run through it towards the other box fixed at the top. When the animal entered the top box, boxes were switched and the procedure was repeated.

Animals were marked by white non-toxic paint dots on the tip of the snout, the centre of the pectoral and pelvic girdles, mid-hand and mid-foot, and on all the joints of fore and hind limbs (Fig. 1). In *G. gecko*, the mid-hand and mid-foot are the first limb segments that hit the substrate and the last that leave it (respectively before and after the digits touch and leave the substrate, see Russell, 1975). Therefore, we decided to put markers at the level of the metatarsal and metacarpal bones.

Running and climbing sequences were recorded from above with a NAC-1000 high-speed video system set at 500 frames. A mirror fixed on a wooden support immediately lateral to the glass-tunnel at an angle of 45° provided a simultaneous lateral view. Animals were given at least 15 minutes of rest between successive trials. Only sequences where the animals ran straight and continu-

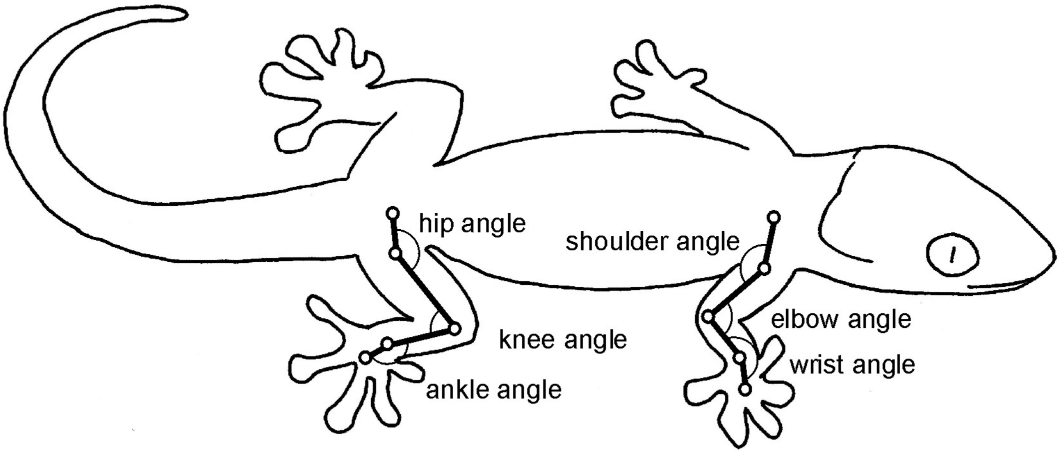

Fig 1. – Landmarks (white dots) and segments (bars) used to calculate the three-dimensional angles in *Gekko gecko*. The angles used in the analysis are indicated**.**

ously were retained for further analysis. From the positions of the marker on the snout tip, early and late in these sequences, an estimate of running speed was obtained. Based on these estimates, nine climbing sequences were selected for specimens 1 and 2 (Table 1) representing a velocity range as wide as possible. Inducing horizontal running was more difficult in these two specimens. Animals preferred to run on the side-walls of the corridor or simply sat on the side-walls enclosing the tunnel. We obtained only 5 and 2 running bouts respectively. Eight additional running bouts were added from the third specimen (Table 1).

We calculated the angles (3D) between the limb segments (based on the digitised 3D-coordinates of the markers) as indicated on Fig. 1 at the time when the feet touched and left the substrate as this corresponds to the extreme leg configurations. The relationship with forward speed (obtained from the linear regression of the pelvic marker) was established by means of least squares linear regression analysis. T-tests were performed to explore the difference between the joint angles at lift-off and touch-down (and at mid-stance and mid-swing for knee and elbow) and to compare the shoulder, the elbow and the wrist with the hip, the knee and the ankle respectively. A t–test was also performed to see if joint angles are affected by substrate inclination. If the angles were speed dependant, analysis of covariance (ANCOVA, velocity as covariate) was used.

Three climbing and level running sequences of specimen 1 were selected, which covered a speed range (from about 0.60 to 0.90 m/s). Within 1 cm/s the climbing speed was identical to the level running speed. The markers were digitised frame by frame and the 3D-joint angles were calculated as mentioned above. Profiles were smoothed with a zero-phase shift digital low-pass filter (WINTER, 1990; cut-off frequency = 25 Hz). The shoulder, the elbow and the wrist angles were plotted against the relative fore limb cycle (%FF; see Figs 2,3). Similarly, the hip, the knee and the ankle angle were plotted against the relative hind limb cycle (%HF; see Figs 2,3). Zero % corresponds to the time that the fore limb touches the substrate.

RESULTS

General kinematic pattern

Fig. 2 illustrates how the three-dimensional angles within the fore limbs and the hinds limbs vary during their respective stride cycle at three different climbing speeds. The angular patterns for comparable level running speeds by the same individual are represented in Fig. 3.

As soon as the fore foot hits the substrate (0% of the cycle), the extended elbow (± 150°) flexes 40° to 50°. This maximal elbow flexion is reached at all speeds at about 35% of the fore limb cycle. Thereafter, the elbow extends again for the remainder of the stance phase. At lift-off the elbow starts to flex until about – 30% of the fore limb cycle. The amount of flexion during the swing phase is, however, considerably smaller than that observed during stance. This difference appears to become larger with increasing speed. The elbow thus shows a double flexion-extension cycle coinciding with stance and swing. During level running, the elbow shows the same double flexion-extension cycle (with the larger amplitude during stance) as observed for climbing.

At touch-down, the already extended shoulder (± 150°) continues to extend for about 10° during the initial part of stance (± 10% of the limb cycle). Then a sharp flexion of about 60° occurs (retraction of the fore limb), after which the shoulder flexes briefly further (especially at the lowest climbing speed). In the first part of the stance phase fast extension of the shoulder (protraction of the fore limb) takes place. The shoulder thus goes through one simple flexion-extension cycle, which is slightly out of phase with the transitions between stance and swing. At higher running speeds, the pattern of the shoulder angle during level running is very similar to that observed during climbing. At the lowest speed, a flexion-extension cycle is also present, but is somewhat more irregular.

