Belgian Journal of Zoology

(formerly : « ANNALES DE LA SOCIÉTÉ ROYALE ZOOLOGIQUE DE BELGIQUE — ANNALEN VAN DE KONINKLIJKE BELGISCHE VERENIGING VOOR DIERKUNDE »)

Published by the « KONINKLIJKE BELGISCHE VERENIGING VOOR DIERKUNDE — SOCIÉTÉ ROYALE ZOOLOGIQUE DE BELGIQUE »

Volume 123 (2)

(December, 1993)

Editor :

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The *Belgian Journal of Zoology* publishes original manuscripts in the field of zoology. The manuscripts are evaluated by the editorial board.

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Manuscripts are to be sent to : Prof. Dr. E. SCHOCKAERT, Department SBG, Limburgs Universitair Centrum, B-3590 Diepenbeek (Belgium).

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 107-112 — Brussels 1993

Manuscript received on 1 February 1993

UNEQUAL CAUDOCEPHALIC OOPLASMIC UPTAKE AND ECCENTRIC FORMATION OF THE SUBGERMINAL SPACE BELOW UNINCUBATED QUAIL BLASTODERMS PRESENTING A KOLLER'S SICKLE

by

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SUMMARY

By radioactive ooplasmic yolk layer labeling during late oogenesis, we demonstrated that below unincubated quail blastoderms the subgerminal space extends much more peripherally in the cranial then in the caudal direction, where it ends abruptly against Koller's sickle. Our autoradiographic and histochemical investigations indicate that Koller's sickle develops by a progressive local colonisation of the centro-caudal subgerminal ooplasm, which does not take place in the cranial diametrically opposite anti-sickle region. The deep paracentral uptake of voluminous ooplasmic areas by large encircling extensions of its cells is a characteristic feature of the sickle region.

Key words : avian ooplasm, quail blastoderm, Koller sickle, caudo-cephalic axis.

INTRODUCTION

The caudal sickle named after KOLLER (1882), already described before by RAUBER (1876), can clearly be observed alive under the stereomicroscope, from the exterior in about 30 % of unincubated laid quail blastoderms (FARGEIX, 1964 ; LUTZ, 1964). It develops in the highest (future caudal) half of the blastodisc of temporally obliquely or vertically placed extracted uterine quail egg yolks (CALLEBAUT, 1991, 1993). From the middle part of the sickle region the primitive streak will develop after early incubation (KOLLER, 1882). We have shown by maternal injections of tritium labelled protein precursors that the semi-solid ooplasmic layers playing a role in the formation of the avian germ disc were disposed in/and around the nucleus of Pander as the peels in an onion-bulb (CALLEBAUT, 1974, 1983). By the use of that labeling method it was possible in the present study to demonstrate an unequal caudocephalically directed uptake of ooplasm in the blastoderm of laid unincubated eggs presenting a Koller's sickle. After appropriate fixation (Calcium

formalin) and staining (Unna), we were able to visualize clearly the massive capture of underlying ooplasm by the encircling movement of the blastomeres in the region of Koller's sickle.

MATERIAL AND METHODS

Fifteen fertilized Japanese quail females, selected for regularly laying eggs with blastoderms presenting a Koller's sickle (Stage 1 ; VAKAET, 1962, 1970), were injected 3 times (every 2 days) with 0,5 mCi L- (4, 5-3H) leucine (164 Ci/mM, Amersham, England).

The eggs laid during the days following the injection were opened. After removal of the surrounding albumen and rinsing in Ringer solution most of their yolks with blastoderms presenting a Koller's sickle were fixed *in toto* in calcium formalin (according to SILVERTON and ANDERSON, 1961). For comparison some yolks were also fixed in Susa after Heidenhain (ROMEIS, 1948) without sublimate, in acetic acid-alcohol (1 : 3 v) or in an acetic acid-formaldehyde 35 %-alcohol 95 % (1 : 4 : 15 v) mixture (AFA).

The localization of Koller's sickle was indicated with a linear charcoal mark on the vitelline membrane just behind the blastoderm rim. After 1 night of fixation at room temperature the egg yolks were placed in tap water (the acetic-acid and AFA fixed blastoderms were placed in 70 % alcohol) and during the following days dehydrated. In 95 % alcohol, the germs still adherent to their vitelline membrane were excised with some surrounding yolk and after clearing in xylene, embedded in paraffin.

Eight µm thick sectioning was performed parallel with the caudocephalic axis of the germ(perpendicular to the linear charcoal mark behind Koller's sickle). The blastoderms in the paraffin were placed vertically, perpendicular to the microtome knife edge during sectioning, to avoid a dorsoventral compression. Comparable sections of similar blastoderms of not injected females were used as controls both before and after the autoradiographic procedure. The radioactively labeled and some control sections were dipped in nuclear emulsion L4 (Ilford, England). After 1 month of exposure in the dark the autoradiographs were developed according to CARO and VAN TUBERGEN (1962). Thereafter the autoradiographs were coloured with Unna.

RESULTS

On the autoradiographs of mediosagittal sections through unincubated blastoderms (fixed in calcium formalin) of eggs laid 6 days after the first and 4 days after the second injection the respectively corresponding labeled ooplasmic layers (layers 1 and 2 on Fig. 1) were clearly seen. In the neighbourhood of the germ their form remained no longer symmetrical as was originally the case in the oocyte. At the future cranial side of the germ (Figs. 1, 2), the second labeled layer was seen

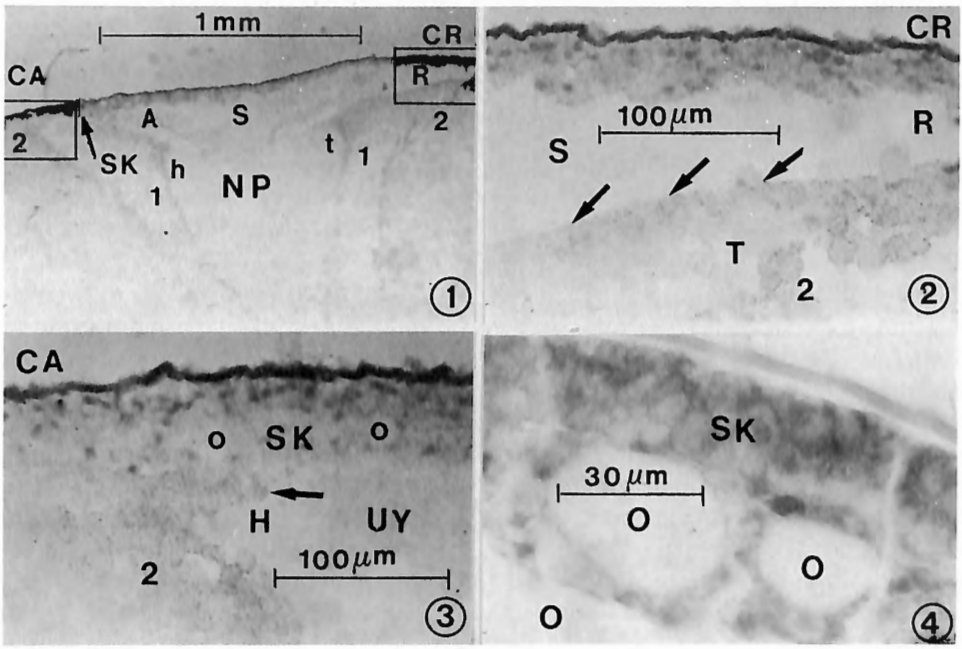

Fig. 1-4. — Microphotographs taken from Unna stained sections of calcium formalin fixed quail blastoderms.

1. — Autoradiograph of a mediosagittal section through an unincubated quail germ on its egg yolk presenting two labeled ooplasmic layers (numbered 1 and 2 formed respectively 6 and 4 days before laying) CA : caudal and CR : cranial side of the germ ; layer 1 is seen to surround the bootshaped nucleus of Pander (NP) ; t : cranial toe-like and h : caudal heel-like part of NP ; S : subgerminal space extending more peripherally as a recess (R) at the cranial side ends abruptly in A (axilla form) since it is closed at the caudal side by the sickle of Koller (SK) ; layer 2 is caudally seen to end against the Koller sickle material (see also Fig. 3) whereas cranially it ends below the cranial shallow recess of the subgerminal space (see also Fig. 2).

2. — Enlargement of the cranial part of Fig. 1 (cranial rectangle). Note the long hook-like recurved part (indicated by 3 arrows) of the labeled ooplasmic layer 2 surrounding a toe-like area (T) of unlabeled ooplasm (UY) below the widely open subgerminal space (S) and its cranial recess (R).

3. — Enlargement of the caudal part of Fig. 1 (caudal rectangle). Note the much shorter hook-like part (arrow on its point) of labeled layer 2 surrounding a heel-like part (H) of unlabeled ooplasm (UY) below the sickle of Koller (SK) ; O : islands of ooplasm without nuclei in Koller's sickle.

4. — Mediosagittal section through sickle of Koller (SK) of unincubated quail blastoderm to show the uptake of voluminous parts of ooplasm (upper o's) by an encircling movement or extension of the sickle cells. The contact zone between the sickle and the underlying ooplasm (lower left O) is seen to be rectilinear.

to form a long hook-like structure below the widely open subgerminal space which extends more peripherally as a narrow recess. By contrast at the future caudal side the hook form was much less developed or absent (Figs.1, 3). Here the subgerminal space was obliterated by the yolk rich cells of Koller's sickle. The first (deepest) layer which surrounds the nucleus of PANDER (1817) (Fig. 1) was seen to present an analogous but less obvious form (parallel with the second labelled layer) corresponding to the bootshape we have previously described (CALLEBAUT 1983, 1987). After autoradiographic processing of similar sections through non radioactive control blastoderms no background labeling was observed.

On the sections through non radioactive calcium formalin fixed control blastoderms which were not submitted to the autoradiographic procedure and were only stained with Unna, the contrast between the cellular borders of the blastoderm and the subgerminal ooplasm was very sharp. So it was clearly seen that voluminous ooplasmic areas were locally taken up into the sickle by an extensive encirclement of its deeper cells (Fig. 4). These areas corresponded to the nuclei free zones seen after autoradiographic coating with nuclear emulsion (Fig. 3). The interface contact zone between the sickle and the underlying ooplasm remained nearly plane (Fig. 4). After fixation in AFA or acetic alcohol and Unna or iron hematoxylin and eosin staining the blastoderms and subgerminal cavity were seen to be somewhat compressed and deformed and the distinction between the blastodermal cell borders and the colonized underlying ooplasm was not well demarcated.

DISCUSSION

The present study indicates that the deep paracentral colonization of voluminous yolky ooplasmic areas by large encircling movements of the blastomeres is a characteristic feature of Koller's sickle region in quail blastoderms. So the Koller's sickle may develop as the result of the deep penetration of blastomeres in the ooplasm of the upper germ wall after the eccentric formation of the area pellucida (CALLEBAUT, 1993) or perhaps also by a more central proliferation of cells obliterating locally the subgerminal space. Unincubated quail eggs treated with 3H-thymidine at room temperature presented an unequal incorporation pattern with a more intensive incorporation at the caudal side of the germ, mainly in the nuclei of Koller's sickle (CALLEBAUT, 1989) indicating their higher DNA synthesis rate.

Although we showed that a cytoplasmic continuity no longer existed between the cells of the unincubated quail blastoderm and the underlying ooplasm, our observations indicated that the deep sickle cells can hold both structures together by means of their prominent protrusions. It is clear that the penetration of the sickle cells is different from that of the more peripheral yolk endoderm which originates later from the outer part of the germ wall (area opaca) and in which according to VAKAET (1962) no cellular boundaries existed.

The present study indicates that at the level of Koller (or Rauber) sickle a larger quantity of centrally localized ooplasm (closer to the original animal pole of the oocyte) is taken up into the germ. So an unequal asymmetric distribution of the original β and/or γ ooplasms (CALLEBAUT, 1987) takes place which can be determining for the further development of the germ. At the end of the intrauterine period some centrifugal expansion occurs in the upper layer forming the main part of the area opaca (CALLEBAUT and MEEUSSEN, 1988). The localization of the sickle of Koller however, remains unchanged. The early or primary eccentricity is somewhat « paradoxical » and is diametrically opposite to the eccentricity usually seen after laying or during the first hours of incubation (CALLEBAUT, 1993). CLAVERT (1960, 1962) and KOCHAV *et al.* (1980) have not seen the parallelism existing between the structure of the avian germ, the subgerminal cavity and the underlying yolk. The latter authors dissected out the germ together with underlying yolk and removed the vitelline membrane before fixation and so disturbed some early spatial relationships. Moreover at that moment, knowledge about the formation of the avian yolk layers in the germ disk was still incomplete. From their study KOCHAV *et al.* (1980) concluded that at the moment of area pellucida formation there occurs a massive cell shedding process. They presumed that all the deeper cells of the germ fall into the subgerminal cavity and finally assemble in its lowest (future cranial) part under influence of gravity. I have never seen any proof of this hypothesis, since after trypan blue induced fluorescent labeling of the yolk in quail eggs the labeled cells or yolk masses, both in the caudal and cranial part of the subgerminal space, always remained localized in the prolongation of the labelled subgerminal yolk layers (CALLEBAUT, 1987). This was also particularly the case for the Koller sickle region in which locally voluminous densely trypan blue labeled yolk masses remained visible, confirming our present observations.

ACKNOWLEDGEMENTS

The author is very grateful to Mrs. E. Van Nueten, Mrs. S. Van Rompaey and Mr. F. De Bruyn for excellent technical assistance and to Mrs. L. Debie for typing the manuscript.

REFERENCES

CALLEBAUT, M. (1974) — La formation de l'oocyte d'oiseau. *Archiv. Biol. (Brux.)*, **85** : 201-233.

CALLEBAUT, M. (1983) — The constituent oocytal layers of the avian germ and the origin of the primordial germ cell yolk. *Arch. Anat. Microsc.*, **72** : 199-214.

CALLEBAUT, M. (1987) — Ooplasmic localization and segregation in quail germs : fate of the four ooplasms. *Arch. Biol. (Brux.)*, **98** : 441-473.

CALLEBAUT, M. (1989) — Incorporation of 3H-thymidine in unincubated quail blastoderms presenting a sickle of Koller. *Med. Sci. Res.*, **17** : 873-874.

CALLEBAUT, M. (1991) — Methods for studying early development of avian germs on their egg yolk in a vertical or inverted position. *Eur. Arch. Biol.*, **102** : 197-199.

CALLEBAUT, M. (1993) — Early eccentricity in gravitationally oriented quail germs. *Eur. J. Morphol.*, **31** : 5-8.

CALLEBAUT, M. and C. MEEUSSEN (1989) — The area opaca of the avian blastoderm is mainly formed by centrifugal expansion. *Med. Sci. Res.*, **16** : 617-618.

CARO, L. and R. VAN TUBERGEN (1962) — High-resolution autoradiography. *J. Cell Biol.*, **15** : 173-188.

CLAVERT, I. (1960) — Déterminisme de la symétrie bilaterale chez les oiseaux IV. Existence d'une phase critique pour la symétrisation de l'œuf. Son stade. *Arch. Anat. Microsc. Morph. Exp.*, **49** : 345-361.

CLAVERT, I. (1962) — Symmetrization of the egg in vertebrates. In : *Advances in morphogenesis 2.* AP, NY London : 27-60.

FARGEIX, N. (1964) — La caille domestique (*Coturnix coturnix japonica*). Ponte et étude de l'œuf au stade non incubé. *Arch. Anat. Histol. Embryol. norm. et exp.*, **1** (4) : 275-281.

KOCHAV S. M. GINSBURG and H. EYAL-GILADI (1980) — From cleavage to primitive streak formation : a complementary normal table and a new look at the first stages of the development of the chick II. Microscopic anatomy and cell population dynamics. *Dev. Biol.*, **98** : 441-473.

KOLLER, C. (1882) — Untersuchungen über die Blätterbindung im Hühnerkeim. *Arch. Mikrosk. Anat., 20* : 171-211.

LUTZ, H. (1964) — Le stade non incubé du blastoderme d'oiseau. *Arch. Anat. Histol. Embryol.*, **47** : 531-537.

PANDER, C. (1817) — *Historiam metamorphoseos quam ovum incubatum prioribus quinque diebus subit* : F.E. Nitribitt, Wirceburgi (69 pp).

RAUBER, A. (1876) — *Über die stellung des Hühnchens im Entwicklungsplan* W. Engelsmann, Leipzig (28 pp).

ROMEIS, W. (1948) — *Mikroskopische Technik.* 15. Aufl. Liebnitz, München (695 pp).

SILVERTON, R. and M. ANDERSON (1961) — *Handbook of Medical Laboratory Formulae.* Butterworths, London (676 pp).

VAKAET, L. (1962) — *Pregastrulatie en gastrulatie der Vogelkiem. Morfologische en experimentele studie.* Arscia, Brussel (244 pp).

VAKAET, L. (1970) — Cinephotomicrographic investigations of gastrulation in the chick blastoderm. *Arch. Biol. (Liège)*, **81** : 387-426.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 113-121 — Brussels 1993

Manuscript received on 4 May 1993

NEW AND RARE SPECIES OF *LECANE* AND *LEPADELLA* (ROTIFERA : LECANIDAE ; COLURELLIDAE) FROM BRAZIL

by

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ABSTRACT

The taxonomy and distribution of some new or rare species of the rotifer genera *Lecane* and *Lepadella* are discussed. *Lecane braziliensis* n. sp. and *Lepadella amazonica* n. sp. are described. The presence of *Lecane dumonti* SEGERS, *L. uenoi* YAMAMOTO, *Lepadella lindaui* KOSTE, *L. bicornis* VASISHT and BATTISH and *L. pterygoida* (DUNLOP) in the neotropical region is reported or confirmed.

Key words : Rotifera, taxonomy, zoogeography, *Lecane, Lepadella,* new species.

RESUMO

A taxonomia e distribuição de algumas espécies, novas, ou raras, de rotiferos dos gêneros *Lecane* e *Lepadella* são discutidas. São descritos duas novas espécies *Lecane braziliensis* n. esp. e *Lepadella amazonica* n. esp. A presença de *Lecane dumonti* SEGERS, *L. uenoi* YAMAMOTO, *Lepadella lindaui* KOSTE, *L. bicornis* VASISHT e BATTISH e *L. pterygoida* (DUNLOP) é registrada ou confirmada para a região neotropical.

INTRODUCTION

The aquatic habitats in the floodplain of the Amazon and Pantanal Rivers have a remarkably high rotifer diversity, equalled only by that of some other tropical floodplain areas such as those of the Niger (Africa : SEGERS *et al.*, 1993) or Murray-Darling (Australia : SHIEL and KOSTE, 1983). Of all these, however, it is the

Amazon basin which has received most attention by workers on Rotifera, especially by HAUER (1965) and KOSTE (e.g., 1972).

One of the sites studied recently is shallow waters on the Island of Maracá, Roraima, Brazil (KOSTE and ROBERTSON, 1990). While studying some replicate samples from the above-mentioned study, we found some specimens of the rotifer genera *Lecane* NITZSCH and *Lepadella* BORY DE ST. VINCENT which needed taxonomic reconsideration. Along with a report on these, some records of rare congeners, apparently not or unsatisfactorily reported from the neotropical region before, are provided.

MATERIAL AND METHODS

Samples are from the Island of Maracá, Roraima, Brazil (18 June 1987, leg. E. N. dos Santos-Silva and B. Robertson), from the Pantanal region : Rio Abobral, Paraguai and Miranda (27-29 August 1985, leg. A. L. de Oliveira-Neto), and from a pond near Lobo Reservoir, São Paulo (3 January 1990, leg. H. J. Dumont). All are qualitative and were taken with a 50, 55 or 67 µm plankton net, and preserved in formalin.

Measurements are in µm.

RESULTS

Lecane braziliensis SEGERS, n. sp.

Figs 1a-c

Type locality : Pond on Maracá Island, Roraima, Brazil.

Types : Female holotype, three female paratypes in the I.N.P.A., Manaus, Brazil (ROT-040, ROT-041), three female paratypes in the collection of the Institute of Animal Ecology, R.U.G.

Description

Female. Loricate species. Dorsal lorica plate anteriorly narrower, medially wider than ventral plate, with a pair of longitudinal folds and some irregular folds. Head aperture margins nearly coincident, straight, dorsally with slightly protruding median part, antero-lateral corners angulate. Ventral plate longer than wide, with incomplete transverse and longitudinal folds, ornamented. Lateral margins smooth, straight, with anterior notch. Lateral sulci deep. Foot plate relatively narrow, coxal plates rounded or irregularly deformed through fixation. Prepedal fold narrow, elongate, posterior margin medially with projection. Foot pseudosegment simple, slightly projecting. Toes fused over proximal half, slightly dilated from medially onwards. Claws completely separated, slightly less than half as long as the toes.

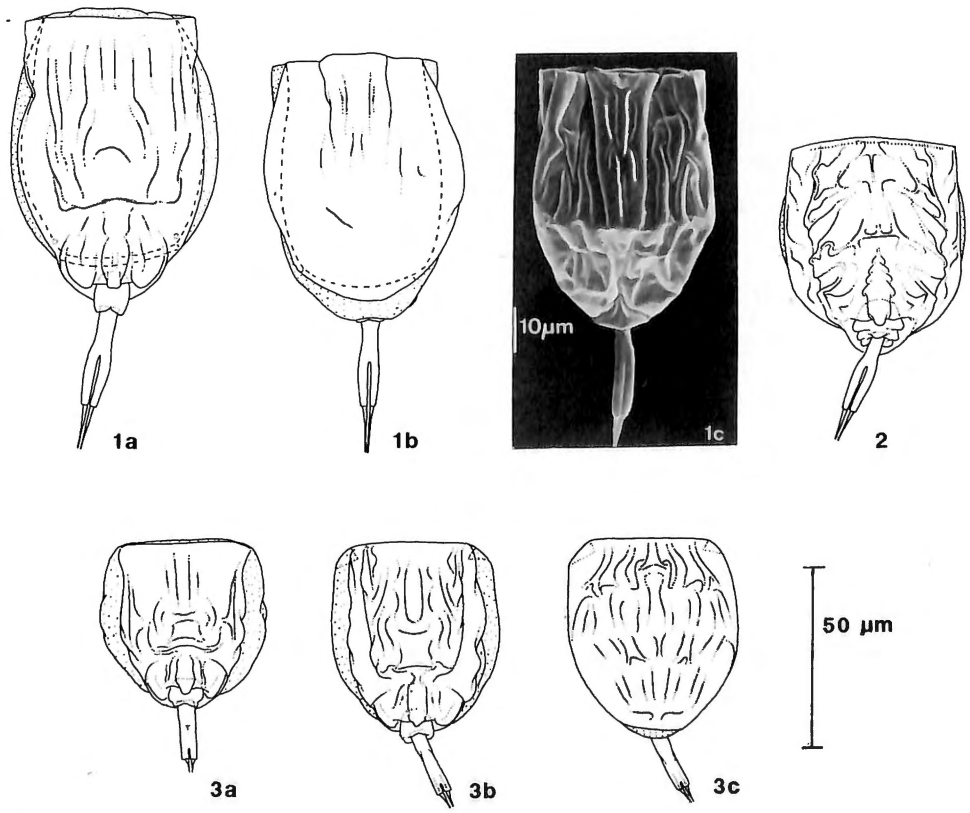
Male unknown.

Measurements

Dorsal plate length 67-74, dorsal plate width 46-57, ventral plate length 69-79, ventral plate width 43-50, toe length (without claws) 24-27 (fused part : 13-14), claw length 8-14.

Differential diagnosis

L. braziliensis n. sp. resembles *L. inopinata* HARRING and MYERS, 1926 and *L. sympoda* HAUER, 1929. The species, however, has a more elongate lorica than these two, and lacks the triangular antero-lateral projections of *L. sympoda*. The great length of its claws (8-14 µm, versus 3-5 µm in *L. inopinata* and 5-7 µm in *L. sympoda*), and the presence of strong longitudinal folds in the anterior region of the dorsal lorica provide an easy diagnostic feature for the species.