For the wrist angle, no obvious patterns can be discerned. The wrist angle appears to change irregularly with

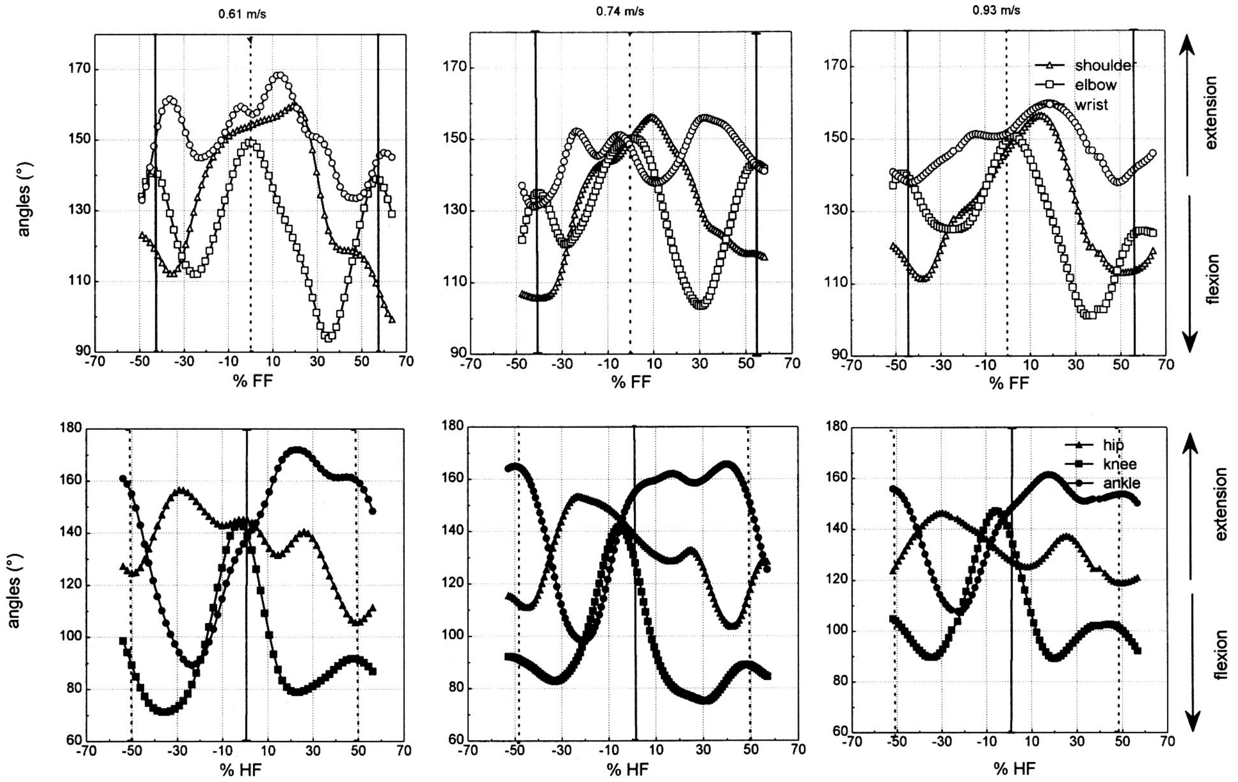

Fig 2. – Three-dimensional angles adjusted to the limb cycle (right body side) of G*ekko gecko* climbing at three speeds (0.61, 0.74 and 0.93 m/s). Shoulder, elbow and wrist are plotted against the fore limb cycle; hip, knee and ankle are plotted against the hind limb cycle. Zero % corresponds to the time when the fore foot hits the substrate. The vertical dashed lines on each plot indicate the time when the foot hits the substrate. The solid lines represent lift-off.

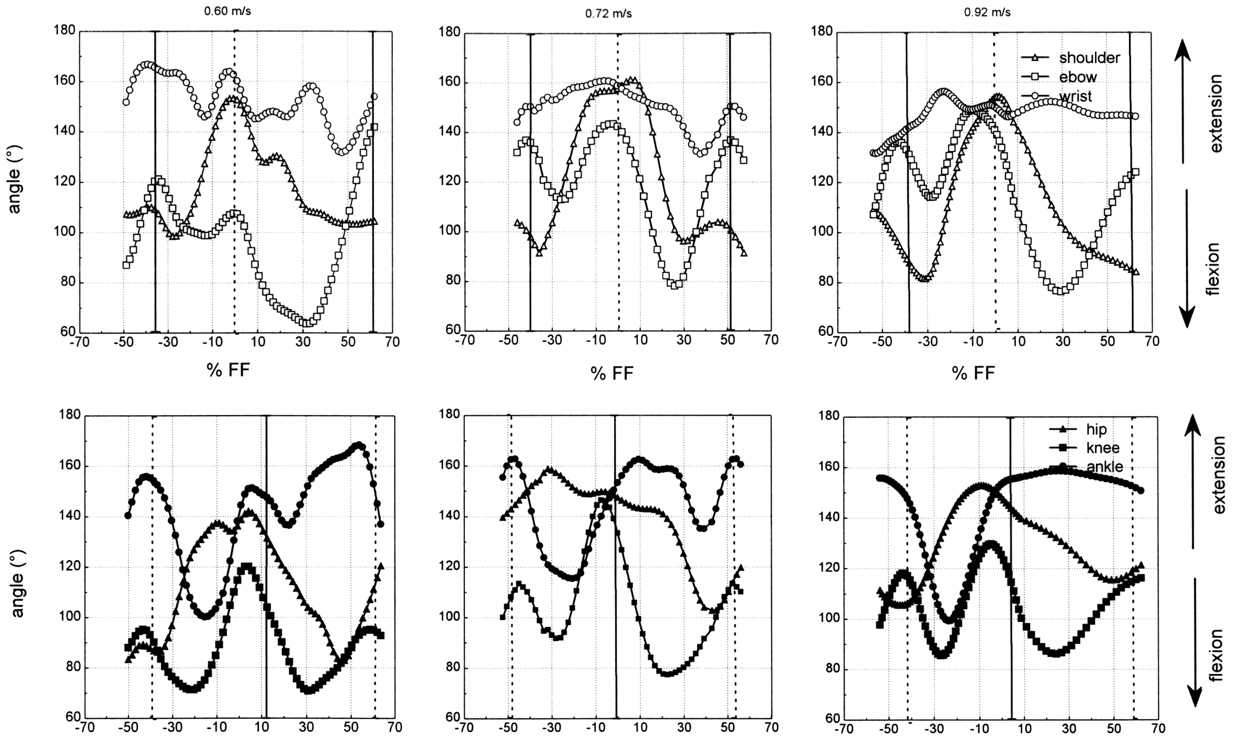

Fig 3. – Three-dimensional angles adjusted to the limb cycle (right body side) of G*ekko gecko* level running at three speeds (0.60, 0.73 and 0.92 m/s). Shoulder, elbow and wrist are plotted against the fore limb cycle; hip, knee and ankle are plotted against the hind limb cycle. 0 % corresponds to the time when the fore foot hits the substrate. The vertical dashed lines on each plot indicate the time when the foot hits the substrate. The solid lines represent lift-off.

speed. At the lowest speed, the wrist angle pattern approximates a double flexion-extension cycle. At the highest speed this pattern reduces to a single flexion-extension cycle. Wrist angle patterns during level running are rather variable as observed during climbing.

When the hind foot touches the substrate, the knee flexes, starting from an angle of about 90°, for only about 10° to 20° during the first 15% of the limb cycle. Thereafter, it extends 60° to 70° for almost the entire stance phase. A small flexion (about 10°) occurs just prior to lift-off. It proceeds in a very rapid flexion of the knee (about 50°) during the first part of the swing phase. Then the knee extends again (about 10°) towards the end of the swing phase. Thus, the knee goes through a double flexion-extension cycle coinciding with stance and swing respectively. In this case, however, both flexion-extension cycles are extremely asymmetric, with the stance phase being characterized by extension and the swing phase by flexion. The pattern of the knee during level running is generally similar to the pattern observed during climbing, although the extension towards the end of stance appears to be somewhat smaller during level running.

During about the first third of stance the hip extends rapidly 30° to 40° starting from an angle of about 120°. During stance, the hip starts to flex, slowly, and continues into the swing phase. About half way through the swing phase a brief period of extension, coinciding with the transition from flexion to extension in the knee, occurs. Overall, the angular rotation in the hip remains small (amplitude about 30° to 40°) and is characterized by a strong temporal asymmetry. The angular rotations in the hip for level running *G. gecko* are somewhat larger than those for climbing animals (about 40° to 50°). The marked brief extension during swing observed in climbing is absent during level running.

Contrary to the wrist, ankle patterns appear more stable during climbing. Over the first half of the stance phase, the ankle flexes from about 160° to about 70°. Next, during the stance phase the ankle extends to about 145° after which the ankle angle remains constant until the next touch-down. The ankle thus shows a single, but temporally strongly asymmetric, flexion-extension cycle. Except at the lowest speed, the ankle pattern for level running is highly similar to that observed during climbing.

Effect of speed

Table 2 summarises the effect of speed on the joint angles at lift-off and touch-down as well as at the time when the foot leaves and hits the substrate (expressed as %

TABLE 2

Relationships between angular variables (at lift-off and touch-down) and velocity for *Gekko gecko* moving on horizontal and vertical substrates. Intercepts and slopes (± se) of least squares regressions (angles = b +a ∗ velocity) are given for those relations that had significant r^2-values. Velocity is expressed in ms^{-1}, angles in degrees.

	level running (N = 18)			**climbing (N = 15)**		
	r^2	**slope ± se**	**intercept ± se**	**r^2**	**slope ± se**	**intercept ± se**
fore foot						
lift-off						
%FF	0.0369	-	-	0.020	-	-
shoulder	0.001	-	-	0.011	-	-
elbow	0.237	-	-	0.001	-	
wrist	0.006	-	-	0.072	-	-
touch-down						
%FF	NT	-	-	NT	-	-
shoulder	0.00002	-	-	0.124	-	-
elbow	0.138	-	-	0.003	-	-
wrist	0.164	-	-	0.0007	-	-
hind foot						
lift-off						
% HF	0.09	-	-	0.061	-	-
hip	0.0004	-	-	0.027	-	-
knee	0.0157	-	-	0.441**	27.76±0.187	72.73±7.23
ankle	0.063	-	-	0.001	-	-
touch-down						
% HF	0.162	-	-	0.072	-	-
hip	0.615***	49.14±10.781	73.18±12.273	0.019	-	-
knee	0.097	-	-	0.079	-	-
ankle	0.513**	-31.39±8.47	173.62±9.648	0.074	-	-

significant at P = 0.01.; * significant at P = 0.001. %FF, timing of touch-down/lift-off expressed as a proportion of the front foot cycle; %HF, timing of touch-down/lift-off expressed as a proportion of the hind foot cycle; NT, not testable as fore foot touch-down was considered as time zero by definition.