Figs 1-3. — 1. *Lecane braziliensis* n. sp. a : ventral view ; b : dorsal view ; c : dorsal view, S.E.M. photograph. — 2. *Lecane dumonti* SEGERS, ventral view. — 3. *Lecane uenoi* YAMAMOTO. 3a, b : ventral views, c : dorsal view.

Etymology

The specific name *braziliensis* is an adjective, derived from the name of the country where the species was found, Brazil.

Distribution

Several *L. braziliensis* n. sp. were found in a sample from the Island of Maracá, a single specimen occurred in a sample of the Rio Miranda, Pantanal region of Brazil.

Lecane dumonti SEGERS, 1993

Fig. 2

Material : Two female specimens from a pond on the Island of Maracá, Roraima, Brazil.

Comments

This remarkable species was recently described from a single locality in Nigeria (Lake Oguta, Imo State : SEGERS, 1993), and can now also be cited from Brazil. The present specimens differ only slightly from Nigerian ones, in being smaller. The distribution of *L. dumonti* is as that of *Lepadella minoruoides* KOSTE and ROBERTSON, 1983 (SEGERS *et al.*, 1993). Formulating a hypothesis that explains this distribution pattern seems at present unjustified.

Measurements

Dorsal plate length 56 (59-69), dorsal plate width 50 (58-67), ventral plate length 59 (66-71), ventral plate width 49 (53-65), toe length (without claws) 24 (23-25) (fused part : 9 (9-13)), claw length 8 (11-14)(Nigerian specimens between brackets).

Lecane uenoi YAMAMOTO, 1951

Figs 3a-c

Synonym : L. rugosa (HARRING, 1914) after KOSTE (1974)

Material : Several female specimens from a pond near Lobo reservoir, São Paulo ; single female specimen from a pond on Maracá Island, Roraima, Brazil.

Comments

L. uenoi is the only *Lecane* combining incompletely fused toes and a dorsal lorica being consistently broader than the ventral lorica. By this, the small species can hardly be confused with any congener. The Brazilian specimens deviate in some minor details from YAMAMOTO's (1951) description of the species. The shape of the head aperture margins differs slightly, variably pronounced ornamentations of the

lorica are present and the claws are parallel, not diverging in the Brazilian specimens. All these characters are, however, known to be subject to intraspecific variation in the genus.

The area of *L. uenoi* is insufficiently documented. The species is only known from its type locality in Japan (Rokujizo pond, Kyoto prefecture : YAMAMOTO, 1951), and from three localities in Brazil.

Measurements

Dorsal plate length 44-53 (50), dorsal plate width 46-48 (48), ventral plate length 47-52 (50), ventral plate width 35- 41 (41), toe length (without claws) 14-18 (14), claw length 4-5 (4)(Japanese specimen between brackets).

Lepadella amazonica SEGERS, n. sp.

Figs 4a-e

Synonym : L. quinquecostata (LUCKS, 1912) after KOSTE (1974) and KOSTE (1978), partim.

Type locality : Pond on Maracá Island, Roraima, Brazil.

Types : Female holotype in the I.N.P.A., Manaus, Brazil (ROT- 042), female paratype in the collection of the Institute of Animal Ecology, R.U.G.

Description

Female. Lorica elongate, width about two thirds of length. Head aperture ventrally a deep V-shaped sinus, dorsally semicircular in anterior view, concave in dorsal view, with stippled collar. Lorica dorsally with three groups of longitudinal carinas : one middorsal and a pair of lateral groups, each group consisting of two blunt carinas, fused caudally in the middorsal group. Edge of lorica laterally slightly curved, caudally nearly straight. Foot with tree distinct pseudosegments, the distal one the longest. A pair of equal-sized toes present.

Male unknown.

Measurements

Lorica length 77-90, width 53-60. Head aperture width 26-32, depth ventrally 15-16, dorsally 5-7. Foot aperture width 15, length 22. Toe length 20-23.

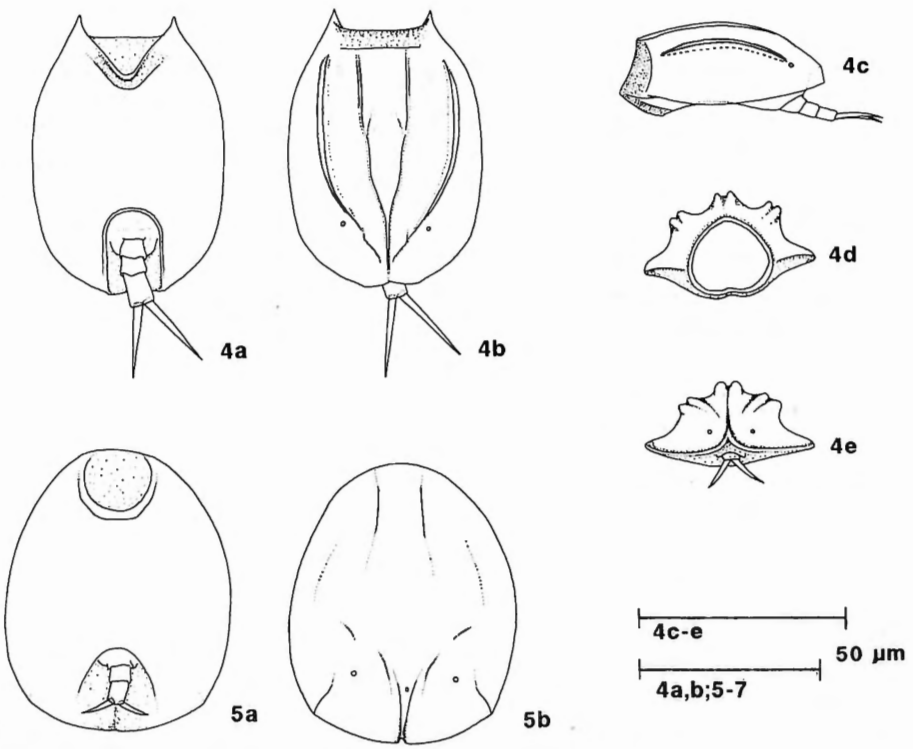
Differential diagnosis

L. amazonica n. sp. is characterised by the configuration and shape of the longitudinal carinas on its dorsal lorica. Three groups of blunt, longitudinal carinas are present : one middorsal group of two carinas, fused distally, and two lateral ones. In this, the species differs from *L. quinquecostata* (LUCKS, 1912) (see figs 10a-g in SEGERS *et al.*, 1992), which has five sharp, longitudinal carinas (one middorsal,

two intermediate and two lateral), situated at regular distances. Additionally, the general shape of lorica of *L. quinquecostata* clearly differs from *L. amazonica* n. sp. in being flatter and more elongate, and in having a differently shaped head aperture. *L. berzinsi* SEGERS, 1993 (figs 2a-e in SEGERS, 1993) has a similar general shape of lorica, but the disposition of its six sharp, longitudinal carinas in three pairs (middorsal, intermediate and lateral) is different.

Etymology

The specific name *amazonica* is an adjective, derived from the species' area.



Figs 4-5. — 4. *Lepadella amazonica* n. sp. a : ventral view, b : dorsal view, c : lateral view, d : frontal view, e : caudal view. — 5. *Lepadella lindaui* Koste. a : ventral view, b : dorsal view.

Distribution

L. amazonica n. sp. is known from the type locality and from the shore of the Rio Tapajós near Santarém, Brazil. The species appears to be endemic to of the Amazon region.

Affiliation

Although easily distinguished from it, *L. amazonica* n. sp. seems most closely related to *L. berzinsi,* taking into account the similar general shape of lorica and the presence of six carinas in both species. As *L. amazonica* n. sp. and *L. berzinsi* can be considered endemics of South America resp. Africa, the species-pair may represent a case of vicariance.

Lepadella lindaui KOSTE, 1981

Figs 5a, b

Material : Five female specimens from a pond on the island of Maracá, Roraima, Brazil.

Comments

The species closely resembles *L. apsida* HARRING, 1916 by the shape of its lorica and head aperture, but is easily distinguished by the presence of longitudinal ridges on its dorsal lorica.

L. lindaui is known from Australia (Winmurra Billabong) and Africa (Mombasa, Kenya : KOSTE, 1981, Abadaba Lake, Imo State, Nigeria, leg. S. N. Umeham), and now also from Brazil. The species appears to be pantropical.

Lepadella bicornis VASISHT and BATTISH, 1971

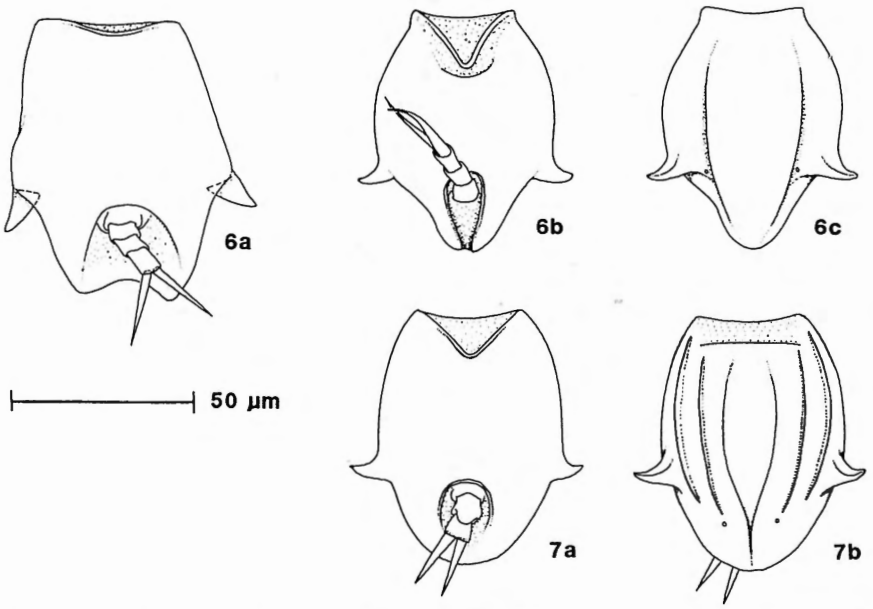
Figs 6a-c

Synonyms : L. ehrenbergii (PERTY, 1850) after KOSTE (1974). *L. pterygoides* (DUNLOP, 1897) (sic.) after BRANDORFF *et al.* (1982), KOSTE (1978), partim. *L. pterygoides* (sic.) after KOSTE (1978), partim.

Material : One specimen of *L. bicornis* in samples from the Rio Abobral and Rio Paraguai each (Pantanal region, Brazil).

Comments

L. bicornis is characterised by its equally-long toes, the presence of lateral projections on the lorica and by its dorsal lorica having a broad, elongate central dome. Other *Lepadella*'s with lateral projections on the lorica are (see KOSTE, 1978 ; 1981) : *L. triptera* EHRENBERG, 1830 f. *alata* MYERS, 1934 ; *L. ehrenbergii* (PERTY, 1850), *L. pterygoida* (DUNLOP, 1897) and *L. minorui* KOSTE, 1981. The first-named differs from *L. bicornis* by its more or less triangular cross- section, with sharp mid-



Figs 6-7. — 6. *Lepadella bicornis* Vassist and Battish. a, b : ventral views, c : dorsal view. — 7. *Lepadella pterygoida* (Dunlop). a : ventral view, b : dorsal view.

dorsal edge. *L. ehrenbergii* has unequally long toes, *L. pterygoida* is characterised by the presence of six longitudinal ridges on its dorsal lorica (Figs 7a-b). *L. minorui* has a lorica covered with minute spines, bifid lateral projections, and a triangular cross-section with a sharp middorsal crest.

L. bicornis was originally described from North India (VASISHT and BATTISH, 1971). KOSTE (1974) and BRANDORFF *et al.* (1982) figured what appears to be this species from the Amazon region, Brazil (Rio Tapajós and Rio Nhamunda, resp.). The record by BRANDORFF *et al.* (1982) is, according to KOSTE and JOSÉ DE PAGGI (1982), the only record of *L. pterygoida* from the neotropical region. Its presence in South-America can, nevertheless, be confirmed by our record from the Pantanal region, Brazil (Rio Paraguai : Figs 4a-b). *L. pterygoida* can be considered cosmopolitan : records are from Japan (YAMAMOTO, 1960), U.S.A. and U.K. (HARRING, 1916).

ACKNOWLEDGEMENTS

The present study was supported by the Belgian Administration for Development and Cooperation through the « International training course on Lake Zooplankton : A tool in Lake Management » by grants to E. N. dos Santos-Silva and A. L. de Oliveira-Neto.

REFERENCES

BRANDORFF, G.-O., W. KOSTE and N. N. SMIRNOV (1982) — The Composition and Structure of Rotiferan and Crustacean Cummunities of the lower Rio Nhamunda, Amazonas, Brazil. *Stud. Neotrop. Fauna Environ.*, **17** : 69-121.

HARRING, H. K. (1916) — A revision of the rotatorian genera *Lepadella* and *Lophocharis* with descriptions of five new species. *Proc. U. S. Nat. Museum*, **51** : 527-568.

HAUER, J. (1965) — Zur Rotatorienfauna des Amazonasgebietes. *Int. Rev. ges. Hydrobiol.*, **50** (3) : 341-389.

KOSTE, W. (1972) — Rotatorien aus Gewässern Amazoniens. *Amazoniana*, **III** (3/4) : 258-505.

KOSTE, W. (1974) — Zur Kenntnis der Rotatorienfauna der « Schwimmenden Wiese », einer Uferlagune in der Várzea Amazoniens, Brasilien. *Amazoniana*, **V** (1) : 25-59.

KOSTE, W. (1978) — *Rotatoria.* Die Rädertiere Mitteleuropas (Überordnung Monogononta). Begr. v. M. VOIGT, 2 Vols, Gebr. Borntraeger, Stuttgart.

Koste, W. (1981) — Zur Morphologie, Systematiek und Ökologie von neuen monogononten Rädertieren (Rotatorien) aus dem Überschwemmungsgebiet des Magela Creek in der Alligator-River-Region Australiens, N.T. Teil I. *Osnabrücker naturwiss. Mitt.*, **8** : 97-126.

KOSTE, W. and S. JOSÉ DE PAGGI (1982) — Rotifera of the Superorder Monogononta recorded from Neotropis. *Gew. Abwässer*, **68-69** : 71-102.

KOSTE, W. and B. ROBERTSON (1990) — Taxonomic Studies of the Rotifera from Shallow Waters on the Island of Maracá, Roraim, Brazil. *Amazoniana*, **XI** (2) : 185-200.

SEGERS, H. (1993) — Rotifera of some lakes in the floodplain of the River Niger (Imo State, Nigeria). I. New species and other taxonomic considerations. *Hydrobiologia*, **250** : 39-61.

SEGERS, H., N. EMIR and J. MERTENS (1992) — Rotifera from north and northeast Anatolia (Turkey). *Hydrobiologia*, **245** : 179-189.

SEGERS, H., C. S. NWADIARO and H. J. DUMONT (1993) — Rotifera of some lakes in the floodplain of the River Niger (Imo State, Nigeria). II. Faunal composition and diversity. *Hydrobiologia*, **250** : 63-71.

SHIEL, R. and W. KOSTE (1983) — Rotifer communities of billabongs in northern and southeastern Australia. *Hydrobiologia*, **104** : 41-47.

VASISHT, H. S. and S. K. BATTISH (1971) — The rotifer fauna of North India. *Lepadella* and *Colurella. Res. Bull. (N.S.) panjab Univ.*, **22** : 189-192.

YAMAMOTO, K. (1951) — On six new Rotatoria from Japan. *Ann. Zool. Japon.*, **24** (3) : 157-162.

YAMAMOTO, K. (1960) — Plankton Rotatoria in Japanese inland waters. *Hydrobiologia*, **16** (4) : 364-411.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 123-127 — Brussels 1993

Manuscript received on 19 May 1993

ALTICA AENESCENS (WEISE, 1888) (COLEOPTERA : CHRYSOMELIDAE) : A NEW FLEA BEETLE FROM BELGIUM AND HOW TO DISCRIMINATE IT FROM *ALTICA LYTHRI* AUBÉ, 1843

by

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SUMMARY

Altica aenescens (WEISE, 1888) is recorded for the first time from Belgium. A comparison is made between the morphological characteristics of *A. aenescens* and the closely related *Altica lythri* AUBÉ, 1843, especially in what concerns the SEM morphology of the male genitalia.

Key words : Alticinae, Altica sp., characterisation, male genitalia

INTRODUCTION

From the genus *Altica* (Coleoptera : Chrysomelidae) 13 species are known in Northern Europe (LUCHT, 1987), including several groups of sibling species (KEVAN, 1962 ; KRÁL, 1966 ; PHILLIPS, 1979).

KRÁL (1966) gives a detailed overview of the nomenclatural and systematic confusion within the species-complex *A. aenescens* (WEISE, 1888), *A. lythri* AUBÉ, 1843 and *A. ampelophaga* (GUÉRIN, 1859). All are larger species (> 4 mm), without strongly pronounced humeral cali and with two longitudinal keels on the ventral part of the aedeagus. Correct identification of these species is only possible after studying the male genitalia (KRÁL, 1966 ; MOHR, 1966) and from a knowledge of the host plants. *A. aenescens* is a northern species (KRÁL, 1966) feeding on *Betula sp.*. *A. lythri*, which is a very common species in Belgium, feeds on *Epilobium sp.* and *Lythrum salicaria*. *A. ampelophaga* feeds on *Vitis sp.* (KRÁL, 1966) and has a more southern distribution.

DERENNE (1963) only reports *A. lythri* from Belgium. LUCHT (1987) mentions the species from the Benelux, but not from which country.

MATERIAL AND METHODS

Material belonging to the complex discussed by KRÁL (1966), was found in a malaisetrap and two pitfall traps, placed in the nature reserve « Groot Schietveld » (Brasschaat, FS.08), during the month of May 1989, in a habitat dominated by *Calluna vulgaris* and *Erica tetralix*, with several forest patches of *Betula pendula* and *Myrica gale*. Additional animals were caught on *Betula pendula*, using a sweepnet. This material was compared with animals caught on *Epilobium hirsutum* in Deurne.

For identification of the *Altica* species the genitalia were dissected and mounted on aluminium stubs with double sided Scotch tape, sputtercoated with gold and examined with a Phillips Scanning Electron Microscope 515, at an accelerating voltage of 20 kV. The total width (broadest part elytra) and length (frons-apical suture elytra) of the beetles were measured using a Wild Censor (accuracy 0.005 mm) attached to a Wild M5 binocular microscope.

RESULTS

The specimens caught on *Betula sp.* and those found in the malaisetrap were identified as *A. aenescens* (WEISE, 1988), a species new to Belgium. In the malaisetrap 3 males and 9 females were caught. The material swept from *Betula* consisted of 2 males and 34 females. The specimens caught on *Epilobium hirsutum* (7 males and 11 females) were identified as *A. lythri.* Identification is based on study of the male genitalia and knowledge of the hostplant.

All external morphological characters used by Král (1966) to distinguish between *A. aenescens* and *A. lythri*, overlap in variability. In most cases the body coloration of *A. aenescens* shows a violet faint on a dark blue colouration, which is not present in *A. lythri.*

The body lengths (tl) of males and females of the two species do not differ significantly (Mann-Withney U test) (Table 1). Both for males and for females pronotum width (pw) differs significantly between species (Mann-Withney U test, $p < 0.05$) (Table 1).

For a correct identification, a study of the genitalia is necessary. The genitalia of all male specimens were studied using SEM. We give a diagnosis and a clear description of the male genitalia of *A. aenescens* and *A. lythri*, illustrated with SEM pictures. The aedeagi of both species are subtruncate and nipple-shaped at the apex (Fig. 1). Ventrally two longitudinal keels are present. There are no visible differences in the basal foramen. In both species the median apical part on the dorsal side (Fig. 1 : 2, 5) is divided into three subparts. Ventrally both (Fig. 1 : 1, 4) have lateral depressions at the apices.

TABLE 1

Basic statistics of the body measurements. — lythri, *Altica lythri*; aenes, *Altica aenescens*; m, male; f, female; char., character measured; tl, total body length; pw, pronotum width; n, number of animals measured; min., minimum length; max., maximum length; st.dev.; standard deviation; M-W U test, results Mann-Withney U test.

species	sex	char.	n	min.	max.	mean	st.dev.	M-W U test
lythri	m	tl	7	4.175	4.600	4.407	0.148	U = 11.500
aenes.	m	tl	5	4.150	4.925	4.605	0.336	n.s.
lythri	f	tl	10	4.700	5.400	5.103	0.229	U = 45.000
aenes.	f	tl	10	4.700	5.500	5.085	0.257	n.s.
lythri	m	pw	7	2.075	2.250	2.150	0.066	U = 3.500
aenes.	m	pw	5	2.150	2.450	2.305	0.115	$p < 0.05$
lythri	f	pw	10	2.275	2.600	2.465	0.087	U = 23.500
aenes.	f	pw	10	2.325	2.800	2.553	0.128	$p < 0.05$

The aedeagus of *A. aenescens* (Fig. 1 : 4, 5, 6) is parallel-sided and does not broaden at the apex. Both in dorsal and ventral view the aedeagus of *A. lythri* (Fig. 1 : 1, 2, 3) broadens towards the apex.

In ventral view the aedeagus of *A. aenescens* (Fig. 1 : 4) has subapical depressions on both sides proceeding zones of lateral striae which become shorter and fainter and finally disappear halfway along the aedeagus. There is a small median groove that runs for a quarter of the length of the aedeagus starting just behind the apex. Two slender, deep and slightly curved depressions divide the apical third into three zones. In *A. lythri*, in ventral view (Fig. 1 : 1) the subapical depression is also present on both sides, but is deeper and longer than in *A. aenescens*. This depression also proceeds zones of lateral striae, but in this species they are much more strongly developed and extend over half the length of the aedeagus.

In dorsal view the aedeagus of *A. aenescens* (Fig. 1 : 5) has a large median depression at the apex. Between half and three quarters along the aedeagus there is a zone with moderately developed transverse undulations. In *Altica lythri* (Fig. 1 : 2) the zone of transverse undulations is also present, but the central part of the median apical zone is relatively smaller than in *A. aenescens*.

In lateral view the aedeagus of *A. aenescens* (Fig. 1 : 6) is straight and robust. In *A. lythri* (Fig. 1 : 3) the aedeagus is slender (less robust) in lateral view, with

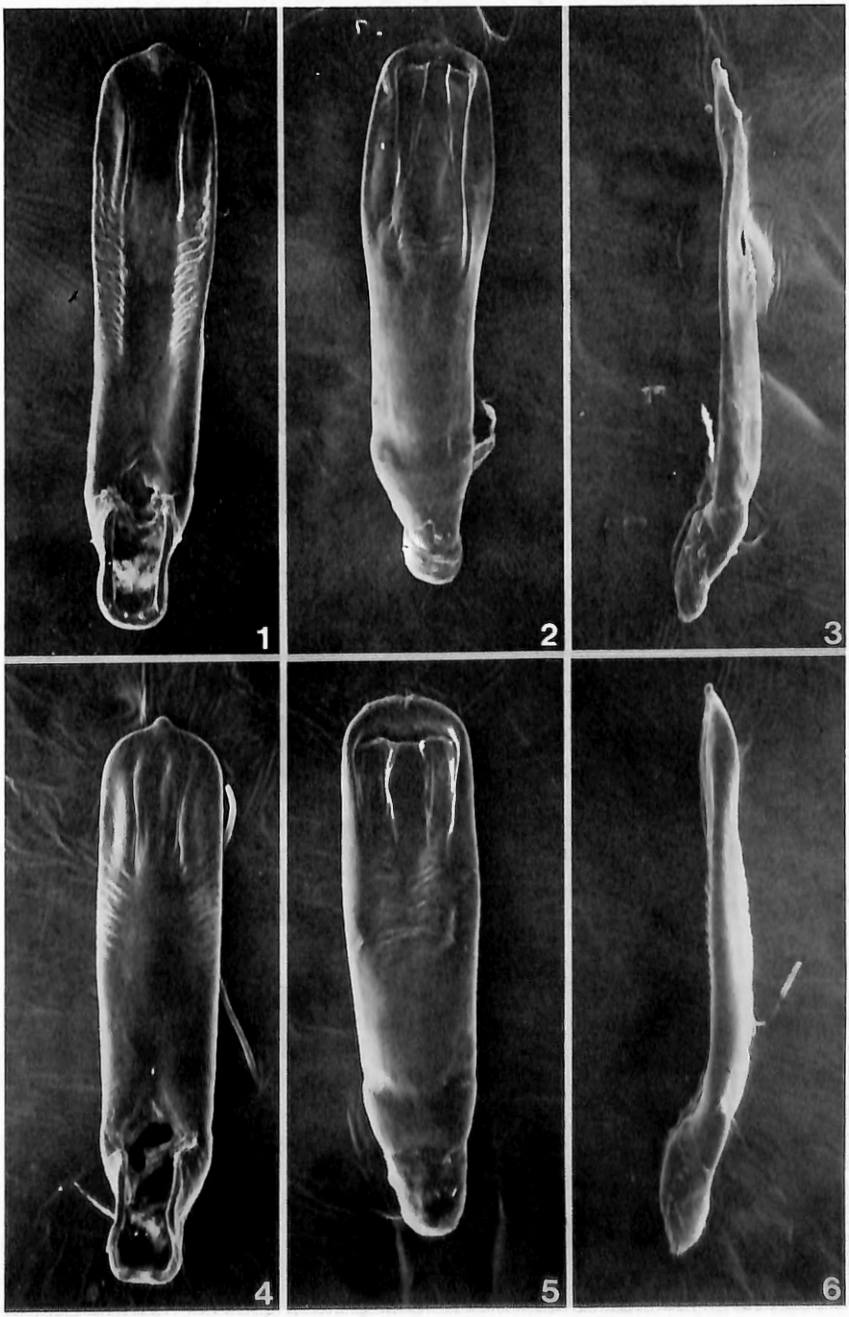

Fig. 1. — Aedeagus *Altica lythri* : 1 : ventral view. 2 : dorsal view. 3 : lateral view. — Aedeagus *Altica aenescens* : 4 : ventral view. 5 : dorsal view. 6 : lateral view.

small lateral margins. The end of the foramen has a « turned-up nose »-like appearance. In *A. aenescens* this uptilting is not as conspicuous.