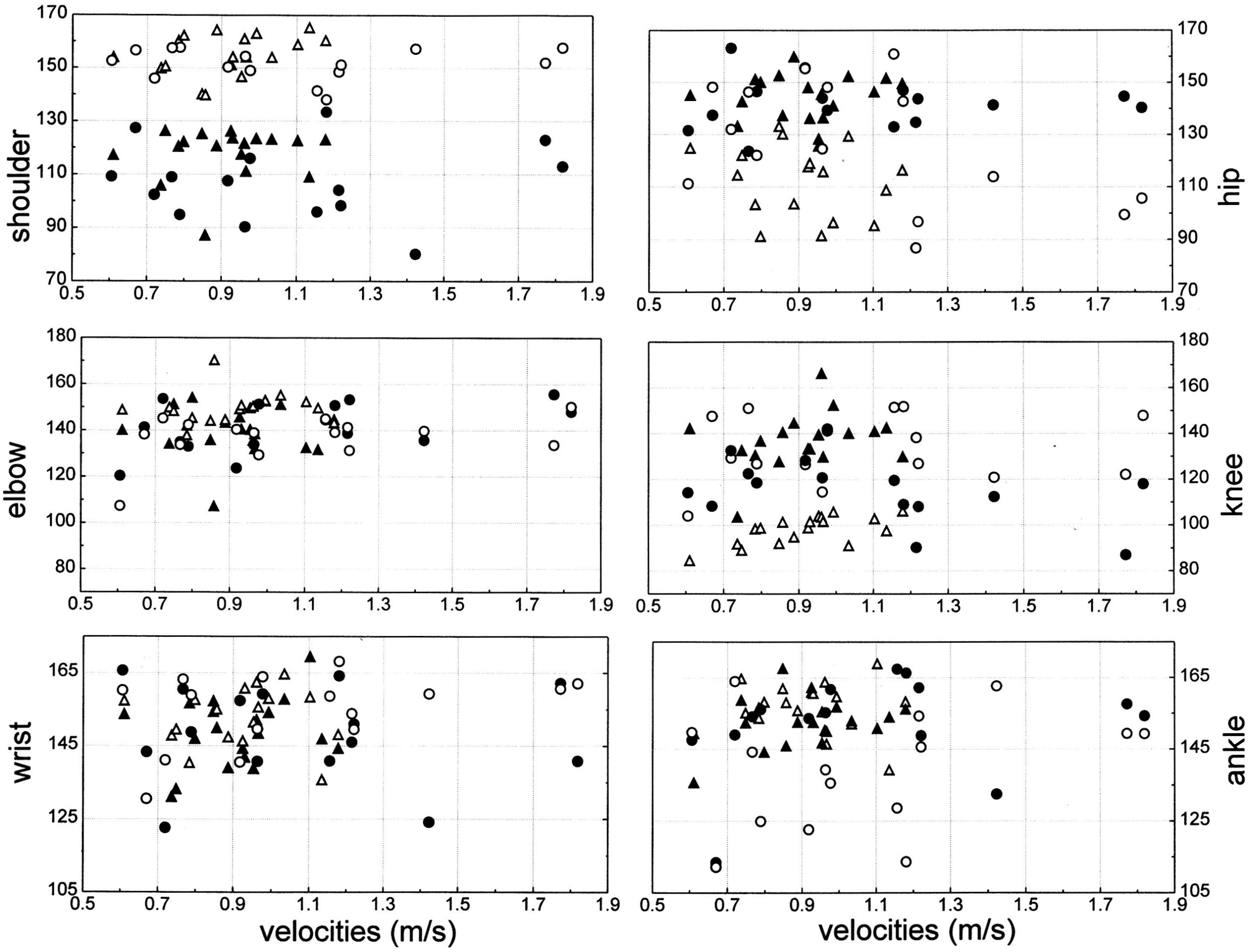

Fig 4. – The three-dimensional angles of the fore and hind limbs of G*ekko gecko* determined at touch-down (open symbols) and at lift-off (filled symbols) versus speed. Triangles and circles represent running vertically and horizontally respectively.

of the stride cycle). During climbing and level running, the joint angles of the fore limbs do not change with speed (all $P > 0.06$; Fig.4). When the hind foot leaves the substrate, none of the hind limb angles change with speed (all $P > 0.25$; Fig.4). However, at touch-down, during level running the hip angle increases ($P < 0.01$) and the ankle angle decreases ($P < 0.01$) with increasing speed (Fig.4). An increase in level running speed from 0.5 to 1 m/s results in an increase by 20% of the hip angle, and a decrease in ankle angle of about 11% (both calculated from the regression equations). During climbing, only the knee angle at hind foot touch-down increases with speed (Table 2). Consequently, an increase in speed from 0.5 to 1 m/s (based on the regression equations) results in an increase of 14 % in knee angle at hind footfall. None of the timing parameters calculated change with speed (all $P > 0.13$).

Hind limb versus fore limb timing

During both climbing and level running, the hind limb leaves the ground after the fore foot hits the substrate (Table 3, paired t-test, $t_{17} = -2.78$, $P = 0.01$ and $t_{14} = -1.04$, $P < 0.01$, for climbing and level running respectively). Additionally, the hind foot touches the substrate before the fore foot leaves it ($t_{17} = 4.28$, $P < 0.01$ and $t_{14} = 3.36$, $P < 0.01$ for climbing and level running respectively).

TABLE 3

Comparison of the timing when the front and hind feet of *Gekko gecko* hit, and leave the substrate (expressed as a proportion of the fore/hind foot cycle respectively). Time zero is defined at front foot contact. Values are means ± standard error.

	vertical		**horizontal**	
	lift-off	**touch-down**	**lift-off**	**touch-down**
front foot	-44.97 ± 2.558	0	-42.88 ± 3.954	0
hind foot	2.057 ± 2.985	-48.22 ± 2.559	5.52 ± 4.301	-46.21 ± 4.692

Difference within limbs

The elbow and the knee flex twice during a cycle, during the stance and the swing phase respectively (Figs 2, 3). Therefore, the elbow and the knee angles cannot only be compared between footfall and lift-off, but also between mid-stance and mid-swing.

During climbing, the elbow is more extended at touch-down than at lift-off (t-test for dependent samples, t_{17} = -2.513, P = 0.02), amounting up to an average of 6.21% difference. However, during level running, touch-down and lift-off, elbow angles are comparable. Additionally, the elbow is consistently more extended at mid-swing than at mid-stance, for both level and vertical running (t-test for dependent sample, climbing t_{17} = 4.42, P < 0.01; level running: t_{14} = 7.61, P < 0.01). On average, at mid-swing the elbow is 11.27% more extended during climbing and 28.9% more extended during level running.

In contrast, the knee is more extended when the hind foot leaves the substrate than at touch-down (t-test for dependent samples, climbing; t_{17} = -13.71, P < 0.01; level running: t_{17} = -4.17, P < 0.01). The average differences are 28.4% and 13.5% during climbing and level running respectively. The knee is also more extended at mid-stance than during mid-swing in climbing (t-test, t_{17} = 4.438, P < 0.01). In level running, mid-stance and mid-swing knee angles are comparable.

Climbing versus level running

The shoulder is more extended during climbing than during level running when the fore foot leaves the substrate (t-test for independent samples, t_{31} = -2.69, P = 0.01), but not when it touches it (t_{31} = -1.55, P = 0.13). On average the shoulder extends 9.5% more during climbing. At lift-off the degree of the elbow extension is comparable for climbing and level running (t_{31} = 0.35, P = 0.72), but the elbow extends further during climbing (t_{31} = -4.07, P < 0.01). At both footfall and lift-off, the wrist angle is identical for horizontal and vertical running (P > 0.5).

At hind foot lift-off, none of the hip, the knee or the ankle angles vary between climbing and level running (t-test, all P > 0.3). At touch-down, however, these angles do change with substrate orientation. The regression lines relating the hip angle at footfall with speed during climbing and level running differ in slopes (Analyse of covariance, $F_{1,29}$ = 6.71, P = 0.015), but not in intercepts ($F_{1,30}$ = 1.28, P = 0.27). The hip angle at footfall increases during level running. The regression lines relating knee and ankle angles with speed do not differ in slopes ($F_{1,29}$ = 0.78, P = 0.3 and $F_{1,29}$ = 2.97, P = 0.09 for the knee and ankle respectively), but do differ in intercepts ($F_{1,30}$ = 16.48, P < 0.01 and $F_{1,30}$ = 12.41, P < 0.01 for the knee and the ankle respectively). On average the knee angle at footfall is larger during level running and that of the ankle is larger during climbing (see Table 4).