The spermatheca of both species is very variable and lack species-specific differences. Both belong to the natural group in which the stem of the spermathecal tube is short (KEVAN, 1962).

DISCUSSION

A. aenescens and *A. lythri* are very closely related. Intraspecific variation of these species is large. This agrees with PHILLIPS (1979) who stated that several morphological characters used to segregate the British *Altica* species are in fact unreliable because of intraspecific variation.

As both species feed on very different hostplants, the hostplant is a reliable means of identification. The male genitalia of the two species show morphological differences and indicate that the animals feeding on the two hostplants, are good biological species. Further research should certainly include a study of the genetic isolation of these species.

ACKNOWLEDGEMENTS

We would like to thank Prof. Dr. D. Scheuermann for providing the necessary working conditions to make the SEM pictures and A. Lemouche for weekly emptying the traps.

LITERATURE

DERENNE, E. (1963) — *Catalogue des coléoptères de Belgique. Fasc. IV. Chrysomeloidea Chrysomelidae*. Société Royale d'Entomologie de Belgique, Bruxelles (104 pp).

KEVAN, D.K. (1962) — The British species of the genus *Haltica* Geoffroy (Col., Chrysomelidae). *Ent. Mon. Mag.*, **98** : 189-196.

KRÁL, J. (1966) — Zur Kenntnis der paläarktischen *Altica*-Arten 3. *Entom. Blätter*, **62** : 53-61.

LUCHT, W.H. (1987) — Katalog. In : *Die Käfer Mitteleuropas*. FREUDE, H., HARDE, K.W. and LOHSE, G.A. (Eds.). Goecke & Evers, Krefeld. 1-342.

MOHR, K.H. (1966) Familie : Chrysomelidae. In : *Die Käfer Mitteleuropas*. FREUDE, H., HARDE, K.W. and LOHSE, G.A. (Eds.). Goecke & Evers, Krefeld, **9** : 95-298.

PHILLIPS, W. M. (1979) — A contribution to the study of species relations within the chrysomelid genus *Altica* Müller in Britain. *Zool. J. Linn. Soc.*, **66** (3) : 289-308.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 129-134 — Brussels 1993

Manuscript received on 25 May 1993

FIVE LINYPHIIDAE NEW TO EUROPE, WITH DESCRIPTION OF *PELECOPSIS POOTI* SP. N. (ARANEAE : LINYPHIIDAE)

by

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SUMMARY

Pelecopsis pooti sp. n. is described from the south of Spain. *Lepthyphantes ritae* BOSMANS, *Oedothorax tingitanus* (SIMON), *Pelecopsis coccinea* (O.P. CAMBRIDGE) and *Typhochrestus bifurcatus* SIMON are new to Europe and Spain.

Key words : Linyphiidae, Europe, distribution, *Pelecopsis*.

RÉSUMÉ

Pelecopsis pooti sp. n. est décrite du sud de l'Espagne. *Lepthyphantes ritae* BOSMANS, *Oedothorax tingitanus* (SIMON), *Pelecopsis coccinea* (O.P. CAMBRIDGE) et *Typhochrestus bifurcatus* SIMON sont nouveaux pour l'Europe et l'Espagne.

INTRODUCTION

Whereas a larger part of North African Linyphiidae is actually fairly well known by a series of papers on this subject (BOSMANS, 1985a, 1985b, 1991 ; BOSMANS and ABROUS, 1990, 1992 ; BOSMANS and BOURAGBA, 1992 ; BOSMANS and DE SMET, 1993), the linyphiid fauna of mediterranean Europe remains poorly studied.

MATERIAL AND METHODS

In the collections of the Institut royal des Sciences naturelles de Belgique (IRSNB), the collection of Piet Poot (CPP) and the collection of the junior author five species were discovered of which one is new to science, and four new to Spain

and Europe. The new species is described below, and the distribution data of the four others are presented.

RESULTS

Pelecopsis pooti sp. n.

(Figs 1-8)

Type material

Holotype male from Spain, Huelva, Matalascañas, in dunes, 8.IV.1988, R., M. and J. Jocqué leg. (IRSNB). Paratypes : 2 ♂♂ 5 ♀♀, same data (IRSNB) ; ibidem, 1 ♂ 1 ♀, 17.IV.1991, P. Poot leg. (CPP).

Diagnosis

Closely related to other members of the *P. bucephalus* group particularly to *P. bicornuta* HILLYARD, 1980, *P. bucephala* (O.P. CAMBRIDGE, 1875) and *P. modica* HILLYARD, 1980, occurring in the same region. Males differ by the shape of the cephalic tubercle and the tibial apophysis without additional teeth ; females can be distinguished by the small posterior tubercles and the rectangular postero-median plate in the epigyne.

Description

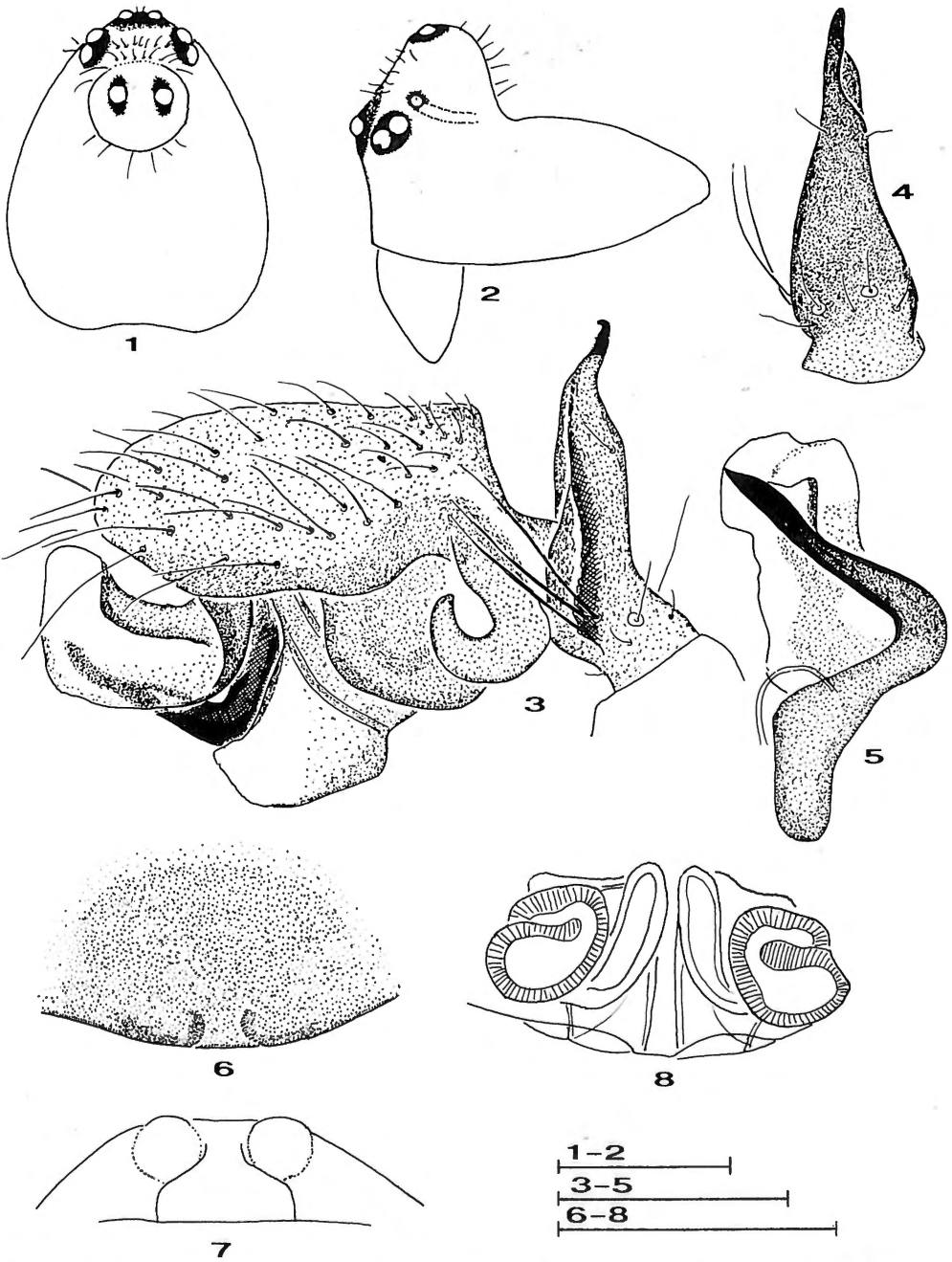
Measurements (in mm). Male : total length 2.3 (2.1-2.3) ; cephalothorax 1.10 (0.91-1.10) long, 0.80 (0.74-0.80) wide. Female : total length 2.1-2.3 ; cephalothorax 0.90-0.96 long, 0.74-0.80 wide. Legs :

	Fe	Pa	Ti	Mt	Ta	TbMtI
I	0.72	0.23	0.60	0.54	0.36	0.62
IV	0.88	0.22	0.74	0.68	0.36	—

Colour. Cephalothorax reddish brown, striae, margin and eye region darkened ; sternum brownish black ; legs yellowish orange ; abdomen black, with purplish black scutum.

Cephalothorax. (Figs 1-2). Male : with well-developed cephalic lobe provided with long hairs ; region of anterior median eyes protruding, region between median eyes flattened ; posterior median eyes separated by 2.5 times their diameter ; sulci small, narrower than the diameter of a lateral eye, continuing posteriorly into a narrow groove ; thoracic part with punctate striae.

Sternum. Moderately punctate ; reticulated, especially at sides.



Figs 1-8. *Pelecopsis pooti* sp. n. — 1. Male cephalothorax, dorsal view. — 2. Idem, lateral view. — 3. Male palp, retrolateral view. — 4. Male palpal tibia, dorsal view. — 5. Embolic division, prolateral view. — 6. Epigyne, ventral view. — 7. Idem, posterior view. — 8. Vulva. [Scale lines : 0.5 mm (1-2) ; 0.2 mm (3-8)].

Legs. Male : without dorsal spines. Female : all tibiae with 1 dorsal spine, as long as the diameter of the segment.

Scutum. Covering 9/10 of the abdominal dorsum, densely punctated.

Male palp (Figs 3-5). Tibia provided with a long antero-dorsal apophysis, without additional teeth ; protegulum produced anteriorly ; embolus at angle of 90° to median part of radix, terminally widened ; tailpiece rounded posteriorly.

Epigyne (Figs 6-7). Obscure, with two small posterior tubercles. Postero-median plate rectangular.

Vulva. Fig. 8.

Distribution

Only known from the Atlantic coast in Andalucia in southern Spain.

Pelecopsis coccinea (O.P. CAMBRIDGE, 1875)

Material examined

Spain, Cadiz, Tarifa, 1 ♂ 3 ♀♀, P. Poot leg. (CPP, CRB).

Distribution

This species was described from an unknown locality in Morocco (O.P. CAMBRIDGE 1875). In their revision of the *Pelecopsis* species of North Africa, BOSMANS and ABROUS (1992) were unable to add new localities. It is cited here for the first time in Europe.

Oedothorax tingitanus (SIMON, 1884)

Material examined

Spain, Malaga, San Pedro Alcantara, 4♂♂, V.1963, G. Fagel leg. (IRSNB).
Cadiz, Tarifa, 2 ♂♂ 2 ♀♀ III.1992, P. Poot leg. (CPP, CRB).

Distribution

This species was cited from Morocco (SIMON, 1884 ; DENIS, 1968) and from Algeria (SIMON, 1894). According to BOSMANS (1985a) it is common in marshy places in the North of Tunisia, Algeria and Morocco. New to Europe.

Typhochrestus bifurcatus SIMON, 1884

Material examined

Spain, Granada, Anjaron, 4 ♂♂ 10.V.1961, G. Fagel leg. (IRSNB).

Distribution

Described from one locality in Algeria (SIMON, 1884), this species appeared to be common in N.E. Algeria and N. Morocco (BOSMANS and ABROUS, 1990). New to Europe.

Lepthyphantes ritae BOSMANS, 1985

Material examined

Spain, Cadiz, Tarifa, 1 ♀, IV.1990, P. Poot leg. (CPP).

Distribution

Common all over the north of Algeria, and known from one locality in Morocco (BOSMANS, 1985b). New to Europe.

ACKNOWLEDGEMENTS

We are grateful to L. Baert (IRSNB) and P. Poot (Maastricht) for the loan and donation of material.

REFERENCES

BOSMANS, R. (1985a) — Etudes sur les Linyphiidae nord-africaines, II. Le genre *Oedothorax* BERTKAU en Afrique du Nord, avec une revision des caractères diagnostiques des mâles des espèces ouest-paléarctiques. *Biol. Jb. Dodonaea*, **53** : 58-75.

BOSMANS R. (1985b) — Etudes sur les Linyphiidae nord-africaines, III. Les genres *Troglohyphantes* JOSEPH et *Lepthyphantes* MENGE en Afrique du Nord (Araneae : Linyphiidae). *Revue arachnol.*, **6** : 135-178.

BOSMANS, R. (1991) — Etudes sur les Linyphiidae nord-africaines, IV. Le genre *Sintula* SIMON en Afrique du Nord (Araneae : Linyphiidae). *Rev. arachnol.*, **10** : 21-51.

BOSMANS, R. and ABROUS, O. (1990) — Studies on North African Linyphiidae, V. The genus *Typhochrestus* SIMON, 1884 in North Africa (Araneae : Linyphiidae). *Bull. Inst. r. Sci. nat. Belgique*, **60** : 19-37.

BOSMANS, R. and ABROUS, O. (1992) — Studies on North African Linyphiidae, VI. The genera *Pelecopsis* SIMON, *Trichopterna* KULCZYNSKI and *Ouedia* gen. n. (Araneae : Linyphiidae). *Bull. Br. arachnol. Soc.*, **9** : 65-85.

BOSMANS, R. and BOURAGBA, N. (1992) — Trois nouvelles Linyphiidae de l'Atlas Algérien, avec la description du mâle de *Lepthyphantes djazairi* BOSMANS, et la redescription de *Lepthyphantes homonymus* DENIS (Araneae). *Bull. Ann. Soc. r. belge Ent.*, **128** : 245-262.

BOSMANS, R. and DE SMET, K. (1993) — Etudes sur les Linyphiidae nord-africaines, I. Le genre *Walckenaeria* BLACKWALL en Afrique du Nord (Araneae : Linyphiidae). *Rev. arachnol.*, **10** : 21-51.

CAMBRIDGE, O.P. (1875) — On some new species of *Erigone*. *Proc. zool. Soc. London*, **1875** : 190-224.

DENIS, J. (1968) — Notes d'aranéologie marocaine. X. Les erigonides du Maroc. *Bull. Soc. Sci. nat. phys. Maroc*, **47** : 379-390.

SIMON, E. (1884) — *Les arachnides de France*, **5** (3) : 421-885. Roret, Paris.

SIMON, E. (1894) — *Histoire naturelle des Araignées*, **1** (3) : 488-760. Rovet, Paris.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 135-157 — Brussels 1993

MORPHOLOGY OF THE PECTORAL GIRDLE IN *POMATOSCHISTUS LOZANOI* DE BUEN, 1923 (GOBIIDAE), IN RELATION TO PECTORAL FIN ADDUCTION

by

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SUMMARY

Like most gobies, *Pomatoschistus lozanoi* is a benthic fish species. During locomotion the pectoral fin adduction is of great importance in generating a forward propulsion. Several specimens of *Pomatoschistus lozanoi* were dissected, cleared with staining and sectioned with staining, in order to examine the morphology of the pectoral girdle-apparatus. In this paper a detailed description is given of the skeletal elements, the musculature and the ligaments of the pectoral girdle-apparatus. The pectoral fins of gobies seem better adapted to powerful adduction than a generalised teleost. The proximal radials form a large rigid shoulder plate with a long distal margin on which a high pectoral fin articulates. The fin muscles are strongly developed and assure, together with the large pectoral fin, powerful — drag based — pectoral propulsion. The morphological adaptations for powerful adduction, however, are at cost of the maneuvering abilities of the pectoral fins.

Keywords : Pomatoschistus lozanoi, morphology, pectoral fin, adaptation, locomotion.

INTRODUCTION

Pomatoschistus lozanoi (Fig. 1) is one of the most abundant fishes in the European coastal waters, occuring from the Wadden Sea up to South-Portugal and around the British Isles (HAMERLYNCK *et al.*, 1990).

Related to its benthic life style, locomotion occurs by short hops and darts, remaining close to the bottom and frequently resting on it between darts. Propulsion is generated by combined adduction of the pectoral fins and tail beating. Aquarium observations show that pectoral fin adduction is especially important in generating the lift needed for leaving the bottom. The pectoral fins also serve as supporting structures when lying on the bottom, preventing the body from rolling over. The present study provides a description of the pectoral girdle-apparatus and discusses some functional aspects of its adduction.

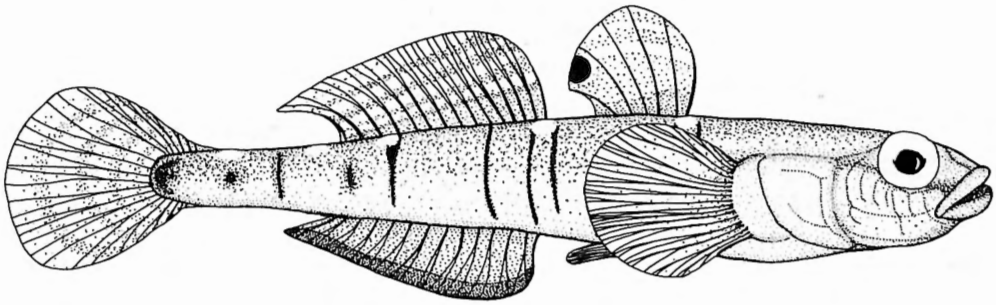


Fig. 1. — Habitus of *Pomatoschistus lozanoi.*

MATERIAL AND METHODS

Four specimens of *Pomatoschistus lozanoi* were identified according to HAMERLYNCK (1990), sexed and measured.

Specimen 1 (male, SL = 51.30 mm, TL = 60.55 mm), specimen 2 (female, SL = 50.70 mm, TL = 59.65 mm), specimen 3 (female, SL = 45.00 mm, TL = 54.00 mm), specimen 4 (male, SL = 44.40 mm, TL = 52.25 mm), specimen 5 (female, SL = 48.65, TL = 56.10) and specimen 6 (male, SL = 50.15 mm, TL = 59.95 mm) were dissected, after being stained with alizarin red S and alcian blue.

Specimen 7 (male, SL = 47.30 mm, TL = 56.90 mm) was cleared and the skeletal elements were stained with alizarin red S and alcian blue, as described by HANKEN and WASSERSUG (1981), but the trypsin was replaced with a 2 % KOH solution.

Specimen 8 (female, SL = 48.10 mm, TL = 56.70 mm) was embedded in Technovit 7100. Serial cross sections (5 µm) were made and stained with toluidin.

Specimens 1 to 7 were studied using a stereoscopic microscope (WILD M5) and specimen 8 was examined using a light microscope (WILD M12).

RESULTS

Osteology

In the skeletal part of the pectoral girdle-apparatus three functional units can be distinguished : (1) the shoulder girdle, which is dorsally attached to the skull and functions as the suspension unit for the shoulder- and finplate ; (2) the shoulder plate, firmly attached to the former element and (3) the actual fin plate, consisting of fin rays that articulate with the shoulder plate.

These skeletal elements consist of cartilage, with corresponding perichondral ossifications, and dermal bones. These elements may be fused or interconnected with short collagen fibres.

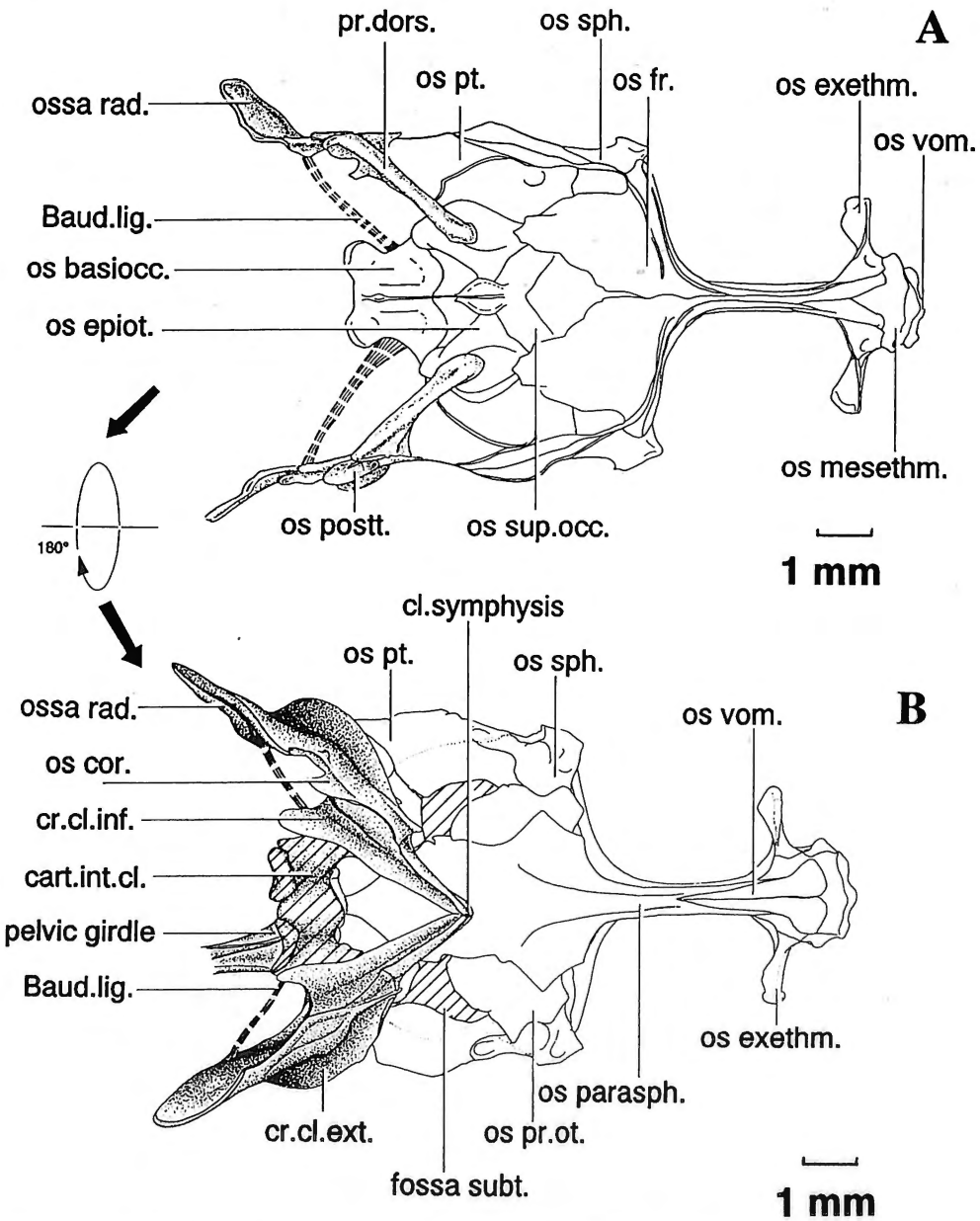


Fig. 2. — Dorsal (A) and ventral (B) view of the neurocranium and pectoral girdle-apparatus in *Pomatoschistus lozanoi* (shaded areas : cartilage). (Abbreviations : see list on p. 153).

The shoulder girdle

os posttemporale (Fig. 2A-B, 3C, 4A-C, 5A-B). The suspension of the pectoral girdle to the skull occurs through the posttemporal bone (Fig. 2A-B) (supraclaviculare I in EGGERT, 1929). This is a dermal bone bearing the posterior oculoscapular canal of the canalis lateralis system (AKIHITO, 1986). Some authors describe this bone as a part of the otic region (MESTERMANN and ZANDER, 1984). Although the posttemporal bone seems to be part of the skull in some primitive fishes (*e.g. Amia calva,* Holostei), according to JARVIK (1980) it is considered as being part of the exoskeletal shoulder girdle.

In *Pomatoschistus,* the posttemporal bone is situated caudolaterally to the skull. It consists of a basal plate with two rostrally directed processes (proc. dorsalis and proc. ventralis). On its lateral face the basal plate bears the oculo-scapular canal. The dorsal and ventral process form a fork with a dorsal and a ventral attachment to the skull (Fig. 2A-B). The rostral tip of the dorsal process is flattened and is firmly connected to the epiotic bone via a syndesmosis (terminology of ANKER, 1989). The processus ventralis is situated at the ventral side of the neurocranium. This process extends rostrally into the ligamentum posttemporalo-intercalare, which is attached to the neurocranium at the intercalar bone (Fig. 5B).

The posttemporal-epiotic syndesmosis allows restricted rotation around a dorsoventral axis. The ligamentum posttemporalo-intercalare allows movements of the ventral process in all directions relative to the neurocranium. The posttemporal and hence the shoulder girdle can thus rotate to a limited extent around a dorsoventral axis.

Among the Gobiidae differences in relative length of the ventral process and the ligamentum posttemporalo-intercalare occur (SPRINGER and FREIHOFER, 1976; SPRINGER, 1983). A possible explanation for these variations is that the ventral process of the posttemporal bone is an ossification of the ligamentum posttemporalo-intercalare.

The supracleithral-posttemporal syndesmosis is situated on the medial side of the basal plate (Fig. 3C). Two attachment zones can be distinguished. The larger one is situated at the lateral side of the supracleithral bone and allows some rotation in the plane of the shoulder girdle. The smaller one forms a rostral border preventing the supracleithrum to slide forward.

os supracleithrum (Fig. 3A-B, 4B-C, 5B). EGGERT (1929) named this dermal bone the supraclavicularia II. The supracleithrum is a dermal bone connecting the posttemporal to the cleithral bone (the major element of the shoulder girdle). In lower actinopterygians it is a sensory canal bone through which the connection between the cranial sensory system and the body lateral sensory system passes (JARVIK, 1980).

In *Pomatoschistus lozanoi,* no sensory canal is situated in the supracleithral bone nor does a lateral line exist (MILLER, 1986). The lateral face of the supracleithral bone is attached to the medial side of the posttemporal bone. The ventromedial side of the supracleithrum is connected to the dorsolateral face of the cleithrum via the

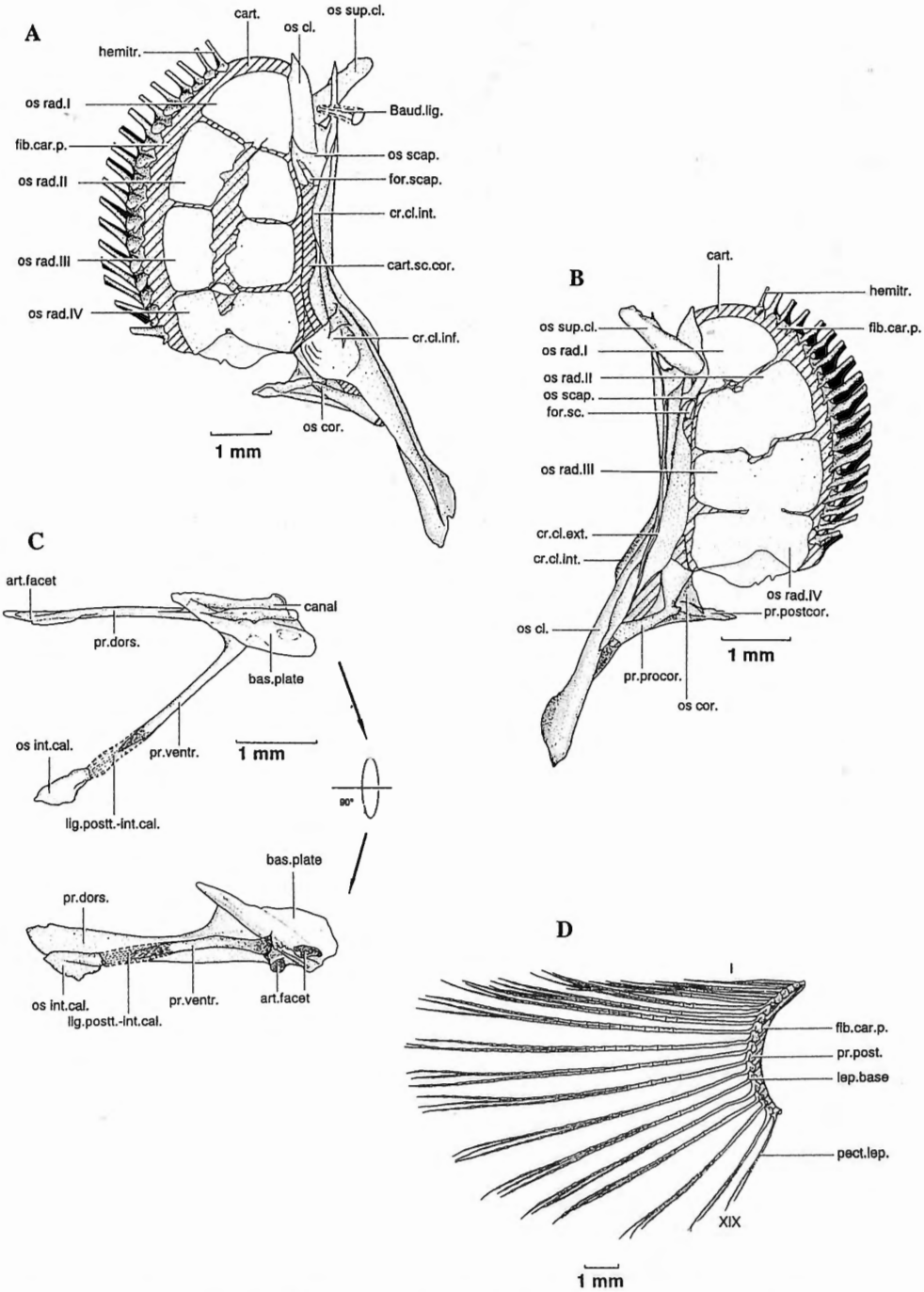


Fig. 3. — Bony elements of the pectoral girdle-apparatus in *Pomatoschistus lozanoi*. — A. Medial view of the shoulder girdle and shoulder plate. — B. Lateral view. — C. Lateral and ventral view of the os posttemporale with the os intercalare. — D. Lateral view of the fin plate. (Shaded areas : cartilage).

supracleithral-cleithral syndesmosis (Fig. 3B). Near the latter, Baudelot's ligament is attached (see below).

os cleithrum (Fig. 2B, 3A + B, 4A-C, 6A-C, 7A + B, 7E + F). This element constitutes the main part of the shoulder girdle. It suspends the endoskeletal elements of the pectoral girdle-apparatus and the pelvic girdle-apparatus. The cleithral bone forms the caudal margin of the branchial cavity, thereby protecting the heart. Dorsally it is attached to the supracleithral bone. Ventrally it forms a symphysis with the ventral tip of the contralateral cleithral bone (Fig. 2B, 6C), this symphysis is lying subdermally (Fig. 4B-C, 6A-C).

Rostral to the supracleithral-cleithral syndesmosis an incision is present through which runs Baudelot's ligament (Fig. 3A ; see below). At the rostral edge of the cleithrum bone three crests are present. The lateral crest (lateral crista cleithralis externa) is situated along the whole length of the cleithral bone, except for the most ventral part (Fig. 3B). The upper medial crest (crista cleithralis interna) extends between the dorsal incision and the coracoid bone. The lower medial crest (crista cleithralis inferior) is situated along the ventral half of the cleithrum. This crest is much higher than the internal cleithral crest (Fig. 3A). The medial faces of the left and right inferior cleithral crest are interconnected by the intercleithral cartilage, thus forming a second connection between the cleithra. The pelvic girdle articulates with the pectoral girdle by the intercleithral cartilage.

The cleithral bone forms a caudal furrow in which the scapulo-coracoidal cartilage is enclosed. This cartilage and its ossifications are attached to the cleithrum by means of collagen fibres.

This cleithral bone is also named the clavicula by MATSUBARA and IWAI (in BIRDSONG, 1975). The os cleithrum and the os claviculum, however, are not homologous : in some primitive Crossopterygians, both can be present (*e.g. Eusthenopteron*) (ROMER and PARSONS, 1986 ; JARVIK, 1980).

os postcleithrum. This dermal element has not been found in *Pomatoschistus lozanoi*, although in other gobiid species it can be present (AKIHITO, 1969, 1986). In *Eusthenopteron* (Crossopterygii) an os anocleithrum is present but whether this bone is homologous to the os postcleithrum remains uncertain (JARVIK, 1980).

Shoulder plate

During ontogeny a single cartilaginous shoulder plate develops. Later on this plate is subdivided into the proximal scapulo-coracoid cartilage and the distal radials (MERTENS, 1971, unpublished document).

cartilago scapulo-coracoideum (Fig. 3A-B, 7F). This cartilage is fixed in the distal furrow of the cleithral bone by collagen fibers. In this hyaline cartilage two ossification centres are present : a dorsal os scapulum and a ventral os coracoideum. In gobies the central part of the cartilage is not ossified, thus separating the scapular bone from the coracoid bone (AKIHITO, 1963, 1967).

os scapulum (Fig. 3A). This perichondral bone, which is perforated by a foramen scapulae, is the dorsal ossification of the scapulo-coracoid cartilage. In gobiid fishes a gradation in the ossification of the dorsal part of the scapulo-coracoid cartilage occurs. According to AKIHITO (1963, 1967) four types of scapular bones can be distinguished within the Gobiidae. In *Pomatoschistus lozanoi,* the ventral border of the foramen scapulae is not lined with an ossification (Fig. 3A), corresponding with type II in AKIHITO (*op. cit.*).

Distally the scapular bone articulates with the ventral part of the uppermost proximal radial bone and the dorsal part of the second proximal radial bone of the shoulder plate (Fig. 3A).

The scapular foramen is situated just below the overlapping dorsal part of the cleithral bone (Fig. 3B). Through this foramen runs a trunk of three connected nerve fibers, i.e. the spinal nerves I, II and III (MERTENS, 1971, unpublished document).

os coracoideum (Fig. 2B, 3A-B, 6C, 7B, 7E-F). Lateral to the lower medial crest lies this ventral ossification centre of the scapulo-coracoid cartilage. The perichondral ossification starts early during the ontogeny (JOLLIE, 1983).

The triangular coracoid bone consists of a vertical plate possessing two ventral processes (Fig. 3A-B). The processus procoracoideus is pointed ventrorostrally, articulating with the caudal side of the cleithral bone. The processus postcoracoideus is directed caudally, up to almost half the length of the shoulder plate. This process forms the ventral border for the coracoradial muscle fibers.

The dorsal non ossified part of the coracoid borders onto the rostral side of the ventralmost radial bone. The number of radial bones articulating with the coracoid bone is species specific (SPRINGER and FRASER, 1976; JARVIK, 1980; MERTENS, 1971, unpublished document).

ossa radialia proximalia (Fig. 2A-B, 3A-B, 7F). The four radial bones in *Pomatoschistus lozanoi* form the major part of the shoulder plate. Variable terminology has been used to describe these perichondral bones. Generally the term 'radialia' is used (MERTENS, 1971, unpublished document; BIRDSONG, 1975; SPRINGER and FRASER, 1976; JARVIK, 1980; MESTERMANN and ZANDER, 1984). Other authors use 'actinost' to indicate these elements (GOSLINE, 1971; HUSSAIN, 1981; AKIHITO, 1969). Also used is the name 'pterygophore' which is very much confusable with the term 'pterygiophore', the latter refering to the basal bony elements supporting the unpaired fins (LAGLER *et al.*, 1962).

The radial bones are the ossifications of the cartilaginous radials (see above) (JOLLIE, 1983). In *Pomatoschistus lozanoi,* the ossification is not complete, in such a way that the central region of the medial side of the three ventralmost radial bones remains cartilaginous (Fig. 3A).

In most fishes these radial bones are bar-like. In *Pomatoschistus lozanoi,* however, these bones are laterally compressed, and form plates instead of bars. The ventralmost and dorsalmost radial bones are triangular, the former bearing a ventral bony lamella (Fig. 3B-C). The two central bones are somewhat rectangular.

The radial bones are interconnected by collagenous fibres, thus forming one rigid plate.

Both lateral and medial fin muscles lie on the proximal radial bones, running from the cleithral or coracoid bone to the fin rays.

ossa radialia distalia. These small spherical structures are perichondral bones, situated distally to the proximal radial bones. They are completely surrounded by the fibrocartilage pad (hence they are not visible on the drawings), thus acting as supporting structures for this pad.

fibrocartilage pad (Fig. 3A-B, 7F). This pad forms a pliable but firm articulation border for the fin rays, situated along the distal margin of the proximal radial bones. Due to the curvature of the pad it is possible for the marginal fin rays to make a large angle between each other (GEERLINK, 1989).

Fin plate

lepidotrichia (Fig. 3A-B, 3D, 7D). In *Pomatoschistus lozanoi,* only soft, segmented fin rays are present, which are connected to each other by a dermal membrane. The number of pectoral fin rays varies at least between species. In *Pomatoschistus lozanoi,* nineteen pectoral fin rays are present. They act as supporting structures for the propulsion-generating fins.

The fin rays consist of two hemitrichia, each of which can be subdivided in three parts : a basal element, an unsegmented stem and a distal part, which is segmented into hemisegments.

In a transverse section, the hemitrichs are curved with their convex sides facing to each other. Opposite hemitrichs are connected by collagenous intra-lepidotrich ligaments, except at their base where they remain separated (GEERLINK and VIDELER, 1987).

At their base the hemitrichs are flattened and are provided with a processus posterior and a processus internus. The posterior process serves as an insertion site for the abductor and adductor muscles of the fin plate. The internal process which is situated at the medial sides of the hemitrichs, anchors the fin ray into the fibrocartilage pad (GEERLINK, 1989).

In *Pomatoschistus lozanoi,* the pectoral (and pelvic) fin rays are dichotomously branched (Fig. 3D, 6A). In the pectoral lepidotrichs maximally two branching points are present. Starting dorsally, the first and second rays are not branched. The third and nineteenth fin rays both have one braching point, all the others have two. The branching in those hemitrichs follows a certain pattern : in fin rays four to eleven the second branching point is situated in the ventralmost branch. The second branching point in fin ray twelve to eighteen is situated on the dorsal branch.

The attachment of the fin rays to the fibrocartilage pad allows the rays to rotate around two axes. Restricted rotation is possible around a horizontal axis going through the base of each fin ray. This rotation enables a dorsoventral motion of

the pectoral fin rays resulting in enlarging and reducing the fin surface. The second rotation axis runs through the fibrocartilage pad between the bases of the fin ray. Rotation around this axis results in adduction and abduction of the fin plate.

Myology

In this publication nomenclature is used as in WINTERBOTTOM (1974). For synonymy we refer also to WINTERBOTTOM (1974).

Body muscles attached to the shoulder girdle-apparatus

Epaxial and hypaxial body muscles are attached to the pectoral girdle : dorsally the musculus lateralis superficialis and ventrally the musculus obliquus inferioris.

m. lateralis superficialis (Fig. 4A-C, 7A). This part of the body musculature lies ventrolaterally to the epaxial muscles, attaching to the dorsocaudal side of the posttemporal bone. These lateral muscles extend to the tail region. Contraction of these muscles will presumably rotate the shoulder girdle backwards.

m. obliquus inferioris (Fig. 4A-C, 6A-B, 7A). This ventralmost body muscle runs along the pelvic girdle-apparatus and joins the contralateral oblique muscle at the ventral tip of the cleithral bone.

Ontogenetically the oblique muscle arises from those fibers of the hypaxial muscles which are orientated in an anteroventral to a posterodorsal direction. The medial fibers of this muscle are attached to the caudal side of the ventral tip of the cleithral bone (Fig. 7A). The lateral fibers insert on a myocomma, separating the inferior oblique muscle from the sternohyoid muscle (Fig. 6A-B) (WINTERBOTTOM, 1974).

Some dorsolateral fibers of the inferior oblique muscle (on the second myomere starting rostrally) insert anteriorly on the postcoracoid process of the coracoid bone (Fig. 4B-C, 6A-B).

In *Pomatoschistus lozanoi,* the fibers of the inferior oblique muscles lie lateral to those of the superior oblique muscle, which seems contradictory. According to WINTERBOTTOM (1974), the position of these two muscles, in relation to each other, can vary in teleost fishes. In general the inferior oblique muscle is situated medially to the superior one. Both muscles fuse at the tail region.

Muscles between the shoulder girdle-apparatus and the neurocranium

m. levator pectoralis (Fig. 4B-C, 5A-B, 7A-B). This muscle arises from the epaxial muscles and becomes completely separated from them. In some primitive fishes the medial fibers are still continuous with the epaxial muscles (WINTERBOTTOM, 1974). In *Pomatoschistus lozanoi,* two subdivisions are distinguishable : a pars lateralis and a pars medialis. Both are situated at the lateral side of the caudoventral region of the skull.

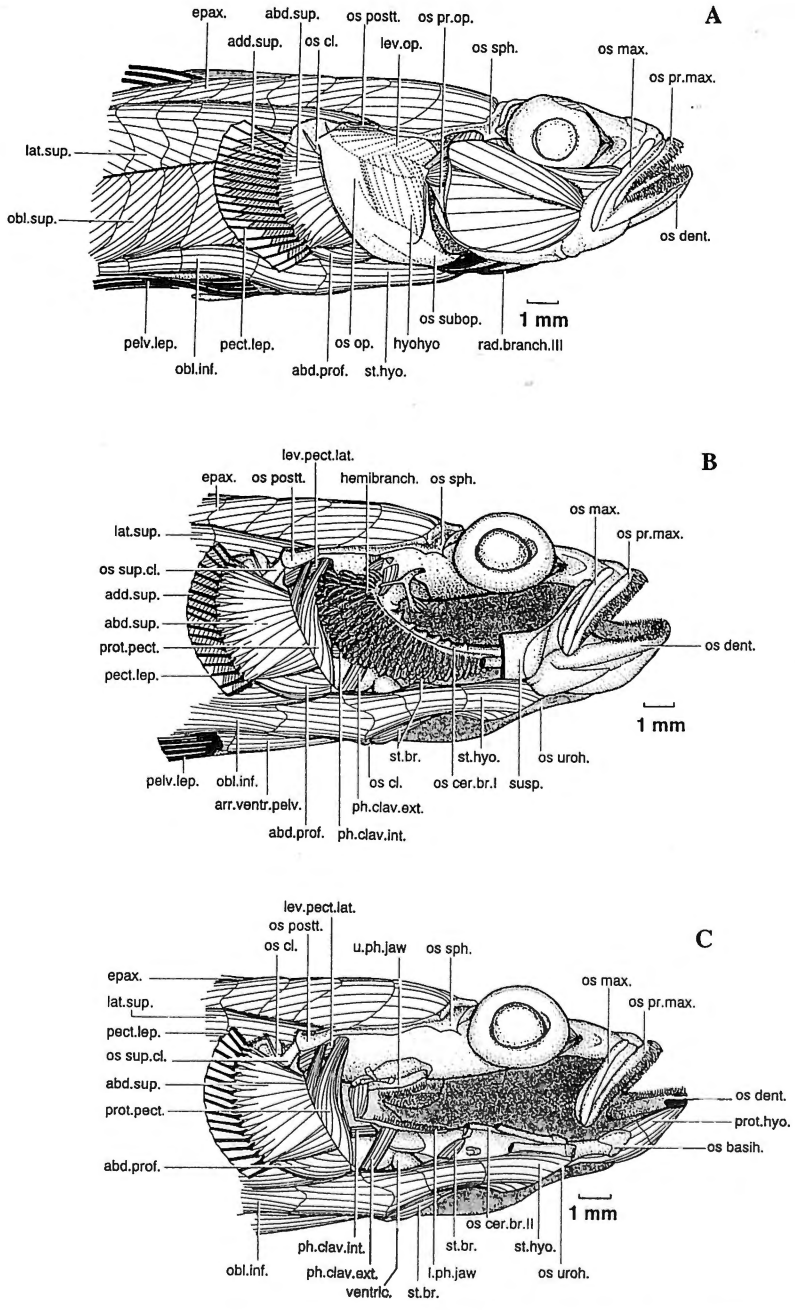


Fig. 4. — Lateral view of the body muscles and the muscles of the pectoral girdle-apparatus.

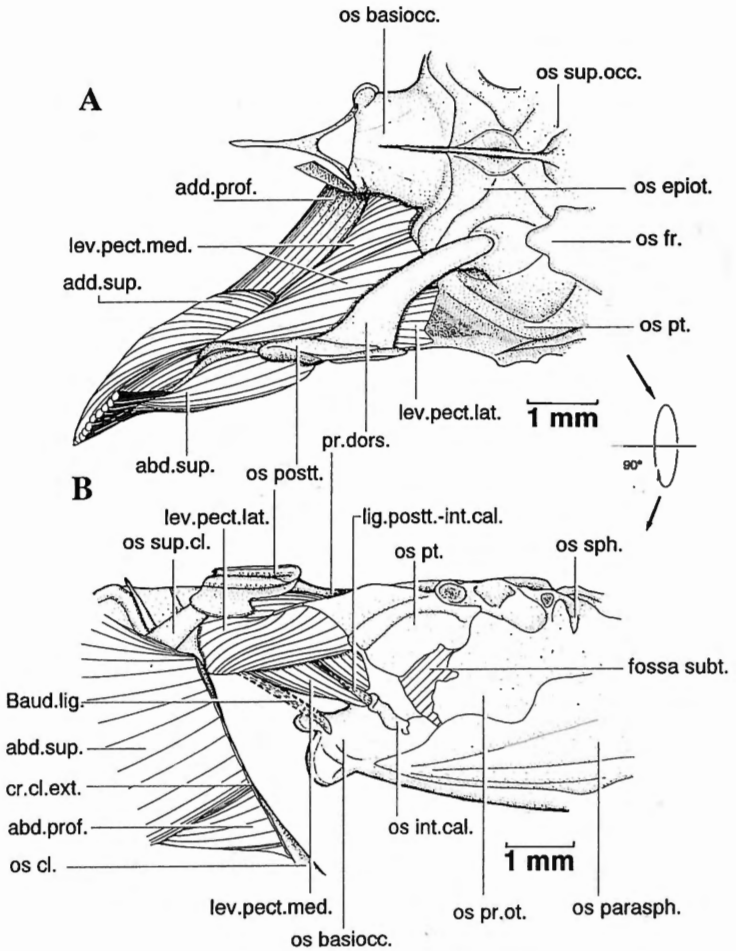


Fig. 5. — Detailed view of the musculus levator pectoralis in dorsal view (A) en lateral view (B). (Shaded areas : cartilage).