TABLE 4

Mean values (± SE) of the amount of joint angles at lift-off and touch-down in *Gekko gecko* when running and climbing.

	vertical		**horizontal**	
	lift-off	**touch-down**	**lift-off**	**touch-down**
shoulder	118.22±9.676	155.12±7.691	106.90±14.313	151.33±6.040
elbow	139.91±10.896	149.17±7.085	141.27±11.042	137.07±9.930
wrist	148.18±9.545	152.90±7.64	148.46±13.482	154.65±10.478
hip	144.92±8.130	113.33±13.62	141.684±9.665	126.237±23.41
knee	137.15±12.482	98.09±6.1819	133.37±14.987	115.35±14.220
ankle	152.69±7.094	156.91±7.008	152.00±13.674	139.74±16.368

DISCUSSION

Zaaf and co-workers (2001) observed that *G. gecko* takes somewhat larger strides at a lower frequency while climbing, and smaller front limb steps while running on the horizontal. Duty factors are constant over speed, but are somewhat larger during running, while during climbing sprawling is significantly larger. Based on these findings Zaaf et al. (2001) concluded that the spatial aspects of climbing are kept fairly constant and that this strategy is retained when switching to a horizontal substrate. In the following section, we examine in more detail how the joint angles change between climbing and running.

The hip angle at the time when the hind foot leaves the substrate shows the same amount of extension whether the animal is running or climbing (table 4). However, at touch-down the hip angle increase slightly with speed during level running. By increasing the hip angle with speed at footfall during level running, *G. gecko* presumably modifies the point of contact of the foot with the substrate in order to deliver force. Although we do not provide a direct measurement on the femur retraction-protraction and rotation, it is likely that that the higher hip angle on the level surface means that the femur is less protracted at touch-down (see Fig.1). Probably, this difference in protraction is a consequence of the postural change that takes place when *G. gecko* shifts to a horizontal surface. Zaaf et al. (2001) showed that sprawling was reduced on the flat (probably to reduce potential friction with the surface), which might constrain femoral protraction. As the degree of sprawling decreases with increasing level running speeds, the velocity effect on the hip angle at touch-down supports this hypothesis. Reilly & Elias (1998) found similar results in the alligator when it changed from a sprawling gait to a high walk. In this species, a greater femoral excursion in the sprawling gait (in comparison with the high walk) is realised by a greater femur protraction just prior to touch-down. This is similar to what happens in sprawled climbing by *G. gecko*. The stronger protraction of the femur may thus allow a more anterior placement of the hind foot, which can increase the step length. This is, however, not observed in *G. gecko* (see ZAAF et al., 2001), which implies that the larger upper limb rotation is counteracted by decreased rotations at the level of other joints (e.g. smaller knee extension). Moreover, the movement of the femur is not restricted to simple retraction-protraction, but it can also rotate about its long axis to generate thrust (i.e. JAYNE & IRSCHICK, 1999). According to these authors, the amount of femoral rotation is minimised on inclined surfaces in the generalized lizard *Dipsosaurus dorsalis,* to keep the body close to the substrate. However, in contrast to *G. gecko, D. dorsalis* reduces its degree of sprawling on inclined surfaces.

Our results show that the shoulder and hip react differently to the physical demands imposed by the substrate orientation. Whereas the femur is more protracted at touch-down on the vertical substrate, and retracts equally far whether *G. gecko* is running or climbing, the humerus excursion is reduced on the vertical substrate as a result of a decrease of the degree of retraction at lift-off. This suggests that front steps are smaller on the vertical substrate, but this appears to be compensated for by the increased elbow extension at touch-down (ZAAF et al., 2001). Maybe, the less retracted state of the upper arm is required to ensure a sufficient backward pointing force transmission to the vertical substrate throughout stance.

Both the elbow and the knee show a flexion-extension cycle during both the swing and stance phases of the locomotor cycle. The amount of flexion of the elbow during the stance phase is higher than that occurring during the swing phase. This is undoubtedly linked to the need for fore limb pulling forces just mentioned. This suggests that, contrary to horizontal locomotion by specialised runners where elbow extensor activity can be expected to brake initial elbow flexion during stance, forceful elbow flexor activity (m. brachialis and m. biceps) adds to the propulsion in vertical climbing. ZAAF et al. (1999) showed that these elbow flexors are better developed in *G. gecko* than in a ground dwelling gecko.

At touch-down the amount of the elbow extension was significantly larger on a vertical substrate. This additional extension of the elbow at touch-down during climbing results in a more anterior placement of the foot. Thus, tensile flexor forces in the elbow are ensured over a larger distance.

As for the elbow, the knee angles at lift-off were comparable between level running and climbing (Table 4, Fig. 4). However, at touch-down, and unlike what is observed for the elbow, the amount of the knee extension was larger on the level than on a vertical substrate (Table.4, Fig. 4). This can clearly be related to the more parasagittal leg posture on the horizontal substrate. Through a reduction in the degree of flexion at touch-down, forceful pushing can dominate the stance phase. Obviously, the reduced excursion in the knee during climbing is compensated for by the increased femoral retraction (see above). Despite differences in limb postures and morphology, the knee is in many vertebrates, lizards and others, more flexed at touch-down when the animal is locomoting on an incline. For example, in cats (SMITH & CARLSON-KUHTA, 1995), squirrel monkeys (VILENSKY et al., 1994), turkeys (ROBERTS et al., 1997), and the lizard *Dipsosaurus dorsalis* (JAYNE & IRSCHICK, 1999), the knee was more flexed at touch-down during uphill locomotion. Moreover, ZAAF et al. (2001) show that a specialist level running gecko (*Eublepharis macularius*) reduces the degree of sprawling, and hence flexes its limbs when induced to climb vertically. By doing this, the level runner tries to minimise the distance between the body and the vertical substrate in order to reduce the moment about its centre of gravity and to gain additional friction between the body and the substrate. The specialist climber *G. gecko*, on the other hand, spreads its hind limbs to bring its body closer to the substrate when running vertically (ZAAF et al., 2001). Thus, presumably the decreased extension of the knee at touch-down in climbing *G. gecko* is involved in thrust generation as suggested above. Increased flexion of the knee at touch-down on a vertical substrate probably puts the foot and the lower leg in a position allowing the production of sufficient force to initiate forward propulsion.

The pattern of movement of the wrist shows irregular but generally small flexion-extension cycles during climbing (Fig. 2). For level running, wrist movements seem to be more regular with peaks of extension occurring mostly at lift-off and touch-down (Fig. 3, at least for the first two speeds). As *G. gecko* raises its body from the ground during level running by reducing the degree of sprawling, and by increasing the flexion of the elbow at touch-down (see higher), the observed flexion-extension movement at the wrist could be a mechanism for generating thrust by ultimate palmar flexion. On a vertical substrate, however, thrust generation through palmar flexion-extension movements seems more difficult. The fact that the wrist angle does not change over the cycle during climbing suggests that the front foot is rotated while the fore limb is retracted as was observed on high-speed recordings.