The shorter musculus levator pectoralis pars lateralis originates from the caudal margin of the pterotic bone of the neurocranium (Fig. 5A-B). This bundle runs medially to the basal plate of the posttemporal bone, ventrally to the dorsal process and laterally to the ventral process. It inserts on the rostral margin of the cleithral bone. At the caudalmost tip of the pterotic bone a small tendon is present on which the fibers of the lateral part insert.

The musculus levator pectoralis pars medialis originates more ventrally to the base of the skull, at the exoccipital bone, close to the intercalar bone (Fig. 5B). Distally, this muscle encloses the ventral process of the posttemporal bone as well as the distal part of Baudelot's ligament. The fibers are attached to the medial side

of the supracleithral bone and the rostral side of the cleithral bone, just before the insertion site of the superficial adductor muscle of the pectoral fin.

m. protractor pectoralis (Fig. 4B-C, 7B). This muscle connects the rostral side of the shoulder girdle with the lateral side of the neurocranium.

During ontogeny the protractor muscle arises from the levator arcuum branchialum 'Anlage' (WINTERBOTTOM, 1974). This sheet-like muscle is attached to the rostrolateral margin of the crista cleithralis externa of the cleithral bone. The insertion is spread over the total length of the crest. Dorsally, the muscle is separated into two smaller bundles, a rostral one inserting on the ventral side of the lateral margin of the pterotic bone of the neurocranium, and a caudal one inserting on the basal plate of the posttemporal bone (Fig. 4B-C). Contraction of this protractor muscle will presumably generate a forward rotation of the pectoral girdle-apparatus around a horizontal axis.

Muscles between the shoulder girdle-apparatus and the hyoid arch

m. sternohyoideus (Fig. 4A-C, 6A-B, 7A). This muscle lies ventrally between the ventral tip of the cleithral bone and the urohyal bone.

The sternohyoid muscle develops from the ventral part of the hypobranchial muscle plates of the first few spinal myomeres (WINTERBOTTOM, 1974). The fibers of the sternohyoid are musculously attached to the lateral sides of the urohyal bone (Fig. 4B-C, 6B). This dermal bone is the ossification of the tendon plate between the rostral tips of the contralateral sternohyoid muscles (VERRAES, 1973). It is connected to the distal tips of the hyoid bars by ligaments (MERTENS, 1971, unpublished document; LELE and KULKARNI, 1939).

Caudally, the lateral fibers of the sternohyoid muscle are separated from the inferior oblique muscle by a myocomma (Fig. 4B-C, 6A-B). The medial fibers insert on the rostral side of the ventral tip of the cleithral bone (Fig. 7A). This muscle forms the ventral border of the branchial cavity, lying between the two hyoid rami. The basal elements of the branchial arches meet just above the sternohyoid muscle.

Ventrally the sternohyoid muscle is subdivided by one myocomma. However, on the lateral side of the muscle a middle third muscle segment is present. The myocommata separating this subdivision are continuous with the ventral myocomma.

The sternohyoid muscle, together with the cleithral bone and the inferior oblique muscle, participates in a four bar system which is used in suction feeding (AERTS and VERRAES, 1984; MULLER, 1987).

Muscles between the shoulder girdle-apparatus and the branchial arches

m. sternobranchialis (Fig. 4B-C, 6A-C). In some fishes the medial and mediodorsal fibers of the sternohyoid muscle become separated forming the sternobranchial muscle (WINTERBOTTOM, 1974).

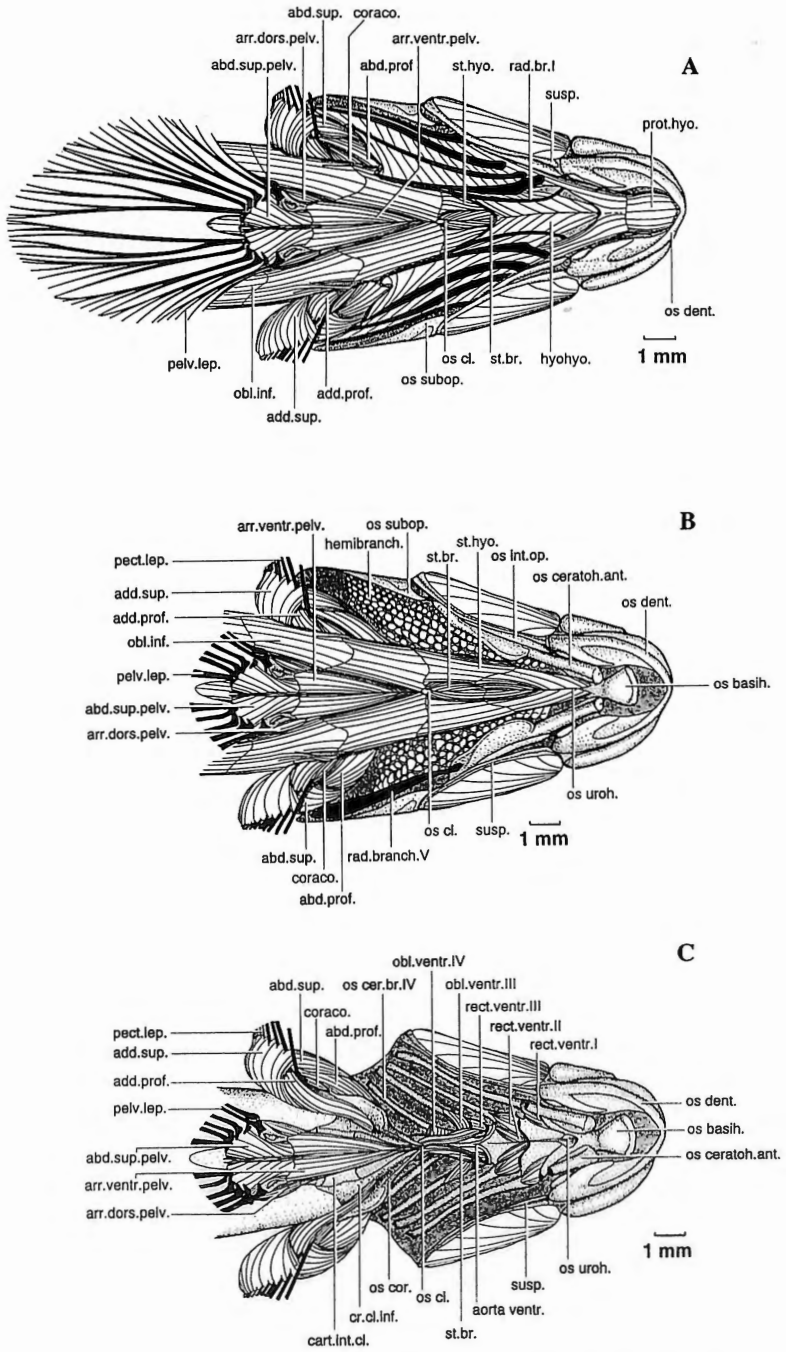


Fig. 6. — Ventral view of the body muscles and the muscles of the pectoral girdle-apparatus.

Caudally the muscle is attached to the ventral tip of the cleithral bone, medially to the attachment of the fibers of the sternohyoid muscle (Fig. 6C). In *Pomatoschistus lozanoi,* the fibers of the sternobranchial muscle rostrally form two separate bundles : a dorsal one inserting on the hypobranchial bone III (Fig. 6C), and a ventral one inserting on the caudal border of the urohyal bone (Fig. 6B). The latter lies between the two sternohyoid muscles and is subdivided by a myocomma.

m. pharyngoclavicularis externus (Fig. 4B-C). This muscle is the first of two muscles connecting the lower pharyngeal jaws to the pectoral girdle.

According to WINTERBOTTOM (1974), during ontogeny the pharyngoclavicular muscle becomes divided from the fifth branchial arch muscle plate. Later during development this muscle becomes separated in an external portion (pharyngoclavicularis externus) and an internal portion (ph. clav. internus). In *Pomatoschistus lozanoi,* the external muscle attaches on the ventrorostral part of the external crest of the cleithral bone, ventral to the insertion site of the pectoral protractor muscle. The small external muscle bundle runs anterodorsally, attaching to the lateral side of the lower pharyngeal jaw, lateral to its ventrolateral crest (Fig. 4C).

m. pharyngoclavicularis internus (Fig. 4B-C, 7A). Medially to the external pharyngoclavicular muscle passes the internal muscle. It also connects the lower pharyngeal jaw with the shoulder girdle.

The fibers are attached to the rostral side of the external crest of the cleithral bone, medially to the ventral fibers of the pectoral protractor muscle. The fibers are directed horizontally. They insert on the ventral side of the lower pharyngeal jaw, medially to the ventrolateral crest of the jaw.

Muscles between the shoulder girdle and the fin plate

m. abductor superficialis (Fig. 4A-C, 5A-B, 6A-C). The lateralmost muscle plate of the shoulder plate is the superficial abductor muscle.

According to WINTERBOTTOM (1974), during ontogeny a muscle plate develops laterally to the shoulder plate. The lateral fibers become separated from the medial ones, forming the superficial abductor muscles. In some primitive fishes the lateral fibers are not completely separated from the medial ones (*e.g. Elops*) (WINTERBOTTOM, 1974). The medial fibers form the musculus adductor profundus.

In *Pomatoschistus lozanoi,* the superficial abductor muscle originates along the upper three quarters of the margin of the external cleithral crest. Caudally the muscle is tendinously attached to the posterior process of the lateral hemitrichs, except for the ventralmost fin ray where there is no insertion.

Contraction of this abductor muscle, together with the deep abductor muscle, will generate a forward rotation of the fin rays. When the pectoral fins are used to support and stabilise the fish on the bottom, the fin rays are in an abducted position.

Within the Gobiidae a subdivision of this superficial muscle may be present in a pars superficialis and a pars profundus (EGGERT, 1929). This division is also present in other fish groups (*e.g.* Labridae) (GEERLINK, 1989). In *Pomatoschistus lozanoi,* a clear subdivision could not be distinguished.

m. abductor profundus (Fig. 4A-C, 5B, 6A-C, 7A). Medially to the superficial abductor muscle and more oblique directed is the deep abductor muscle.

In *Pomatoschistus lozanoi,* the insertion of this muscle on the cleithral bone is situated medially to the attachment of the superficial muscle on the external crest (Fig. 7A). This insertion site is spread over the lower half of the crest. The fibers run posterodorsally to the base of each lateral hemitrich. Contraction will result in the abduction of the fin rays.

m. adductor superficialis (Fig. 4A-C, 5A, 6A-C, 7B-D). This medialmost ('medial' is relative to the body axis, not to the shoulder plate) muscle of the shoulder plate originates dorsally on the shoulder girdle, adjacent to the insertion of the m. levator pectoralis pars medialis, and inserts on the fin rays.

During ontogeny a muscle plate is formed at the medial side of the shoulder plate. Its medial fibers form the superficial adductor muscle, whereas the lateral ones form the deep adductor muscle. The adductor muscle may not be completely subdivided (*cfr.* abductor) in some primitive fishes (*e.g. Elops*) (WINTERBOTTOM, 1974).

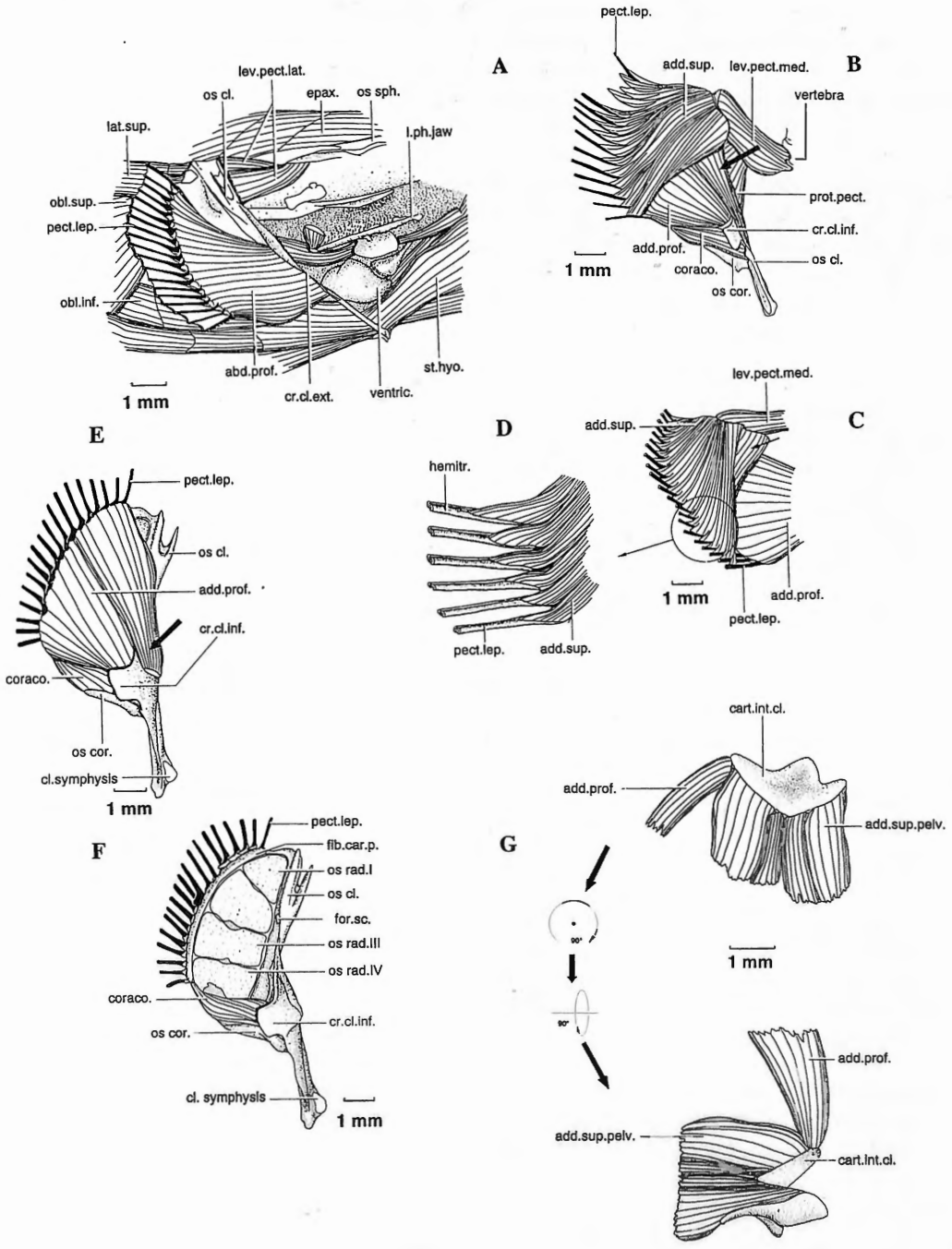
In *Pomatoschistus lozanoi,* the insertion site of the superficial adductor muscle is situated caudally to the insertion of the medial part of the pectoral levator muscle. It comprises the medial side of the basal plate of the posttemporal bone, the anteromedial side of the supracleithral bone and the dorsomedial side of the cleithral bone. Distally the fibers of the adductor muscle are attached to the medial side of the fin ray stem. This insertion is situated at some distance from the base of the ray (Fig. 4A, 7C-D), resulting in a larger lever for the adductor muscle compared to a basal insertion. Thus the momentum on the fin increases which enlarges the adduction force.

In *Pomatoschistus lozanoi* and some other fishes the superficial fibers are differently orientated with regard to the deeper ones. The dorsal superficial fibers are attached to the more ventral fin rays whereas the ventral, deeper fibers run to the more dorsal fin rays (Fig. 7C, small arrow).

Contraction of this muscle is believed to rotate the fin rays backward.

m. adductor profundus (Fig. 5A, 6A-C, 7B-C, 7E-G). This muscle is situated between the superficial adductor muscle and the shoulder plate. The caudal insertion is at the bases of the medial hemitrichs. The deep adductor muscle is rostrally attached at two different places, thus dividing the muscle in two parts.

The ventral part of the muscle originates from the coracoid and the cleithral bones (Fig. 6C, 7B, 7E). The dorsal fibers are attached to the dorsorostral tip of the intercleithral cartilage (Fig. 7E, 7G). Rostrally, these two muscle parts are separated by the crista cleithralis inferior.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obl.sup.
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obl.inf.
abd.prof.
cr.cl.ext.
ventric.
st.hyo.
1 mm
B
pect.lep.
add.sup.
lev.pect.med.
vertebra
prot.pect.
cr.cl.inf.
add.prof.
coraco.
os cl.
os cor.
1 mm
C
lev.pect.med.
add.sup.
add.prof.
pect.lep.
1 mm
D
hemitr.
pect.lep.
add.sup.
E
pect.lep.
os cl.
add.prof.
cr.cl.inf.
coraco.
os cor.
cl.symphysis
1 mm
F
pect.lep.
fib.car.p.
os rad.I
os cl.
for.sc.
os rad.III
os rad.IV
coraco.
cr.cl.inf.
os cor.
cl. symphysis
1 mm
G
cart.int.cl.
add.prof.
add.sup.pelv.
1 mm
90°
90°
add.prof.
add.sup.pelv.
cart.int.cl.

m. coracoradialis (Fig. 6A-C, 7B, 7E-F). This ventralmost muscle of the shoulder plate connects the coracoid bone with the ventralmost radial bone.

According to WINTERBOTTOM (1974) no data are available concerning the ontogeny of this muscle. Possibly it arises from a part of the hypaxial muscles.

In *Pomatoschistus lozanoi,* the muscle lies ventrally to the shoulder plate, between the deep abductor and deep adductor muscles (Fig. 6A-C). The fibers of the coracoradial muscle originate from the dorsal side of the coracoid bone and the caudal side of the cleithral bone, medially to its inferior medial crest (Fig. 7E-F). Distally the fibers insert on the ventrocaudal tip of the ventralmost radial bone, right below the ventralmost fin ray.

As yet, it is difficult to suggest a possible function for this muscle, since it inserts on, in our opinion, firmly connected and hardly movable skeletal elements.

Ligaments

Ligamentum posttemporalo-intercalare (Fig. 3C, 5B). This ligament is continuous with the ventral process of the posttemporal bone (Fig. 3C). The ligament is attached to the intercalar bone of the neurocranium. The length of this ligament, in relation to the length of the ventral process varies interspecifically, as already stated in the description of the ventral process of the posttemporal bone.

Baudelot's ligament (Fig. 2A-B, 3A, 5B). In Pomatoschistus lozanoi, this strong ligament is situated between the medial side of the shoulder girdle and the caudoventral side of the neurocranium. It is attached medially on the shoulder girdle, on that part of the supracleithral bone that is left uncovered by the cleithral incision (Fig. 3A). The attachment site on the neurocranium is the ventromedial side of the basioccipital bone (Fig. 5B).

In the literature not many functions for this ligament are proposed. In cyprinids this ligament functions as a rotation axis for the lower pharyngeal jaws SIBBING (1976). However, in gobies the pharyngeal jaws do not 'articulate' with this ligament.

Fig. 7. — Muscles of the shoulder plate. — A. Lateral view of the musculus abductor profundus. — B. Medial view of the adductor muscles (arrow indicating the position of the profound adductor muscle fibers attaching to the intercleithral cartilage). — C. Idem as B. but showing the crossing of muscle fibers of the musculus adductor superficialis (small arrow). — D. Detailed view of the insertion of the musculus adductor superficialis on the fin ray stem. — E. Medial view of the musculus adductor profundus (arrow indicating the dorsal muscle fibers that insert on the intercleithral cartilage). — F. Medial view of the musculus coracoradialis. — G. Detailed view of the insertion of the dorsal fibers of the musculus adductor profundus on the intercleithral cartilage. (Shaded areas : cartilage).

DISCUSSION

As the pectoral fins are very important in locomotion and as supporting structures when resting on the bottom, some morphological adaptations are discussed below.

Forward propulsion through pectoral fin adduction is exerted according to a drag based mechanism (WEBB and BLAKE, 1985). Contraction of the pectoral fin adductor muscles results in a backward rotation of the fin during the powerstroke. A forward rotation is generated during the non-propulsive recovery stroke through contraction of the abductor muscles. In some other teleost fishes, a dorsoventral movement of the pectoral fins produces the forward propulsion (*e.g.* Labridae, Pomacentridae). In these lift based propulsion mechanisms the pectoral fin rays show an undulating motion which requires a large mobility of the rays and its supporting structures (WEBB and BLAKE, 1985).

During the powerstroke in pectoral fin adduction, large forces are exerted on the skeletal elements of the pectoral girdle. In order to withstand such forces, some strengthening morphological adaptations are present. In generalised teleosts, the radial bones are bar-like structures, attached to each other with connective tissue. GEERLINK (1983) showed that in *Coris formosa* (Labridae) the proximal radials have a considerable degree of movability with the scapulo-coracoid plate and with each other.

In *Pomatoschistus lozanoi* and some other benthic fishes (Gobiidae : EGGERT, 1929 ; AKIHITO, 1986, Cottidae : GREGORY, 1933 and Bleniidae : BRANDSÄTTTER *et al.*, 1990), the radials are plate like structures that are firmly connected to each other and to the scapulo-coracoid plate by short collagen fibers. Thus a rigid shoulder plate is formed. However, the rigidity of the radials considerably reduces the ability for precise maneuvering.

The propulsion force can be increased by altering several parameters such as enlarging the propulsion generating surface, enlarging the proportion of adductor muscles or increasing the contraction power of the adductor muscles. According to AKIHITO (1986 : Fig. 6) and GEERLINK (1983 : Fig. 1B) the proximal radials in gobies are greatly enlarged compared to generalised teleosts. Thus the distal border of the shoulder plate and hence the fin base are relatively larger in gobies. The shape of the fin is trapeziform (compared to triangular in *Coris formosa*). A broader fin base implicates a larger resistance against torque along a proximal-distal axis during powerful fin adduction. In *Pomatoschistus lozanoi,* the surface of the pectoral fin is also strongly enlarged by the branching of the fin rays. The enlarged plate-like shoulder plate provides ample space for large fin muscles (ab- and adductors). The contraction force of the superficial adductor muscle is increased through a distally moved insertion site on the fin rays. The insertion of the superficial adductor muscles is musculous on the stem of the fin rays, in contrast to a tendinous insertion in *Coris formosa* (GEERLINK, 1989). The rather distal attachment will create a large momentum on the fin rays, resulting in a large adduction force. Together with the large reaction force on the fin plate, this results in a strong forward propulsion. The musculous insertion on the fin rays may be an indication

that the extent to which the individual rays can be moved independently is smaller in gobies than in *Coris formosa* (GEERLINK, 1989). Again this is in favour of powerful fin adduction and at cost of maneuvrability of the fin rays.

CONCLUSIONS

The pectoral fins of gobies seem to be better adapted to powerful adduction than those of generalised teleosts. The proximal radials form a large rigid shoulder plate with a long distal margin on which a high pectoral fin articulates. The fin muscles are strongly developed and assure, together with the large pectoral fin, powerful drag-based pectoral propulsion. The morphological adaptations for powerful adduction, however, are at cost of the maneuvering abilities of the pectoral fins.