The amount of the ankle extension is comparable between lift-off and touch-down during level running. However, during climbing the hind foot hits the substrate more extended than when it leaves the ground (Fig. 4, Table 4). Again this must be related to the large sprawling during climbing. In a sprawled leg, initial plantar contact is only possible with largely extended ankles, whereas in a more parasagittal limb posture (as used for level running), plantar contact requires a more flexed ankle. However, in the alligator, REILLY & ELIAS (1998) found that the ankle was more flexed at touch-down during a sprawling gait, and in *Dipsosaurus dorsalis* the ankle angle was not affect in uphill running (JAYNE & IRSCHICK, 1999).

In most reptiles the ankle flexes early during the stance phase and a biphasic flexion-extension is observed during the stance and swing phase respectively (BRINKMAN, 1981; GATESY, 1991; REILLY & DELANCEY, 1997a;

REILLY & ELIAS, 1998; JAYNE & IRSCHICK, 1999). As mentioned already, flexion extension during stance is important for propulsion (REILLY, 1995, REILLY & DELANCEY, 1997a,b). Probably, the flexion of the ankle after lift-off is required for level runners so that their long digits do not hit the substrate while their feet are moving forward. Our data show that the ankle in *G. gecko* only flexes significantly during the propulsive phase. During limb protraction, no significant change in the ankle angle was observed. As the digits in *G. gecko* are capable of hyperextension (RUSSELL, 1975, 1976) they can compensate for the lack of ankle extension.

In the light of the hypotheses formulated in the introduction, we summarise the results as follows. To a large extent, *G. gecko* conserves the angular patterns of the leg joints when shifting from its preferred vertical substrate to the horizontal. However, like the spatio-temporal gait characteristics (see ZAAF et al., 2001) some small changes do show up. We group these differences into two categories. Changes such as the altered hip, ankle or wrist angles probably result from the reduction in sprawling when the animal movies on a horizontal surface; these could be considered as behavioural accommodations to movement on a level surface. Reduced sprawling is needed to lift the body above the surface and the observed alterations are thus an inherent consequence of this. A second category of changes can be linked to the absence of the specific constraints on propulsion in climbing, when the animal moves over ground (i.e. pulling forces at the fore limbs, continuous pushing at the hind limbs). The changes observed at the level of the knee, the elbow and the shoulder belong to this group. Climbing in *G. gecko* thus seems to go along with extensive morphological specialisation allowing good performance on both vertical and horizontal substrates. Yet, despite these morphological specialisations few alterations in the movement patterns are observed (ZAAF et al., 2001; this study).

REFERENCES

ASHLEY-ROSS, M.A. (1995). Patterns of hindlimb motor output during walking in the salamander *Dicamptidon tenebrosus*, with comparisons to other tetrapods. *J. Comp. Physiol.*, A177: 273-285.

AUTUMN, K., W.P. CHANG, R. FEARING, T. HSIEH, T. KENNY, L. LIANG, W. ZESCH & R.J. FULL (2000). Adhesive force of a single gecko foot-hair. *Nature*, 405: 681-685.

BAUER, A.M., A.P. RUSSELL, & G.L. POWELL (1996). The evolution of locomotor morphology in *Rhoptropus* (Squamata: Gekkonidae): functional and phylogenetic considerations. *Afr. J. Herpetol.*, 45: 8-30.

BRINKMAN, D. (1981). The hind limb step cycle of Iguana and primitive reptiles. *J. Zool.* (*Lond.*), 193: 91-103.

CARTMILL, M. (1985). Climbing. In: M. HILDEBRAND, D.M. BRAMBLE, K.F. LIEM & B.D. WAKE (eds). *Functional Vertebrate Morphology.* Harvard University Press, Cambridge: 73-88.

FARLEY, C.T. (1997). Maximum speed and mechanical power output in lizards. *J. exp. Biol.*, 200: 2189-2195.

FARLEY, C.T. & M. EMSCHWILLER (1996). Efficiency of uphill locomotion in nocturnal and diurnal lizards. *J. exp. Biol.,* 199: 587-592.

GARLAND, T. JR. & J.B. LOSOS (1994). Ecological morphology of the locomotor performance in squamate reptiles. In: WAINWRIGHT & REILLY (eds), *Ecological morphology. Integrative organismal biology*. The University of Chicago Press, Chicago: 243-250.

GATESY, S.M. (1991). Hindlimb movements of the American alligator (*Alligator mississippiensis*) and postural grades. *J. Zool., Lond.*, 224: 577-588.

HUEY, R.B. & P.E. HERTZ (1982). Effect of body size and slope on sprint speed of a lizard (*Stellio* (*Agama*) *stellio*). *J. exp. Biol.*, 97: 401-409.

HUEY, R.B. & P.E. HERTZ (1984). Is a jack-of-all temperatures a master of none? *Evolution*, 38: 441-444.

IRSCHICK, D.J. & B.C. JAYNE (1998). Effects of incline on speed, acceleration, body posture and hindlimb kinematics in two species of the lizard *Callisaurus draconoides* and *Uma scoparia*. *J. exp. Biol.,* 201: 273-287.

IRSCHICK D.J. & B.C. JAYNE (1999). Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *J. exp. Biol.*, 202: 1047-1065.

JAKSIC, F.M., H. NÚÑEZ & F.P. OJEDA (1980). Body proportions, microhabitat selection, and adaptive radiation of *Liolaemus* lizards in central Chile. *Oecologia*, 45: 178-181.

JAYNE, B.C. & R.V. ELLIS (1998). How inclines affect the escape behaviour of a dune dwelling lizard, *Uma scoparia. Anim. Behav.*, 55: 1115-1130.

JAYNE, B.C. & D.J. IRSCHICK (1999). Effect of incline and speed on the three-dimentional hindlimb kinematics of a generalized iguanian lizard (*Dipsosaurus dorsalis*). *J. exp. Biol.,* 202: 143-159.

LEVINS, R. (1968). *Evolution in changing environments: some theoretical explorations.* Princeton University Press, New Jersey (120 pp).

MILES, D.B. (1994). The covariation between morphology and locomotory performance in Sceloporine lizards. In: VITT & PIANKA (eds), *Lizard ecology. Historical and experimental perspectives,* Princeton University Press, New Jersey: 207-236.

PIANKA, E.R. & H.D. PINAKA (1976). Comparative ecology of twelve species of nocturnal lizards (Gekkonodea). In the west Australian desert. *Copeia,* 1976: 125-142.

POUNDS, J.A. (1988). Ecomorphology, locomotion and microhabitat structure: Patterns in a tropical mainland *Anolis* community. *Ecol. Monograph*, 58: 299-320.

REILLY, S.M. (1995). Quantitative electromyography and muscle function of the hind limb during quadrupedal running in the lizard *Sceloporus clarki*. *Zoology*, 98: 263-277.

REILLY, S.M. & DELANCEY, M.J. (1997a). Sprawling locomotion in the lizard *Sceloporus clarkii*: the effect of speed on gait, hindlimb kinematics and axial bending during walking. *J. Zool., Lond.,* 243: 417-433.

REILLY, S.M, & M.J DELANCEY (1997b). Sprawling locomotion in the lizard *Sceloporus clarkii*: Quantitative kinematics of a walking trot. *J. exp. Biol.*, 200: 753-765.

Reilly, S.M. & J.A. Elias (1998). Locomotion in *Alligator mississippiensis*: kinematics effect of speed and posture and their relevance to the sprawling-to-erect paradigm. *J. exp. biol.,* 201: 2559-2574.

Roberts,T.J., R.L. Marsh, Weyand, P.G. & C.R. Taylor (1997). Muscular force in running turkeys: the economy of minimizing work. *Science*, 275: 1113-1115.

Russell, A.P. (1975). A contribution to the functional analysis of the foot of the tokay, *Gekko gecko* (Reptila: Gekkonidae). *J. Zool., Lond.,* 176: 437-476.

Russell, A.P. (1976). Some comment concerning interrelationships among gekkonine geckos. In: Bellairs & Cox (eds), *Morphology and biology of reptiles*, Academic Press, London: 217-244.

Sinervo, B. & J.B. Losos (1991). Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard population. *Ecology*, 72: 1225-1233.

Smith, J.L. & P. Carslon-Kuhta (1995). Unexpected motor patterns for hind limb muscles during slope walking in the cat. *J. Neurophysiol.*, 74: 2211-2215.

Smith, J.N.M. & A.A. Dhondt (1980). Experimental confirmation of heritable morphological variation in a natural population of song sparrows. *Evolution*, 34: 1155-1158.

Snyder, R.C. (1952). Quadrupedal and bipedal locomotion of lizards. *Copeia*, 1952: 64-70.

Snyder, R.C. (1962). Adaptation for bipedal locomotion in lizards. *Am. Zool.*, 2:191-203.

Van Damme, R, P. Aerts & B. Vanhooydonck (1997). No trade-off between sprinting and climbing in two populations of the lizards *Podarcis hispanica* (Reptilia: Lacertidae). *Biol. J. Linn. Soc.*, 60: 493-503.

Van Damme, R. & B. Vanhooydonck (2001). Origins of interspecific variation in lizard sprint capacity. *Funct. Ecol.*, 15: 186-202.

Vanhooydonck, B. & R. Van damme (2001). Evolutionary tradeoffs in locomotor capacities in lacertid lizards: are splendid sprinters clumsy climbers ? *J. Evol. Biol.*, 14: 46-54.

Vilensky, J.A., A.M. Moore & J.N. Libii (1994). Squirrel monkey locomotion on inclined treadmill: implications for the evolution of gait. *J. Hum. Evol.,* 26: 375-386.

Zaaf, A. (2000). *Climbing and level running in geckoes: conflict, compromise or concurrence*. Unpublished PhD thesis, University of Antwerp.

Zaaf, A., A. Herrel, P. Aerts & F. De Vree (1999). Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habit (Lepidosaurians). *Zoomorphology*, 219: 11-22.

Zaaf, A., R. Van Damme, A. Herrel & P. Aerts (2001). Spatio-temporal gait characteristics of level and vertical locomotion in a ground-dwelling and a climbing gecko. *J. exp. Biol.*, 204: 1233-1246.

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SHORT NOTE

First record of the Pontocaspian invader *Hypania invalida* (Grube, 1860) (Polychaeta: Ampharetidae) in the River Meuse (Belgium)

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KEY WORDS: *Hypania invalida*, Ampharetidae, Polychaeta, invasive species, first record, Meuse River, macrozoobenthos, freshwater

Hypania invalida (Grube, 1860) is known as a pontocaspian species (1) whose origin, distribution and migration upstream the river Danube have been described by several authors (2, 3, 4, 5, 6). The building of dams on the river Danube has favoured high densities at Ybbs-Persenbeug and Jochenstein, Austria (7), at Gabcikovo-Nagymaros, border between Slovakia and Hungary (8, 9, 10) and at Portile de Fier, Rumania (11). Recently, after the opening of the canal Danube – Main in September 1992, *H. invalida* escaped from the Danube basin and invaded the Main, the Rhine and the Moselle basins (6, 7, 12) and reached the Netherlands in 1995 (13). *H. invalida* has now invaded the river Meuse, and was first recorded in 2000 in its Belgian section.

Macrozoobenthos sampling is part of a routine monitoring network for the study of the biodiversity and for the assessment of biological quality of watercourses in Wallonia (Belgium). In the River Meuse this monitoring started in 1991. Intensive sampling methods were used at five stations in the 2000 campaign (from August 22nd to September 15th): 1 Heer, 2 Lustin, 3 Gives, 4 Chokier and 5 Lixhe (from upstream to downstream respectively, Fig. 1).

Fig. 1. – Location of the sampling sites (1 = Heer, 2 = Lustin, 3= Gives, 4 = Chokier and 5 = Lixhe).

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The presence of an island at Heer (Ile d'Androssart) and at Gives (Ile des Chanoines) allows the sampling in a channel closed to ships and well protected from navigation. Chokier and Lustin to a smaller extend are subjected to disturbances caused by navigation (heavy waves, bottom disturbed by propellers). Lixhe station is located 500 m downstream from a hydroelectric power station in shallow, non navigable waters. The banks were sampled with a handnet (500 µm mesh size on a metal frame 30 x 26 cm) and with three artificial substrates (strong nylon net bags – mesh size 1 cm – filled with 5 litres of 4 to 8 cm pebbles, submerged at a depth of about 1 m and left in place for 34 days). The main channel was sampled at a depth of 4 m with a triangular dredge (side size 30 cm, 500 µm mesh size) and by scuba diving (10 litres material collected under water with a small spade in a 500 µm mesh size handnet). Local conditions did not allow either dredging in station 5 or diving in stations 4 and 5.