ABBREVIATIONS TO THE FIGURES

Skeletal elements

art.facet	= articulation facet
bas.plate	= basal plate
cart.	= cartilago
cart.int.cl.	= cartilago intercleithralis
cart.sc.cor.	= cartilago scapulo-coracoideum
cl.symphysis	= cleithral symphysis
cr.cl.ext.	= crista cleithralis externa
cr.cl.int.	= crista cleithralis interna
cr.cl.inf.	= crista cleithralis inferior
fib.car.p.	= fibrocartilage pad
for.sc.	= foramen scapulae
fossa subt.	= fossa subtemporalis
hemitr.	= hemitrichium
l.ph.jaw	= lower pharyngeal jaw
lep.base	= lepidotrichium base
os basih.	= os basihyale
os basiocc.	= os basioccipitale
os cer.br.	= os ceratobranchiale
os ceratoh.ant.	= os ceratohyale anterior
os cl.	= os cleithrum
os cor.	= os coracoideum
os dent.	= os dentale
os epiot.	= os epioticum
os exethm.	= os exethmoideum
os fr.	= os frontale
os int.cal.	= os intercalare
os int.op.	= os interoperculare
os max.	= os maxillare
os mesethm.	= os mesethmoideum

os op. = os operculare
os parasph. = os parasphenoideum
os postt. = os posttemporale
os pr.max. = os praemaxillare
os pr.op. = os praeoperculare
os pr.ot. = os prooticum
os pt. = os pteroticum
os rad. = os radiale
os scap. = os scapulum
os sph. = os sphenoideum
os subop. = os suboperculare
os sup.cl. = os supracleithrum
os sup.occ. = os supraoccipitale
os uroh. = os urohyale
os vom. = os vomerale
ossa rad. = ossa radialia
pect.lep. = pectoral lepidotrichia
pelv.lep. = pelvic lepidotrichia
pr.dors. = processus dorsalis of the os posttemporale
pr.post. = processus posterior of the lepidotrichium base
pr.postcor. = processus postcoracoideus
pr.procor. = processus procoracoideus
pr.ventr. = processus ventralis of the os posttemporale
rad.branch. = radius branchiostegus
susp. = suspensorium
u.ph.jaw = upper pharyngeal jaw

Muscles

abd.prof. = musculus abductor profundus
abd.sup. = musculus abductor superficialis
abd.sup.pelv. = musculus abductor superficialis pelvicus
add.prof. = musculus adductor profundus
add.sup. = musculus adductor superficialis
add.sup.pelv. = musculus adductor superficialis pelvicus
arr.dors.pelv. = musculus arrector dorsalis pelvicus
arr.ventr.pelv. = musculus arrector ventralis pelvicus
coraco. = musculus coracoradialis
epax. = epaxial muscles
hyohyo. = musculus hyohyoideus
lat.sup. = musculus lateralis superficialis
lev.op. = musculus levator operculi
lev.pect.lat. = musculus pectoralis pars lateralis
lev.pect.med. = musculus pectoralis pars medialis
obl.inf. = musculus obliquus inferioris
obl.sup. = musculus obliquus superioris
obl.ventr. = musculus obliquus ventralis
ph.clav.ext. = musculus pharyngoclavicularis externus
ph.clav.int. = musculus pharyngoclavicularis internus
prot.hyo. = musculus protractor hyoidei

prot.pect. = musculus protractor pectoralis
rect.ventr. = musculus rectus ventralis
st.br. = musculus sternobranchialis
st.hyo. = musculus sternohyoideus

Ligaments

Baud.lig. = Baudelot's ligament
lig.postt.-int.cal. = ligamentum posttemporalo-intercalare

Other

hemibranch. = hemibranchium
ventric. = ventriculus
aorta ventr. = aorta ventralis

REFERENCES

AERTS, P. and W. VERRAES (1984) — Theoretical analysis of a planar bar system in the telostean skull : the use of mathematics in biomechanics. *Annls Soc. r. zool. Belg.*, **114 (2)** : 273-290.

AKIHITO, PRINCE (1963) — On the scapula of gobiid fishes. *Japanese Journal of Ichthyology*, **11 (1-2)** : 1-26.

AKIHITO, PRINCE (1967) — Additional research on the scapula of gobiid fishes. *Japanese Journal of Ichthyology*, **14** : 167-182.

AKIHITO, PRINCE (1969) — A systematic examination of the gobiid fishes based on the mesopterygoid, postcleithra, branchiostegals, pelvic fins, scapula and suborbital. *Japanese Journal of Ichthyology*, **16 (3)** : 93-114.

AKIHITO, PRINCE (1986) — Some morphological characters considered to be important in gobiid phylogeny. In : *Indo-Pacific Biology : Proceedings of the Second International Conference on Indo-Pacific Fishes*. UYENO, T., R. ARAI, T. TANIUCHI and K. MATSUURA (Eds.) : 629-639.

ANKER, G. Ch. (1989) — The morphology of joints and ligaments in the head of a generalized *Haplochromis* species : *H. elegans* TREWAVAS, 1933 (Teleostei, Cichlidae). *Netherlands Journal of Morphology*, **39 (1-2)** : 1-40.

BIRDSONG, R. S. (1975) — The osteology of Microgobius signatus Poey (Pisces : Gobiidae), with comments on other gobiid fishes. *Bull. Fla. State Mus. Biol. Sci.*, **19 (3)** : 135-187.

BRANDSTÄTTER, R., B. MISOF, C. PAZMANDI and G. P. WAGNER (1990) — Micro-anatomy of the pectoral fin in blennies (Blenniini, Blenioidea, Teleostei). *Journal of Fish Biology*, **37** : 729-743.

EGGERT, B. (1929) — Die Gobiidenflosse und ihre Anpassung an das Landleben. *Zeitschrift für Wissenschaftliche Zoologie*, **133 (1-2)** : 411-440.

GEERLINK, P. J. (1983) — The pectoral fin kinematics of *Coris formosa* (Teleostei : Labridae). *Netherlands Journal of Zoology*, **33** : 515-531.

GEERLINK, P. J. (1989) — Pectoral fin morphology : a simple relation with movement pattern ? *Netherlands Journal of Zoology*, **39 (3-4)** : 166-193.

GEERLINK, P. J. and J. J. VIDELER (1987) — The relation between structure and bending properties of teleost fin rays. *Netherlands Journal of Zoology,* **37 (1)** : 59-80.

GOSLINE, W. A. (1971) — *Functional morphology and classification of teleostean fishes.* Publ. Honolulu, The University Press of Hawaï (208 pp).

GREGORY, W. K. (1933) — Fish skulls. A study of the evolution of natural mechanics. *Transactions of the American Philosophical Society,* **23 (2)** : 75-481.

HAMERLYNCK, O. (1990) — The identification of *Pomatoschistus minutus* and *Pomatoschistus lozanoi* (Pisces, Gobiidae). *Journal of Fish Biology,* **37** : 723-728.

HAMERLYNCK, O., P. VAN DE VYVER and C. R. JANSSEN (1990) — The trophic position of *Pomatoschistus lozanoi* (Pisces, Gobiidae) in the southern bight. *Trophic Relationships in the Marine Environment* : 183-190.

HANKEN, J. and R. WASSERSUG (1981) — The visible skeleton. A new double-stain technique reveals the native of the « hard » tissues. *Functional Photography,* **16** : 22-26.

HUSSAIN, M. (1981) — Osteological study of girdles in five families of flatfishes (Pleuronectiformes) with notes on their phylogeny. *Hydrobiologia,* **85** : 85-91.

JARVIK, E. (1980) — *Basic structure and evolution of vertebrates.* Volume I. Publ. Harcourt Brace Jovanovich, Academic Press (575 pp.).

JOLLIE, M. (1983) — Development of the head skeleton and pectoral girdle of salmons, with a note on the scales. *Canadian Journal of Zoology,* **62 (9)** : 1757-1778.

LAGLER, K. F., J. E. BARDACH and R. R. MILLER (1962) — *Ichthyology.* Publ. John Wiley and sons, Inc (545 pp.).

LELE, S. H. and R. D. KULKARNI (1939) — The skeleton of *Periophtalmus barbarus* (Linn.). II. Branchial arches, vertebral column and appendicular skeleton. *Journal of the University of Bombay,* **7 (5)** : 123-134.

MESTERMANN, K. D. and C. D. ZANDER (1984) — Vergleichende osteologische Untersuchungen an *Pomatoschistus*-Arten (Gobioidei, Pisces). *Zool. Jb. Anat.,* **111** : 501-542.

MILLER, P. J. (1986) — Gobiidae. In : *Fishes of the Northern Atlantic and the Mediteranean.* Volume 3. WHITEHEAD, P. J. P., M.-L. BAUCHOT, J.-C. HUREAU, J. NIELSEN and E. TORTONESE : 1019-1085.

MULLER, M. (1987) — Optimization priciples applied to the mechanism of neurocranium levation and mouth bottom depression in bony fishes (Halecostomi). *Journal of Theoretical Biology,* **126** : 343-368.

ROMER, A. S. and T. S. PARSONS (1986) — *The vertebrate body.* Sixth edition. Publ. Saunders College Publishing. The Dryer Press (679 pp.).

SIBBING, F. A. (1976) — Pharyngeal mastication in *Cyprinus carpio* (L.). *Rev. Inst. Püches marit.,* **40 (3-4)** : 744-745.

SPRINGER, V. G. (1983) — *Tyson belos,* new genus and species of western Pacific fish (Gobiidae, Xenisthminae), with discussions of gobioid osteology and classification. *Publ. Smitsonian Institute Press,* **390** : 1-40.

SPRINGER, V. G. and T. H. FRASER (1976) — Synonymy of the fish families Cheilobranchidae (= Alebatidae) and Gobiesocidae, with descriptions of two new species of *Alabes. Publ. Smithsonian Institution Press,* **234** : 1-23.

SPRINGER, V. G. and W. C. FREIHOFER (1976) — Study of the monotypic fish family Pholidichthyidae (Perciformes). *Publ. Smithsonian Institute Press,* **216** : 1-40.

VERRAES, W. (1973) — Bijdrage tot de functioneel-morfologische studie der koponderdelen van *Salmo gairdneri* Richardson, 1836 (Pisces, Teleostei) gedurende de postembryonale ontogenie, met bijzondere aandacht voor het cranium en de kopspieren. *Ph.D. thesis, University of Ghent* : two volumes (242 pp.) (in Dutch).

WEBB and BLAKE, M. (1985) — Swimming. In : *Functional vertebrate morphology.* HILDEBRAND, M., D. M. BRAMBLE, K. F. LIEM and D. B. WAKE (Eds.). Publ. The Belknap Press of Harvard University Press, Cambridge, Massachusettes and London, England : 110-128.

WINTERBOTTOM, R. (1974) — A discriptive synonymy of the striated muscles of the Teleostei. *Proc.Acad.Nat.Sci.(Phil.),* **125 (12)** : 225-317.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 159-163 — Brussels 1993

Manuscript received on 25 June 1993

NOTES ON THE ABERRANT VENOM GLAND MORPHOLOGY OF SOME AUSTRALIAN DOLICHODERINE AND MYRMICINE ANTS (HYMENOPTERA, FORMICIDAE)

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SUMMARY

Two Australian species of *Dolichoderus* Lund, and one of *Leptomyrmex* Mayr (both subfamily Dolichoderinae), have venom glands with two long, slender secretory filaments. In this regard they resemble previously analysed ants of the subfamily Myrmicinae, rather than other dolichoderines. Alternatively, four *Meranoplus* Smith species (subfamily Myrmicinae) have short, knob-like filaments, like those of previously reported dolichoderines, and unlike other myrmicines. Features of venom gland morphology are thus less constant or diagnostically reliable for these subfamilies than was previously supposed.

Keywords : venom gland, morphology, *Dolichoderus, Leptomyrmex, Meranoplus.*

INTRODUCTION

The ant subfamily Dolichoderinae, with its apparent sister-group the Aneuretinae (TRANIELLO and JAYASURIYA, 1981), is characterized by the distinctive and peculiar configuration of its abdominal exocrine glandular system (BILLEN, 1986). These ants alone have a Pavan's gland, and their pygidial glands are so hypertrophied as to have been previously regarded as separate 'anal glands', which were thought uniquely to characterize them. The venom gland of these ants has also been considered unique in possessing two very short knob-like secretory filaments, which is considered to characterize the Dolichoderinae (HÖLLDOBLER and WILSON, 1990). Morphological descriptions of the dolichoderine venom gland are available for representatives of the genera *Azteca, Bothriomyrmex, Dolichoderus, Iridomyrmex, Liometopum* and *Tapinoma* (PAVAN, 1955 ; PAVAN and RONCHETTI, 1955 ; BLUM and HERMANN, 1978b ; BILLEN, 1986). Ants of other subfamilies have long, slender venom gland filaments, with only minor variations in structure, even across subfamilies (BLUM and HERMANN, 1978a). Long filaments have never been reported

from the Dolichoderinae, and dolichoderine-like short lobate filaments have not been recorded from the Myrmicinae, except for an unidentified Australian *Meranoplus* (HÖLLDOBLER, 1988).

MATERIAL AND METHODS

Foraging worker ants of the following relevant species were collected, and later dissected for gross examination of their exocrine glands. In this list bracketed specific names refer to species groups, rather than to a particular included species. The *Dolichoderus (scabridus)* group comprises the Australian species of the subgenus *Diceratoclinea* of WHEELER (1935), and the *D. (doriae)* group those of WHEELER's subgenus *Acanthoclinea*. Both subgenera were synonymized under *Dolichoderus* by BROWN (1973). The two series of the *Meranoplus (diversus)* group are probably conspecific. One-degree geographical coordinates and state codes are given for each locality, following TAYLOR (1987). At least 5 worker specimens were examined from each series, and dealate females in addition from series 4. Appropriately labelled voucher specimens, identified by R.W.T. are in the Australian National Insect Collection (ANIC), where those species believed to be undescribed are placed under the formal collection numbers indicated.

1. *Dolichoderus (scabridus)* Roger	Batemans Bay (35/151), NSW
2. *Dolichoderus (doriae)* Emery	Mongarlowe (35/149), NSW
3. *Leptomyrmex erythrocephalus* (F.)	Mongarlowe (35/149), NSW
4. *Meranoplus (diversus)* Smith	Darwin (12/130), NT
5. *Meranoplus (diversus)* Smith	Yulara (25/131), NT
6. *Meranoplus* sp. 11 (ANIC)	Poochera (32/134), SA
7. *Meranoplus* sp. 12 (ANIC)	Darwin (12/130), NT
8. *Meranoplus* sp. 13 (ANIC)	Darwin (12/130), NT

RESULTS AND DISCUSSION

All *Dolichoderus* and *Leptomyrmex* specimens were found to have venom glands with two long slender secretory filaments, each up to 2.5 mm in length, with a fairly constant diameter of around 40 µm. These open through the convoluted gland, in the mid-dorsal region of the gland reservoir, and their bases are approximated (Fig. 1A). The *scabridus* and *doriae* groups of *Dolichoderus* are apparently closely related lineages, which differ from 'mainline' *Dolichoderus* species (i.e. those of the erstwhile subgenus *Hypoclinea* Mayr) in possessing paired propodeal, or propodeal plus pronotal spines, respectively. The palearctic *D. quadripunctatus* (L.) is the type species of *Hypoclinea*. It has typically dolichoderine bulbous venom gland filaments (BILLEN, 1986). It is possible, therefore, that long filaments distinguish the Australian *(scabridus)/(doriae)* phylad, which could support reassessement of the status of *Diceratoclinea* and *Acanthoclinea*. Unfortunately we have been unable to study any Australian species of « *Hypoclinea* ».

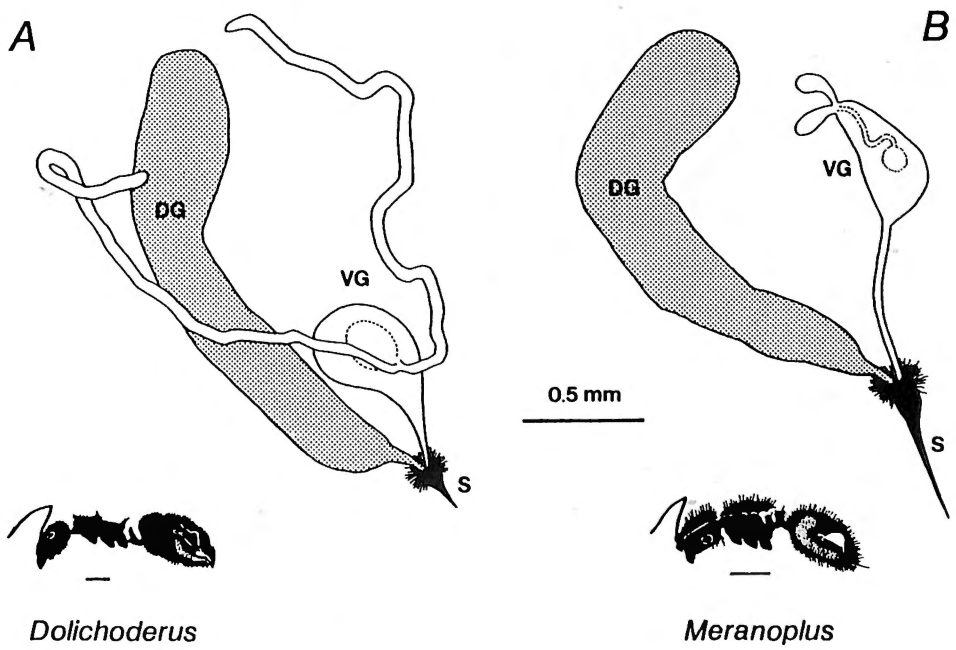

Fig. 1. — General morphology of the sting shaft (S), venom gland filaments and reservoir (VG), and Dufour's gland (DG) in representative Australian *Dolichoderus* (A) and *Meranoplus* (B) species. The stippled outline in the venom gland reservoir indicates the position of the convoluted gland (scale bar for ant profiles = 1 mm).

The four *Meranoplus* species examined differ greatly in size and habitus. All possessed venom glands with a pair of almost bulbous filaments, the largest 0.2 mm long. All bulbs were more or less similar in diameter, measuring 40 to 50 µm. They also open through the convoluted gland, but do so at the apex of the reservoir sac (Fig. 1B). The tubiform Dufour's gland is extremely large in all these *Meranoplus* specimens, where it is by far the most voluminous gastral organ. Behavioural observations revealed it to be the source of long-lasting trail orienting pheromones after the ants have been stimulated by the short-living venom gland secretion, while the Dufour gland in addition elicits a strong repellent effect in other ant species (HÖLLDOBLER, 1988). Despite the voluminous size of the Dufour gland, no associated volatile materials like those found in other ants could be detected in these *Meranoplus* species (MORGAN and BILLEN, unpubl.). Although only a few species have been formally named (TAYLOR, 1987), *Meranoplus* is very species rich, diverse and common in Australia, especially in arid and semi-arid areas, where most species appear to harvest seeds. The glandular morphology presumably relates to these characteristics of distribution and habit.

The very long venom gland filaments in *Dolichoderus* and *Leptomyrmex* are markedly unlike the short, bulbous organs found in all previously examined

Dolichoderinae and, until now, thought to characterize the subfamily (PAVAN, 1955 ; HÖLLDOBLER and WILSON, 1990). The reverse is true of the *Meranoplus* venom glands. Here the short, knob-like filaments are quite unlike the long, slender organs previously reported from other myrmicine ants (BLUM and HERMANN, 1978a), and resemble those of most dolichoderines. The occurrence of lobate venom gland filaments was also noticed for an undescribed Australian *Meranoplus* species (HÖLLDOBLER, 1988), but without any further comments on this aberrant morphology for a myrmicine ant.

These observations by no means challenge the classification of the genera involved, since they otherwise conform fully to the diagnoses of their subfamilies. The similarities involved may well be due to homoplasy. Nonetheless they do demonstrate that venom gland morphology is much less consistent in these ants than was previously supposed.

ACKNOWLEDGEMENTS

We thank Dr. A.N. Andersen for providing the Darwin *Meranoplus* series, and Renate Sadler for curating the voucher specimens. The Belgian Fund for Scientific Research supported the visit of J.B. to Australia.

REFERENCES

BILLEN, J. (1986) — Morphology and ultrastructure of the abdominal glands in dolichoderine ants (Hymenoptera, Formicidae). *Ins. Soc.*, **33** : 278-295.

BLUM, M.S. and H.R. HERMANN (1978a) — Venoms and venom apparatuses of the Formicidae : Myrmeciinae, Ponerinae, Dorylinae, Pseudomyrmecinae, Myrmicinae, and Formicinae. In : BETTINI, S. (Ed.). *Arthropod Venoms*. Springer, Berlin-Heidelberg-New York : 801-869.

BLUM, M.S. and H.R. HERMANN (1978b) — Venoms and venom apparatuses of the Formicidae : Dolichoderinae and Aneuretinae. In : BETTINI S. (Ed.). *Arthropod Venoms*. Springer, Berlin-Heidelberg-New York : 871-894.

BROWN, W.L. (1973) — A comparison of the Hylean and Congo - West African rain forest ant faunas. In : MEGGERS B.J., E.S. AYENSU and W.D. DUCKWORTH (Eds.). *Tropical forest ecosystems in Africa and South America : a comparative review*. Smithsonian Institution Press, Washington : 161-185.

HÖLLDOBLER, B. (1988) — Chemical communication in *Meranoplus* (Hymenoptera : Formicidae). *Psyche*, **95** : 139-151.

HÖLLDOBLER, B. and E.O. WILSON (1990) — *The Ants*. Belknap Press of Harvard University Press, Cambridge, Massachusetts, pp. 732.

PAVAN, M. (1955) — Studi sui Formicidae. I. Contributo alla conoscenza degli organi gastrali dei Dolichoderinae. *Natura (Milano)*, **46** : 135-145.

PAVAN, M. and G. RONCHETTI (1955) — Studi sulla morfologia esterna e anatomia interna dell'operaia di *Iridomyrmex humilis* MAYR e ricerche chimiche e biologiche sulla iridomirmecina. *Atti Soc. It. Sc. Nat.*, **94** : 379-477.

TAYLOR, R.W. (1987) — A catalogue of the ants of Australia, New Caledonia, and New Zealand. *CSIRO Aust. Div. Entomol. Rep.*, **41** : 1-92.

TRANIELLO, J. and A.K. JAYASURIYA (1981) — Chemical communication in the primitive ant *Aneuretus simoni* : The role of the sternal and pygidial glands. *J. Chem. Ecol.*, **7** : 1023-1033.

WHEELER, W.M. (1935) — Myrmecological notes. *Psyche*, **42** : 151-160.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 165-192 — Brussels 1993

Manuscript received on 17 July 1993

RELATIONS PHYLOGÉNÉTIQUES DES GONORHYNCHIFORMES (OSTARIOPHYSI)

par

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RÉSUMÉ

Les relations phylogénétiques des Gonorhynchiformes fossiles et actuels sont revues et modifiées. Le sous-ordre des Gonorhynchoidei comprend les familles Gonorhynchidae (Actuel et Tertiaire), Charitosomidae (Crétacé supérieur) et Judeichthyidae (Crétacé supérieur). Le sous-ordre des Chanoidei est paraphylétique. Le genre *Chanos* est considéré comme le groupe-frère de l'ensemble Kneridae + Phractolaemidae + Gonorhynchoidei, ce dernier sous-ordre incluant formes actuelles et fossiles. La position de *Ramallichthys* est rediscutée ainsi que l'intégration de l'ordre Gonorhynchiformes dans le super-ordre Ostariophysi.

Mots-clés : Ostariophysi, Gonorhynchiformes, cladistique.

Phylogenetical relationships of the Gonorhynchiformes (Ostariophysi)

SUMMARY

The relationships of the fossil and living Gonorhynchiformes are reviewed and modified. The families Judeichthidae (Upper Cretaceous), Charitosomidae (Upper Cretaceous) and Gonorhynchidae (Tertiary and Recent) belong to the suborder Gonorhynchoidei. The suborder Chanoidei is paraphyletic. The genus *Chanos* is considered the sister-group of Kneriidae + Phractolaemidae + Gonorhynchoidei, the last one including fossil and recent forms. The phylogenetic position of *Ramallichthys* is reviewed so the place of Gonorhynchiformes inside the Ostariophysi.

Keywords : Ostariophysi, Gonorhynchiformes, cladistics.