Hypania invalida (Grube, 1860) (Fig.2), identified according to "Die Tierwelt Deutschlands" (14), was collected in three stations: Heer, Gives and Chokier. The length of the largest specimen was 13.9 mm after fixation. Only one specimen was collected at Heer, close to the French border, by scuba diving. The other techniques did not provide any polychaetes. Close to the bank, the oxygen concentration was 6.4 mg l^{-1}, pH 8.22, conductivity 443 µS cm^{-1} and temperature 19.5 °C. At Gives, about 20 specimens were collected by dredging, ten within the artificial substrates and about 250 by scuba diving. The oxygen concentration was 6.5 mg l^{-1}, pH 8.10, conductivity 495 µS cm^{-1} and temperature 20.8 °C. The bottom of the river at both Heer and Gives was sampled at a depth of 4 m on gravel and stones covered with a few mm to a few cm of sludge. At Chokier, one artificial substrate yielded one specimen. The oxygen concentration was 6.4 mg l^{-1}, pH 8.08, conductivity 586 µS cm^{-1} and temperature 24.2 °C.

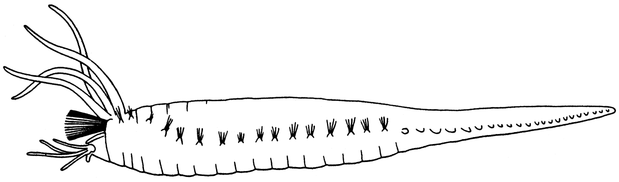

Fig. 2. – Aspect of *Hypania invalida* with partly visible tentacles (most individuals after fixation have their tentacles retracted in the mouth). Total length = 12 mm.

H. invalida is considered as an active filter feeding species (3, 15) but can also work as a deposit feeder (3). It is a eurytopic species, which has been found from hyporhithron to hypopotamon (15). It is one of the characteristic species of the eupotamon (vs parapotamon) and avoids the plesiopotamon (8, 16). It lives within a muddy tube on various substrates with a preference for gravel to silt deposits (3, 4, 5, 16, 17). Its populations can quickly build up to high densities (>10000 ind m^{-2}) in favourable conditions i.e. after the building of a dam (11, 17). Such conditions are met in the Meuse adapted for navigation in Wallonia.

Hypania invalida is one among the recent invaders that were collected in the Walloon Meuse (Belgium) during the same campaign: others were *Corbicula fluminea* (Müller, 1774) (since 1994 in Lanaye close to the Dutch border; in stations 1, 3 and 4 in 2000), *Hemimysis anomala* (Sars, 1907) (stations 1, 2 and 3), *Dikerogammarus* sp, *Echinogammarus* sp and *Corophium curvispinum* (Sars) (stations 1, 2, 3 and 4).). *C. curvispinum* co-occurred with *H. invalida*. The co-occurrence of these two species was also noticed in Bulgaria and Rumania (4, 5).

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REFERENCES

1. Illies, J. (1978). *Limnofauna europaea*. 2. Auflage. Gustav Fischer Verlag, Stuttgart.
2. Kothé, P. (1968). *Hypania invalida* (Polychaeta Sedentaria) und *Jaera sarsi* (Isopoda) erstmals in der deutschen Donau. *Arch. Hydrobiol.*, Suppl. 34: 88-114.
3. Manoleli, D. (1975). On the distribution, biology and origin of Polychaeta from the Danube and the Danube Delta. *Trav. Mus. Hist. Nat. Grigore Antipa*, 16: 24 – 33.
4. Popescu-Marinescu, V. (1980). Données concernant les polychètes dulçaquicoles des eaux de la Roumanie. *Trav. Mus. Hist. Nat. Grigore Antipa*, 21: 131-138.
5. Russev, B & Marinov, T. (1964). The fauna of polychaetes and leeches in the Bulgarian Danube sector [in Bulgarian]. *Izv. Zool. Inst, Sofia*, 15: 191-197.
6. Titizer, T., Schöll, F., Banning, M., Haybach, A. & Schleuter, M. (2000). Aquatische Neozoen im Makrozoobenthos der Binnenwasserstrassen Deutschlands. *Lauterbornia*, 39: 1-72.
7. Titizer, T. (1997). Ausbreitung aquatischer Neozoen (Makozoobenthos) in den europäischen Wasserstrassen, erläutert am Beispiel des Main-Donau-Kanals *Schriftenreihe des Bundesamtes für Wasserwirtschaft*, 4: 113-134.
8. Krno, I., Sporka, F., Matis, D., Tirjakova, E., Halgos, J., Kosel, V., Bulankova, E. & Illesova D. (1999). Development of zoobenthos in the Slovak Danube inundation area after the Gabcíkovo Hydropower Structures began operating In: *Gabcikovo part of the hydroelectric power project of enviromental impact review (evaluation based on six year monitoring).* Ed. Comenius University of Bratislava, Chap. 11.
9. Makovinska, J. (1999). The Danube water quality between Bratislava and Visegrad (1989-1997). In: *Gabcikovo part of the hydroelectric power project of environmental impact review (evaluation based on six year monitoring).* Ed. Comenius University of Bratislava, Chap. 8.
10. Nagy, S. (1999). Composition of macrozoobenthos of the Cunovo reservoir with respect to trophical potential for fish communities. In: *Gabcikovo part of the hydroelectric power project of environmental impact review (evaluation based on six year monitoring).* Ed. Comenius University of Bratislava, Chap. 15.

11. POPESCU-MARINESCU, V. (1992). Les Populations d'*Hypania invalida* (Grube) dans la région Portile de Fier, avant et après la création du lac d'accumulation. *Rev. roum. Biol., Sér. Biol. Anim.*, 37: 131-139.
12. SCHMIDT, W.-D., KAISER, I. & SCHULLER, I. (1998). Zwei Neuankömmlinge aus der Donau – *Hypania invalida* (Polychaeta) und *Jaera istri* (Isopoda) – haben den ganzen Main besiedelt. *Lauterbornia*, 33:121-123.
13. KLINK, A.G. & BIJ DE VAATE, A. (1996). *Hypania invalida* (Grube 1860) (Polychaeta: Ampharetidae) in the lower Rhine – new to the Dutch fauna. *Lauterbornia*, 25: 57-60.
14. HARTMANN-SCHRÖDER, G. (1971). Annelida, Borstenwürmer, Polychaeta. In: *Die Tierwelt Deutschlands,* 58, Ed. DAHL. Gustav Fischer Verlag, Jena.
15. MOOG, O. (1995). *Fauna aquatica austriaca Version 1995.* Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Wien.
16. SPORKA, F. (1998). The typology of floodplain water bodies of the Middle Danube (Slovakia) on the basis of the superficial polychaete and oligochaete fauna. *Hydrobiologia*, 386: 55-62.
17. WEBER, E. (1964). Süsswasserpolychaeten in der österreichischen Donau. *Arch. Hydrobiol.*, Suppl. 27: 381-385.

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