INTRODUCTION

Les Gonorhynchiformes, placés depuis 1970 dans les Ostariophysi (ROSEN et GREENWOOD, 1970) étaient classiquement divisés en deux sous-ordres : Gonorhynchoidei et Chanoidei. Les premiers regroupaient le genre actuel, marin, *Gonorhynchus* auquel semblaient être reliées les formes fossiles *Notogoneus* de l'Eocène des USA et d'Europe (PERKINS, 1970 ; GRANDE, 1984), *Charitosomus* du Crétacé supérieur du Liban (VON DER MARCK, 1885 ; WOODWARD, 1901 ; GAYET, 1986), *Judeichthys* du Crétacé supérieur d'Israël (GAYET, 1985a) et, d'après FINK et FINK (1981), les formes actuelles d'eau douce (*Kneria, Parakneria, Phractolaemus, Cromeria* et *Grasseichthys*) très spécialisées. A côté des Gonorhynchoidei, les Chanoidei regroupaient le genre actuel marin, *Chanos* Lacépède, 1803 (connu depuis l'Aptien de Petraroia en Italie et les genres *Parachanos* du Wealdien de Guinée et du Gabon (ARAMBOURG et SCHNEEGANS, 1935 ; TAVERNE, 1974b), *Aethalionospsis* du Wealdien de Belgique (TAVERNE, 1981), *Tharrhias* de l'Aptien du Brésil (OLIVERAS, 1978 ; PATTERSON, 1984a ; BRITO et WENZ, 1990), *Dastilbe* de l'Aptien du Brésil et d'Afrique (SANTOS, 1947 ; PATTERSON, 1984a ; GAYET, 1989), *Rubiesichthys* du Crétacé inférieur d'Espagne (WENZ, 1984) et *Prochanos* (BASSANI, 1879) du Crétacé supérieur (RADOVČIČ, 1975) de l'Isle de Lesina en Dalmatie. Le genre *Ramallichthys* Gayet, 1982, présente des caractères indiscutablement de Gonorhynchiformes mais aussi des caractères appartenant (d'après FINK et FINK, 1981) aux Cypriniformes. De ce fait, sa position systématique a d'abord été laissée *incertae sedis* entre ces deux groupes (GAYET, 1982). L'étude détaillée de ce genre (GAYET, 1986) conduisait, en revanche, dans la mesure où l'on acceptait sans discussion le cladogramme des Ostariophysi de FINK et FINK (1981), à le placer dans les Cypriniformes. *Ramallichthys* est revu dans le cadre de ce travail et sa position phylogénétique est rediscutée. Enfin, le genre *Chanopsis* Casier, 1961, du Crétacé inférieur du Zaïre, anciennement placé dans l'ordre des Gonorhynchiformes, est maintenant considéré comme un Osteoglossiforme (TAVERNE, 1984). PATTERSON (1984a) estime que *Tharrhias* et probablement les formes fossiles du Crétacé inférieur, *Dastilbe*, *Parachanos* et *Aethalionopsis* (*Rubiesichthys* Wenz, 1984 n'était pas encore publié) ne sont pas assignables à un sous-groupe actuel. Les Chanidae se limiteraient donc au seul genre *Chanos*, ce dernier étant considéré, par FINK et FINK (1981) et PATTERSON (1984a), comme groupe-frère de *Gonorhynchus* et des formes africaines actuelles ; le sous-ordre des Chanoidei se limiterait désormais à cette famille et au seul genre *Chanos*.

De nombreuses formes fossiles ont été citées dans la littérature car considérées comme appartenant aux Chanidae ; le lecteur se reportera à PATTERSON (1984a) qui en donne une liste exhaustive. Cependant, la médiocrité de leur préservation et l'absence d'étude récente de ces fossiles, ne permettent pas d'utiliser leurs caractères dans le cadre de ce travail ; ne sont donc considérés ici que les genres dont l'appartenance aux Gonorhynchiformes est certaine et/ou ceux dont l'étude permet des comparaisons.

MATÉRIEL ÉTUDIÉ

Tout le matériel étudié provient des laboratoires suivants :

Amèrican Museum of Natural History, New York (USA) : AMHN.

Centre des Sciences de la Terre, Lyon I (ACT : Gayet collection personnelle) Villeurbanne (France) : FSL.

Institut de Géologie, Münster (Allemagne).

Muséum national d'Histoire naturelle, Paléontologie, Paris (France) : MNHN.

Smithsonian Institution, Washington (USA) : USNM.

The Hebrew University of Jerusalem (Ein Yabrud), Jerusalem (Israël) : EY.

Matériel fossile et actuel de comparaison

• *Ramallichthys orientalis* Gayet, 1982 : EY 25, 41, 133d et g, 134, 381, 386 (holotype) 425, du Cénomanien de Ramallah en Israël (préparés à l'acide).

• *Judeichthys haasi* Gayet, 1985a : EY 432 (holotype) du Cénomanien de Ramallah en Israël (préparé à l'acide).

• *Hakeliosomus hakelensis* (Davis, 1887) : AMNH-4523-3746, 3757, 3770, 3856, 3895 et 5859 ; AUB-101791 et 109118 ; MNHN-HAK-110, 111d et g, 112, 113d et g, 114d, 116, 117d et g, 119, 120d et g, 121, 123d et g, 124, 125, 127, 128, 129, 131, 133, 134, 136d et g et 342 du Cénomanien de Hakel au Liban (préparés à l'acide à l'exception des six premiers).

• *Charitosomus formosus* von der Marck, 1885 : spécimen n° 8541 (holotype) et 9925 du Sénonien supérieur de Baumberg (Westphalie) en Allemagne conservé à l'Institut de Géologie de Münster (Allemagne).

• *Charitosomus lineolatus* (Pictet et Humbert, 1866) : MNHN 1939-7-70, 1946-18-221d, -397g, -1265, SHA-137g, 191, 192, 193, 194, 195, 197, 198, 199, 200, 202, 203, 204, 205, 206, 207, 209, 212, 214, 217, 218, 222, 224, 233d et g, 236d et g, 237d (= 1946-18-454d), 241, 244, 245, 248d et g, 249g, 256, 257, 259, 260, 263, 269, 272, 277, 281, 424, 486, 1451, 1452, 1453, 1454, 1455, AMNH-5866 du Santonien de Sahel Alma au Liban. (Seuls les numéros SHA-269 et 486 ont été préparés à l'acide).

• *Charitosomus major* Woodward, 1901 : Spécimen n° MNHN-1939-7-7 ; AMNH-PF-690, UC-2014 et UC-2019 ; USNM-22206 (100305) du Santonien de Sahel Alma au Liban.

• *Charitopsis spinosus* Gayet, 1993a : spécimen n° AMNH-3895 (holotype), n° MNHN-HAK-133, AMNH-3746 du Cénomanien de Hakel au Liban (préparés à l'acide).

• *Notogoneus squamosseus* (Blainville, 1818) : MNHN-Aix-33 ; MNHN-1869-481-16.

• *Notogoneus osculus* Cope, 1885 : MNHN-1869-481-17.

• *Gonorhynchus gonorhynchus* (Linné, 1766) : FSL (ACT) n° 52.

• *Chanos chanos* (Forskål, 1775) : FSL (ACT) n° 53.

DISCUSSION

L'étude cladistique réalisée ici permet de donner la classification suivante pour les Gonorhynchiformes :

Ostariophysi
  Anatophysi
    Gonorhynchiformes
      « Chanoidei » (non-Gonorhynchoidei)
        plésions
          Aethalionopsis Taverne, 1981
          « Groupe-*Tharrhias* »
        Chanidae
          Chanos Lacépède, 1803
        Kneriidae
          Kneria Steindachner, 1866
          Parakneria Poll, 1965
          Grasseichthys Géry, 1964
          Cromeria Boulanger, 1901
        Phractolaemidae
          Phractolaemus Boulanger, 1901
      Gonorhynchoïdei
        plésion
          Ramallichthys Gayet, 1982
        Judeichthyidae
          Judeichthys Gayet, 1985a
        Charitosomidae
          Hakeliosomus Gayet, 1993b.
          Charitosomus von der March, 1885
          Charitopsis Gayet, 1993a
        Gonorhynchidae
          Notogoneus Cope, 1885
          Gonorhynchus Scopoli, 1777

Pour une simplification de nomenclature, les termes suivants seront utilisés : « groupe-*Tharrhias* » (*Tharrhias* + *Parachanos* + *Dastilbe* + *Rubiesichthys*) dont les études anatomiques sont trop succinctes ou en cours ; les « Chanoidei » (groupe paraphylétique représentant *Aethalionopsis*, le « groupe-*Tharrhias* » et *Chanos*). Phylogénétiquement, les Kneriidae et les Phractoaemidae pourraient être considérées comme des Gonorhynchoidei ; néanmoins, il semble préférable de limiter ce terme à *Ramallichthys* + les Judeichthyidae + les Charitosomidae + les Gonorhynchidae, les relations existant entre les différents genres appartenant aux Kneriidae et aux Phractolaemidae, ainsi que celles entre les deux familles, ne paraissant pas encore très claires.

Relations phylogénétiques des Ostariophysi

Les Gonorhynchiformes ayant été réunis aux Ostariophysi (ROSEN et GREENWOOD, 1970 ; FINK et FINK, 1981), il est nécessaire, dans un premier temps, de reconsidérer les synapomorphies qui regroupent ces taxons.

Les caractères Ostariophysi tels qu'ils ont été définis par FINK et FINK en 1981 (signalés F&F dans le texte), et qui sont accessibles chez les formes fossiles, ont déjà été discutés (GAYET, 1986). Ils seront rappelés ici succinctement : ce sont :

- *Absence du dermopalatin (caractère F&F 20)*
- *Absence de supramaxillaires (caractère F&F 41)*
- *Absence d'un arc neural autogène en avant de la première vertèbre (caractère F&F 64)*
- *Division ventrale superficielle du muscle* adductor mandibulae *(caractère F&F 127)*. Ce caractère est observable chez les fossiles par sa zone d'insertion (GAYET, 1993b).

Ces quatre caractères sont acceptés (voir GAYET 1986) et sont effectivement observés chez tous les Gonorhynchiformes fossiles. Notons cependant que trois d'entre eux ne correspondent qu'à des « absences ».

Parallèlement, d'autres caractères définis comme synapomorphie des Ostariophysi par FINK et FINK, (1981) ne se retrouvent cependant que chez certains d'entre eux.

- *Absence du basisphénoïde (caractère F&F 7)*. D'après FINK et FINK (1981), les lamelles observées chez certains Siluriformes et considérées comme un basiphénoïde par KINDRED (1917) et d'autres auteurs, seraient mal interprétées, mais la définition de ces lamelles n'est pas donnée par FINK et FINK. Notons également que PASLEAU (1974) signale la présence d'un basisphénoïde chez *Chanos*. Il semble qu'il soit nécessaire d'être prudent pour le basisphénoïde dont « l'absence » chez les formes fossiles n'est peut être due qu'à la fossilisation.

- *Supraneural correspondant à l'arc neural du premier centrum absent (caractère F&F 58)*. Chez *Hakeliosomus*, un supraneural est présent en avant de la première vertèbre (GAYET 1986 : 37 ; 1993b) et, d'après CHARDON (1968, fig. 18), chez le Siluriforme *Diplomystes*. Chez les Gonorhynchiformes fossiles, ce premier supraneural n'est pas toujours observable en raison d'une mauvaise conservation à ce niveau.

- *Partie dorso-médiale des quatre premiers arcs neuraux élargis, en contact avec l'exoccipital et formant un toit continu au-dessus du canal neural (caractère F&F 63)*. Chez *Phractolaemus*, on note un léger élargissement des premiers arcs neuraux mais ceux-ci ne forment pas de toit continu (THYS VAN DEN AUDENAERDE, 1961, fig. 12). Chez *Kneria* et *Parakneria*, l'élargissement existe mais non le contact étroit avec les exoccipitaux (LENGLET, 1974, fig. 17). De même, un tel élargissement du premier arc neural n'a pas été figuré ni chez *Gonorhynchus* (MONOD, 1963, fig. 56 ; GREENWOOD *et al.*, 1966, fig. 8), ni chez *Chanos* (ROSEN et GREENWOOD, 1970, fig. 3 ; PASLEAU, 1974, fig. 15). Seuls, FINK et FINK, (1981, fig. 6) figurent un fort élargissement chez *Chanos*. Chez *Tharrhias*, il y a un léger élargissement des arcs neuraux mais sans

contact entre eux ni avec le neurocrâne (FINK et FINK, 1981, fig. 6, repris par PATTERSON 1984a, fig 3). Ainsi, l'élargissement des arcs neuraux semble être apparu plusieurs fois au sein des Gonorhynchiformes et par conséquent des Ostariophysi, mais aussi chez d'autres groupes comme les anguilles, pour ne citer qu'elles (BLOT, 1978).

• *Fusion de toutes les épines hémales antérieures à la vertèbre préurale 2 et ce, depuis le stade juvénile, au centrum correspondant (caractère F&F 111).* Les épines hémales de tous les Gonorhynchiformes fossiles, antérieures à la vertèbre préurale 2, sont toutes autogènes ; ce caractère n'est donc valable que pour les formes actuelles des Gonorhynchiformes et pour les Otophysi ; il est apparu plusieurs fois.

• *Vessie natatoire divisée en deux chambres, recouvertes d'une tunique péritonéale* (ROSEN & GREENWOOD, 1970), *attachée aux côtes pleurales des troisième et quatrième vertèbres et suspendue au mésentère dorsal épaissi antérieurement (caractères F&F 54 à 57).* Il n'y a aucune raison de considérer la vessie natatoire indivise des Siluriformes comme équivalente de la seule partie antérieure de celle des autres Ostariophysi (CHARDON, *in litt.*). L'attache en elle même n'est pas observable chez les formes fossiles. Seule une modification de la troisième côte pleurale, et elle seule, l'est. A l'exception d'*Aethalionopsis*, tous les Gonorhynchiformes présentent cette modification et tous les Otophysi présentent une modification des deux premières côtes. Ce caractère d'attache de la vessie natatoire peut donc être accepté comme synapomorphie des Ostariophysi si on le suppose présent chez les Gonorhynchiformes fossiles.

On constate, par conséquent, que la définition des Ostariophysi, incluant les Gonorhynchiformes, n'est basée que sur cinq caractères relativement certains (20, 41, 56, 64 et 127 de FINK et FINK, 1981), dont trois ne sont que des disparitions.

Relations phylogénétiques des Gonorhynchiformes

FINK et FINK (1981) séparent les Gonorhynchiformes des Otophysi sur la base de sept synapomorphies reconnues chez ce premier groupe. Tous les Gonorhynchiformes possèderaient, par ailleurs, six caractères mais rencontrés également chez certains Otophysi. Ces synapomorphies, parmi celles accessibles chez les fossiles, sont :

• *Os et cartilage du septum interorbitaire fortement réduits. L'orbitosphénoïde est absent et les pleurosphénoïdes, petits, sont largement séparés entre eux (caractère F&F 6).* Chez toutes les formes fossiles de Gonorhynchoidei étudiées (GAYET, 1993b), ainsi que chez les « Chanoidei », les Kneriidae et les Phractolaemidae, l'orbitosphénoïde est effectivement absent. Il est, en revanche, plus difficile de définir taille et position des pleurosphénoïdes en raison d'une mauvaise préservation à leur niveau.

• *Les pariétaux des Gonorhynchiformes auraient une taille réduite, « devenant à peine plus grands que les os portant le canal sensoriel » (caractère F&F 10).* Cette réduction des pariétaux, par ailleurs rejetés latéralement par le supraoccipital qui s'insère entre eux, est présente chez toutes les formes fossiles. Vue la configuration du crâne de *Charitopsis* (GAYET, 1993b), il est probable que les pariétaux devaient

également être réduits et rejetés latéralement, mais la mauvaise préservation du neurocrâne à ce niveau ne permet pas de s'en assurer.

Néanmoins, chez aucune forme fossile connue tant « Chanoidei » que Gonorhynchoidei, ces os ne sont réduits « à leur seule portion sensorielle ». Chez le Chanidae *Aethalionopsis* (Crétacé inférieur), les pariétaux sont aussi longs que les ptérotiques (TAVERNE, 1981, fig. 3) et de ce fait ne peuvent être considérés comme étant réduits ; les plus réduits sont vraisemblablement ceux, subrectangulaires, de *Judeichthys* (GAYET, 1985a, fig. 1), de *Hakeliosomus* ou de *Charitosomus* (GAYET, 1993b, fig. 2 et 22) mais ils sont encore suffisamment développés pour séparer totalement les frontaux des épiotiques. De par leur taille et leur position, les pariétaux de ces formes sont semblables à ceux de *Phractolaemus* (THYS VAN DEN AUDENARDE, 1961, fig. 13). Chez *Chanos,* les pariétaux sont trois fois plus larges que le canal sensoriel (PASLEAU, 1974, fig. 12) ; réduits cependant, ils ne séparent plus les frontaux des épiotiques qui entrent de ce fait en contact entre eux sur une faible largeur (*ibid.* ; TAVERNE, 1981, fig. 11 ; obs. pers. chez *Chanos chanos* et, contrairement à FINK et FINK, 1981, fig. 5A). Une même observation peut être faite chez *Gonorhynchus* chez qui les pariétaux sont sensiblement de même taille que le supraoccipital et où les épiotiques entrent en contact avec le frontal unique, immense, fusion des deux frontaux (PASLEAU, 1974 ; obs. pers. chez *Gonorhynchus gonorhynchus*). On constate donc une évolution parallèle des frontaux dans les deux lignées. Même si *Tharrhias* et les autres « Chanoidei » fossiles étaient placés comme groupe-frère de tous les autres Gonorhynchiformes actuels et *Chanos* comme groupe-frère de *Gonorhynchus* et des formes africaines actuelles (PATTERSON, 1984b : 13), il semble impossible de prendre ce caractère — tel que défini par FINK et FINK — comme synapomorphie de tous les Gonorhynchiformes à moins de la faire apparaître deux fois. En revanche, le définir simplement comme « une tendance à la réduction » et à la condition de le faire apparaître après la séparation d'*Aethalionopsis*, devient valable.

• *L'exoccipital seul (chez* Chanos *et* Gonorhynchus*) ou l'exoccipital et le supraoccipital (chez les Kneriidae et probablement chez* Phractolaemus*) présentent un bord cartilagineux postéro-dorsal proéminent absent chez les Otophysi (caractère F&F 14).* D'après CHARDON (1968), ce caractère serait présent également chez certains Siluriformes (*Silurus glanis, Wallago attu, Heterobranchus* sp.). Ce caractère n'a pu être observé chez aucune forme fossile. PATTERSON (1984a : 136) le considère cependant comme une des deux synapomorphies reliant les formes fossiles et que ne possèderait pas le genre *Tharrhias* (et probablement *Dastilbe*, *Parachanos* et *Aethalionospsis*). Il note néanmoins (p. 137) que le joint occipital de *Tharrhias* n'est pas précisément connu.

• *Le suspensorium est allongé dans le plan parasagittal, dans la région située entre le condyle articulaire du carré et l'hyomandibulaire. Corrélativement, il y a allongement de l'interopercule et de la branche inférieure du préopercule (caractère F&F 29).* En fait, si cet allongement apparaît effectivement dès les formes les plus anciennes comme *Aethalionopsis*, il est encore relativement faible puisque l'articulation quadrato-mandibulaire est en arrière de la ligne passant par le milieu de l'orbite (le parasphénoïde représentant l'horizontale). Il va ensuite s'accentuant de *Parachanos* (TAVERNE, 1981, fig. 2, 10), à *Tharrhias* (PATTERSON, 1984b, fig. 2), *Rubiesichthys*

(WENZ, 1984, fig. 2), jusqu'au *Chanos* actuel (TAVERNE, 1981, fig. 11). *Judeichthys* (GAYET, 1985a, fig. 3), *Hakeliosomus* (GAYET, 1993, fig. 18), *Parakneria* (LENGLET, 1974, fig. 2), voire même *Kneria* (*ibid*, fig. 12) et *Gonorhynchus* (PASLEAU, 1974), ne présentent pas un suspensorium beaucoup plus allongé que certains Cypriniformes comme *Microgrex* (GAYET, 1986, fig. 19), bien que l'articulation quadrato-mandibulaire soit située avant le milieu de l'orbite. Une forme comme *Cromeria* (AUBENTON, 1961, fig. 12) apparaît, par ses modifications anatomiques, difficile à comparer. En revanche, un allongement considérable, plus important que celui, maximum, observé chez *Tharrhias* ou *Chanos*, apparaît chez *Charitosomus*, chez *Charitopsis* (GAYET, 1993b, fig. 28 et 40) et chez *Notogoneus* (PERKINS, 1970, fig. 4). En conséquence, ce caractère « allongement du suspensorium » est un caractère qui semble surtout valable chez certaines formes fossiles, à l'exception d'*Aethalionopsis* et de *Hakeliosomus*, mais peut être cependant accepté pour l'ensemble des Gonorhynchiformes (avec disparition chez certaines formes actuelles).

• *Les prémaxillaires seraient des os fins et plats alors que chez la plupart des Téléostéens primitifs et chez les Cypriniformes, les prémaxillaires sont plus épais et plus robustes (caractère F&F 38)*. Le caractère robuste du prémaxillaire de *Gonorhynchus*, tel que l'a défini MONOD (1963 : 259) a déjà été remarqué (GAYET, 1986 : 54). Les prémaxillaires de *Judeichthys* (Gayet, 1985a, fig. 3), *Hakeliosomus* (GAYET, 1993b, fig. 6) et de *Charitosomus* sont semblables à ceux des Ctenothrissiformes (GAUDANT, 1978, fig. 4), c'est-à-dire des os relativement épais, nantis de plusieurs processus qui augmentent leur épaisseur. Seul, le prémaxillaire de *Charitopsis* (GAYET, 1993b, fig. 39) est, comme celui de *Parachanos* et de *Chanos* (TAVERNE, 1981, fig. 10, 11) et des Kneriidae (LENGLET, 1974), plat et fin. Ce caractère ne peut donc pas être considéré comme une synapomorphie des Gonorhynchiformes.

• *Présence « d'organes épibranchiaux » poches bilatérales situées dans la poche branchiale, postérieurement aux 4^e^ épibranchiaux (caractère F&F 46)* (citation de GREENWOOD *et al.*, 1966). Ces organes épibranchiaux semblent beaucoup plus développés chez *Chanos* et chez *Gonorhynchus* (PASLEAU, 1974) que chez les autres Gonorhynchiformes (HOWES, 1985). Par ailleurs, d'après HOWES (1985), les Kneriidae et les Phractolaemidae diffèreraient des Gonorhynchidae dans leur degré d'association des diverticulums épibranchiaux avec les arcs branchiaux postérieurs. Enfin, même si les formes fossiles n'apportent rien quant à une discussion sur ce caractère, il semble que ces organes épibranchiaux soient apparus, bien que différents (PASLEAU, 1974), indépendamment dans les différentes lignées d'Eutéléostéens inférieurs (Osteoglossiformes, Clupeiformes, Cypriniformes, Siluriformes et Gonorhynchiformes) (NELSON, 1967) et leur présence ne peut pas valablement être considérée comme une synapomorphie des Gonorhynchiformes.

• *Arc neural antérieur spécialement agrandi et présentant un contact développé et serré avec l'exoccipital (*Chanos *et* Gonorhynchus*) ou avec l'exoccipital et le supraoccipital (Kneriidae et* Phractolaemus*) (caractère F&F 65)*. Cet agrandissement particulier de l'arc neural antérieur a été contesté pour certaines formes (GAYET, 1986). Quant au contact avec les os cités du neurocrâne, il serait donc dû au développement de ces os ; on en reviendrait alors au caractère 14 (voir ci-dessus). En tout état de cause, si cet agrandissement particulier de l'arc neural antérieur

existait vraiment, pourquoi ne pas le comparer au développement du scaphium des Cypriniformes ? (GAYET, 1986 : 59). Il pourrait alors éventuellement être considéré comme une synapomorphie des Ostariophysi mais non des Gonorhynchiformes seuls.

Parmi les sept synapomorphies définies par FINK et FINK (1981), une seulement (caractère F&F6 : réduction des os et du cartilage du septum interorbitaire) est retenue et est observable chez les formes fossiles. Il convient d'ajouter également la position latérale du prémaxillaire au maxillaire, caractère que possèdent tous les Gonorhynchiformes.

Les six caractères, présents chez tous les Gonorhynchiformes mais aussi chez certains Otophysi (selon FINK et FINK, 1981), sont les suivants :

• *Absence de dents aux mâchoires, contrairement à la plupart des Téléostéens primitifs (caractère apparu parallèlement chez les Cypriniformes) (caractère F&F 42).* FINK et FINK (1981) ne mentionnent pas la présence de dents (apparition probablement secondaire) sur le prémaxillaire de *Gonorhynchus* (MONOD, 1963). Il est vrai que tous les Gonorhynchiformes fossiles sont édentés. Cependant, cette apparition n'est pas connue uniquement chez les Cypriniformes puisque *Lusitanichthys* (GAYET, 1985b) qui, s'il n'appartient pas aux Characiformes (tels que définis actuellement) ni aux Cypriniformes, n'en est pas moins un Otophysi, possède également une mâchoire édentée, tout comme *Chanoides*, considéré également par PATTERSON (1984b) comme un Otophysi. Cette absence de dents aux mâchoires caractérise également les Clupeomorphes considérés comme groupe-frère primitif des Ostariophysi (*in* LAUDER et LIEM, 1983). Ce caractère « mâchoires édentées », présent chez les Gonorhynchiformes (à l'exception de *Gonorhynchus*) mais aussi chez les formes plésions des Otophysi et chez les Cypriniformes, peut être considéré comme un caractère plésiomorphe au niveau des Ostariophysi mais non comme une synapomorphie des Gonorhynchiformes et ne peut donc pas être utilisé ici.

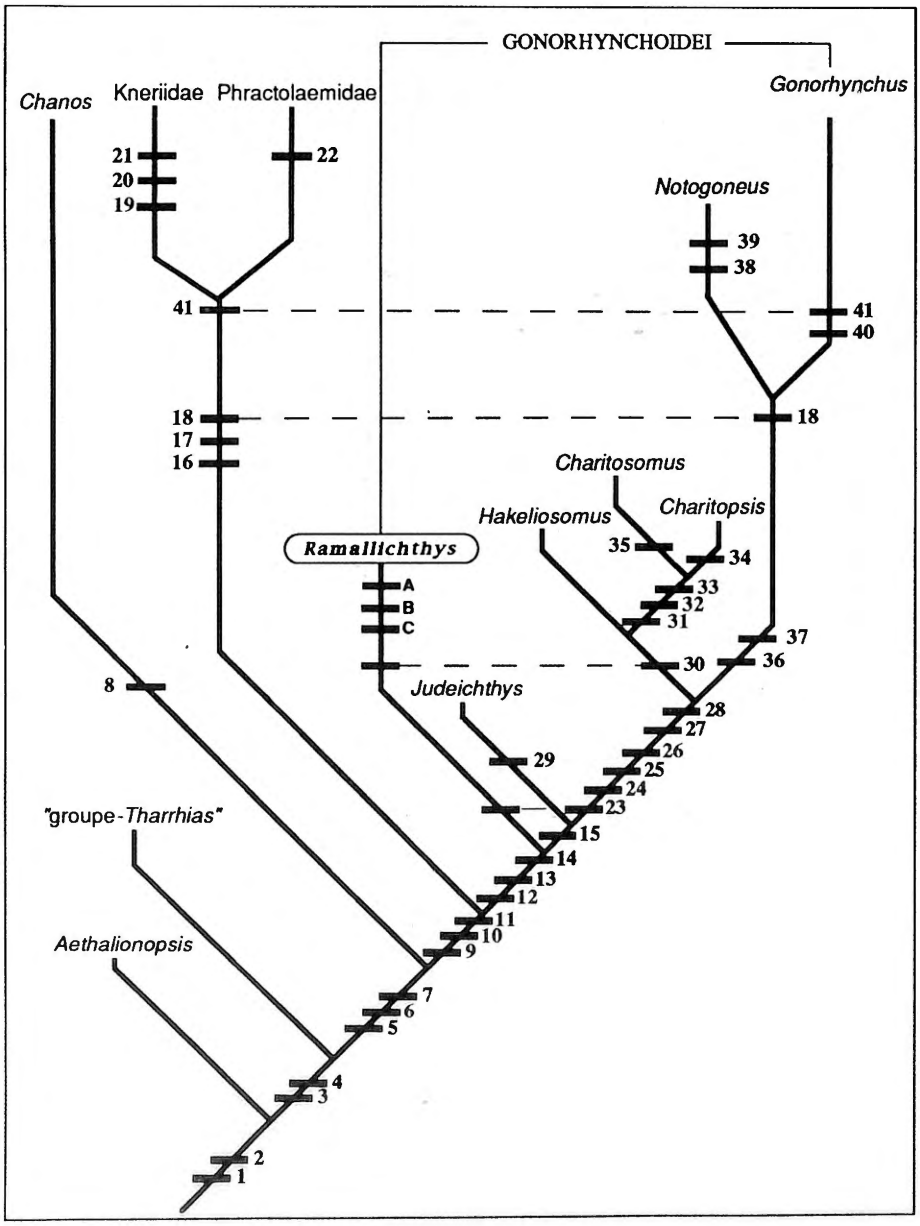
• *Absence de dents des deuxième et troisième pharyngobranchiaux et du basihyal (caractère présent également chez les Cypriniformes et chez les Siluriformes) (caractère F&F 47).* Ce caractère est inaccessible chez les formes fossiles étudiées.

• *Disparition des dents des deux plaques dentées postérieures pharyngobranchiales (caractère apparu également chez les Cypriniformes) (caractère F&F 48).* Les formes fossiles étudiées n'apportent aucun élément.

• *Réduction du nombre de postcleithra (un chez les Cypriniformes, zéro chez les Gonorhynchiformes et les Siluriformes) (caractère F&F 96).* On note cette absence chez tous les Gonorhynchiformes fossiles à l'exception de *Judeichthys* (GAYET 1985a : 76) et *Ramallichthys* (GAYET, 1986, fig. 41). PATTERSON (1984a : 136) considère que *Tharrhias* et les « Chanidae » du Crétacé inférieur n'ont pas ce caractère (ils possèderaient donc un ou plusieurs postcleithra) qu'il utilise pour relier tous les Gonorhynchiformes actuels. Or, TAVERNE (1981 : 967) signale « l'absence de postcleithrum » chez *Aethalionopsis* et SANTOS (1947 : 4) décrit la ceinture pectorale de *Dastilbe elongatus* sans parler de postcleithrum, ce qui peut faire conclure à son absence. Il semblerait, par conséquent, que ce caractère soit apparu plusieurs fois au sein des Gonorhynchiformes, mais aussi au sein des Ostariophysi.

(1) prémaxillaire latéral au maxillaire
(2) réduction os et cartilages du septum interorbitaire, absence orbitosphénoïde, réduction pleurosphénoïdes
(3) réduction pariétaux
(4) fort développement paire de côtes troisième vertèbre
(5) complexe terminal caudal
(6) perte deuxième uroneural
(7) perte postcleithrums
(8) organe épibranchial différent.
(9) perte épine premier arc neural
(10) tendance développement ailes mésethmoïde
(11) tendance disparition ossifications premiers basibranchial et pharyngobranchial
(12) angle branches inégales préopercule égal ou supérieur à 90°
(13) tête hyomandibulaire double
(14) plaques dentées très développées, accolées entoptérygoïde
(15) opercule triangulaire
(16) extension ailes ethmoïdes latéraux
(17) mobilité palatin.
(18) réduction mésethmoïde largement séparé des ethmoïdes latéraux
(19) développement latéral ailes du mésethmoïde
(20) inclinaison ventrale vomer
(21) extention rostrale
(22) apomorphies muscles de la mâchoire
(23) fusion second hypural à ce même complexe
(24) fusion parhypural au complexe caudal terminal
(25) allongement et rétrécissement médian des frontaux
(26) perte processus antérieur hyomandibulaire
(27) présence interhyal ossifié.
(28) écailles striées particulières .
(29) fusion deux premiers hypuraux entre eux
(30) processus rétroarticulaire inférieur très développé
(31) sousopercule épineux
(32) présence processus rétroarticulaire supérieur
(33) rapport position mésethmoïde-vomer
(34) opercule épineux
(35) allongement excessif tête et corps
(36) tête recouverte d'écailles
(37) écailles frangées sur leur bord postérieur
(38) sousopercule incisé
(39) perte plaques dentées endoptérygoïdiennes
(40) fusion frontaux en un frontal unique
(41) fusion arcs neuraux et parapophyses aux vertèbres
(A) présence d'un kinethmoïde
(B) présence de pré-ethmoïdes
(C) articulation palatino-entoptérygoïdienne

Fig. 1. — Cladogramme des relations phylogénétiques des Gonorhynchiformes.


GONORHYNCHOIDEI
Chanos
Kneriidae
Phractolaemidae
Gonorhynchus
Notogoneus
Charitosomus
Hakeliosomus
Charitopsis
Ramallichthys
Judeichthys
"groupe-Tharrhias"
Aethalionopsis
21
20
19
22
41
39
38
41
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A
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• *Réduction du nombre d'épuraux (caractère apparu parallèlement chez les Cypriniformes et les Siluriformes) (caractère F&F 115).* Cette diminution s'observe de manière graduelle chez les « Chanoidei » puisque *Aethalionopsis* possède encore trois épuraux (TAVERNE, 1981), *Rubiesichthys* (WENZ, 1984), *Parachanos*, *Dastilbe* (GAYET, 1989), *Tharrhias* (PATTERSON, 1975), deux, et *Chanos* (FINK et FINK, 1981), un seul. Chez les Gonorhynchoidei, les formes fossiles comme *Hakeliosomus*, *Charitosomus* et *Charitopsis* ne présentent qu'un seul épural (GAYET, 1993b), tandis que chez les formes actuelles *Parakneria* (LENGLET, 1974) et *Grasseichthys* (ROSEN et GREENWOOD, 1970) en possèdent deux et *Kneria* (Lenglet, 1974), *Phractolaemus* et *Gonorhynchus* (ROSEN et GREENWOOD, 1970) un seul. Cette réduction du nombre d'épuraux est donc différente de celle des Cypriniformes et des Siluriformes dont la réduction à un est générale dès l'apparition de ce groupe et ne peut pas être considérée comme synapomorphie des Gonorhynchiformes.

• *Absence de nageoire adipeuse (caractère présent également chez les Cypriniformes et les Gymnotiformes) (caractère F&F 125).* Cette absence nous a paru effective chez les Gonorhynchiformes fossiles étudiés (autant que l'on puisse en être certain en raison des problèmes de fossilisation) ainsi que chez tous les Cypriniformes. En revanche, *Ellisella kirschbaumi* (GAYET et MEUNIER, 1992), seul Gymnotiforme fossile connu, possède une nageoire adipeuse (MEUNIER et GAYET, 1991 ; GAYET *et al.*, in press).

Parmi les caractères pouvant définir les Gonorhynchiformes, bien qu'ils soient apparus parallèlement chez d'autres Ostariophysi, cinq sont acceptés (caractères F&F 42, 47, 48, 96, 125), trois sont accessibles chez les formes fossiles (caractères F&F 42, 96, 125) où ils sont effectivement observés.

Relations phylogénétiques des Gonorhynchiformes entre eux

Ces relations diffèrent selon les auteurs. PATTERSON (1984a) a résumé les différentes interprétations de ces relations et termine sur celle de FINK et FINK (1981) qu'il adopte « Since this is the only published scheme of gonorhynchiform relationships that is supported by characters » (p. 134). PATTERSON propose ainsi quatre possibilités de relations phylogénétiques pour situer les « Chanoidei » au sein des Gonorhynchiformes et opte pour la seconde hypothèse selon laquelle *Tharrhias*, et probablement *Dastilbe, Parachanos* et *Aethalionopsis*, représentent un « stem-group » inassignable à un sous-groupe actuel. Les Gonorhynchiformes actuels seraient alors reliés entre eux par deux caractères : l'absence de postcleithrum et le joint occipital (voir FINK et FINK, 1981, caractères 96 et 14) que ne possèdent pas les formes précédemment citées. Dans ces conditions, l'actuel *Chanos* représenterait le groupe-frère de *Gonorhynchus* + les Kneriidae + les Phractolaemidae Nous avons vu (caractère F&F 96) qu'en fait d'autres formes fossiles, telles *Aethalionopsis, Judeichthys* et probablement *Dastilbe* et *Tharrhias*, possèdent également un postcleithrum. Enfin, HOWES (1985) note qu'aucune synapomorphie n'a pu être mise en évidence au niveau des muscles crâniaux permettant de confirmer la position de *Gonorhynchus* comme groupe-frère des formes africaines actuelles.

Dans l'état actuel de nos connaissances, il est cependant possible de proposer l'hypothèse phylogénétique suivante (Fig. 1) : *Gonorhynchus, Notogoneus, Hakeliosomus, Charitosomus, Charitopsis* et *Judeichthys*, appartiennent au sous-ordre des Gonorhynchoidei (voir ci-après la discussion au sujet de *Ramallichthys)*. Les Kneriidae et les Phractolemidae pourraient cladistiquement être intégrés dans ce sous-ordre ; néanmoins, cette intégration ferait de ce sous-ordre un groupe plus disparate ; nous préférons, de ce fait, limiter le terme Gonorhynchoidei aux formes précédemment citées, les relations entre elles nous paraissant, sinon certaines, du moins plus sûres que celles des Kneriidae et des Phractolaemidae avec ce groupe et les considérer comme groupe-frère des Gonorhynchoidei. En accord avec PATTERSON (1984b), *Chanos* est seul au sein des Chanidae ; *Tharrhias, Dastilbe, Parachanos* et *Rubiesichthys* peuvent être très probablement regroupés dans une même famille (que nous ne créons pas ici dans la mesure où une étude supplémentaire de ces taxa devra être faite ou est en cours) ; *Aethalionopsis* représente le groupe-frère de tous les précédents. Ainsi :

• Tous les Gonorhynchiformes, y compris *Aethalionopsis* possèdent :
— un prémaxillaire placé latéralement au maxillaire **(1)** ;
— la réduction des os et des cartilages du septum interorbitaire, l'absence d'orbitosphénoïde et peut-être la réduction des pleurosphénoïdes **(2).**

• Tous les Gonorhynchiformes, à l'exception d'*Aethalionopsis*, présentent :
— une réduction, plus ou moins importante, des pariétaux, rejetés en arrière par le développement des frontaux et largement séparés par le supraoccipital **(3)** ; les pariétaux d'*Aethalionopsis* sont en fait totalement séparés par le supraoccipital mais contrairement à ceux des autres Gonorhynchiformes, ils ne sont aucunement réduits (Fig. 2) ;
— un développement particulier de la paire de côtes articulées à la troisième vertèbre **(4).**

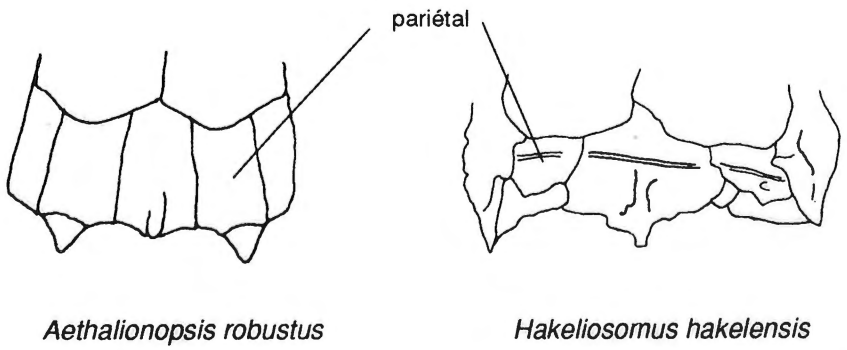

Fig. 2. — Partie postérieure du neurocrâne en vue dorsale. *Aethalionopsis robustus* (d'après TAVERNE, 1981 modifiée) ; *Hakeliosomus hakelensis* (d'après GAYET 1993b, modifiée).

• Tous les Gonorhynchiformes possèdent en commun les trois caractères suivants que l'on ne rencontre pas chez *Aethalionopsis* et le groupe *Tharrhias*. Ce sont :

— un complexe terminal caudal comprenant la fusion des vertèbres préurale 1, urales 2 et 1, de l'arc neural de la vertèbre préurale 1 et du premier uroneural **(5)** (Fig. 3) ;

— la perte d'un deuxième uroneural très long dépassant à l'avant la vertèbre préurale 1 **(6)** (Fig. 3). D'après TAVERNE (1981 : 974) *Aethalionopsis* présente, parmi les « Chanoidei », le stade le moins évolué du squelette caudal axial avec ses vertèbres urales 1 et 2 normales, non fusionnées, et la présence de 3 épuraux. Chez tous les « Chanoidei » fossiles, l'extrémité antérieure du premier uroneural dépasse la deuxième vertèbre préurale (il atteint la troisième vertèbre préurale chez *Aethalionopsis*). On compte trois uroneuraux (peut-être deux seulement chez *Rubiesichthys*) et on note la présence d'un arc neural court de la vertèbre urale 1. Le parhypural et les 6 hypuraux sont tous articulés aux vertèbres préurale 1 (pour le parhypural), urale 1 (pour les hypuraux 1 et 2) et urale 2 (pour les hypuraux 3 à 6) ; le premier hypural n'est pas décroché ;

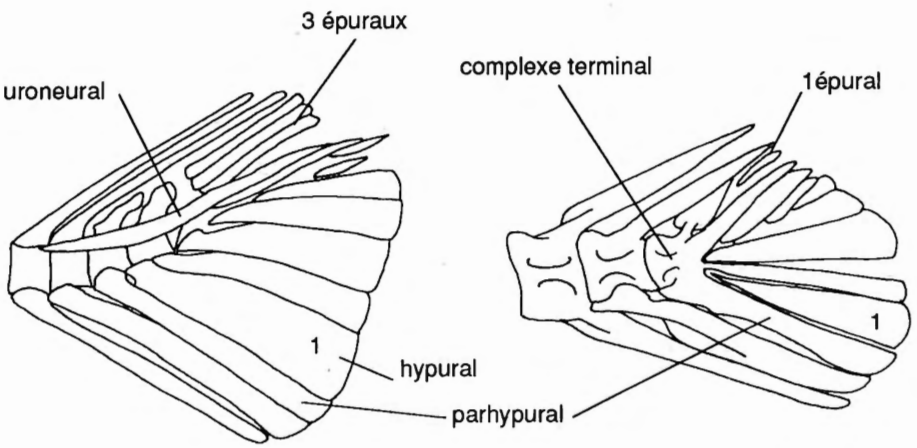

Fig. 3. — Squelette caudal axial : *Aethalionopsis robustus*, d'après TAVERNE, 1981 modifiée) ; *Hakeliosomus hakelensis* (d'après GAYET 1993b, modifiée).

— la perte des postcleithra **(7)**. *Judeichthys* a été décrit (GAYET, 1985a : 76) comme possédant un postcleithrum. Si cette observation est exacte (il n'existe qu'un seul exemplaire et l'observation à ce niveau est difficile), cela oblige à faire apparaître le caractère 7 (perte des postcleithra) quatre fois (*Chanos*, Knériidae + Phractolaemidae, *Notogoneus*, *Gonorhynchus* et les Charitosomidae) ou de le faire réapparaître chez *Judeichthys* (ce qui est une hypothèse plus parcimonieuse). Il serait bon, avant de décider, de trouver et d'étudier plus de matériel. Néanmoins, nous verrons lors de la discussion sur *Ramallichthys* que cette disparition des postcleithra est en fait apparue plusieurs fois.

• *Chanos* se caractérise par une différenciation au niveau de l'organe épibranchial **(8)** (CHARDON, inédit).

• Les Gonorhynchoidei, les Kneriidae et les Phractolaemidae ont en commun des caractères que les formes précédentes et *Chanos* ne possèdent pas :
— la perte de l'épine du premier arc neural (FINK et FINK, 1981 : 304) **(9)** ;
— la tendance au développement des ailes du mésethmoïde **(10)** (Fig. 4) (GAYET, 1993b) ;
— la tendance à la disparition des ossifications des premiers basibranchial et pharyngobranchial **(11)** (FINK et FINK, 1981 : 304). Dans la mesure où il est impossible, jusqu'à présent, d'observer ce dernier caractère chez les formes fossiles, nous l'acceptons et supposons sa présence chez les Gonorhynchoidei fossiles pour des raisons de parcimonie.

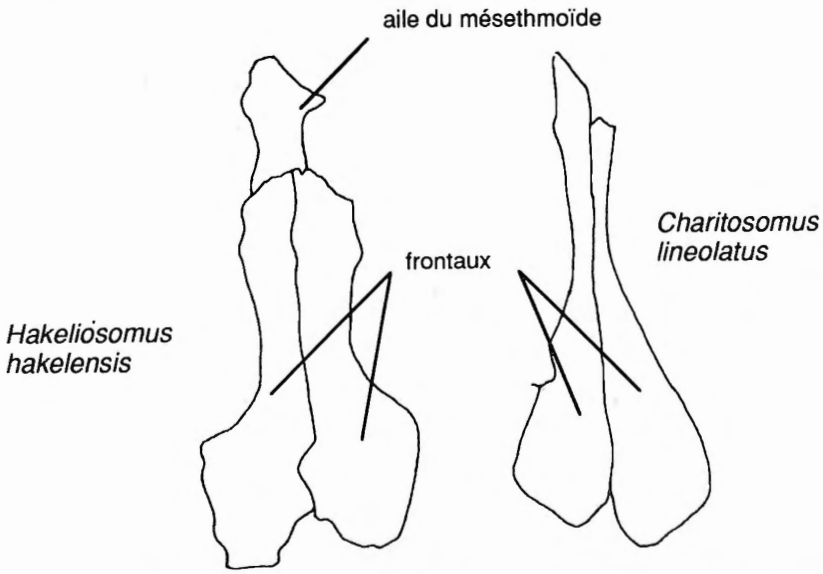

Fig. 4. — Partie médio-antérieure du neurocrâne en vue dorsale (d'après GAYET 1993b, modifiée).

• Les représentants du sous-ordre Gonorhynchoidei (Judeichthyidae, Charitosomidae et Gonorhynchidae) possèdent en commun quatre caractères que ne possèdent pas les « Chanoidei », les Kneriidae et les Phractolaemidae ; ce sont :
— un préopercule dont les deux branches de longueur inégale (la branche inférieure est toujours plus longue que la supérieure) forment entre elles un angle égal ou supérieur à 90° **(12)** alors qu'il est toujours inférieur à 90° chez les « Chanoidei » (Fig. 5). Les Kneriidae possèdent un préopercule dont l'angle des deux branches est nettement supérieur à 90° (LENGLET, 1974) mais les deux branches présentent une longueur égale ;

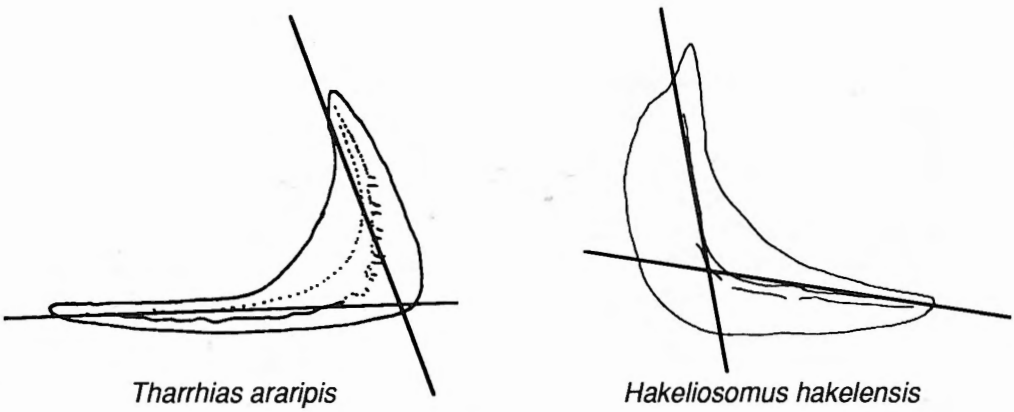

Fig. 5. — Préopercule. *Tharrhias araripis* (d'après PATTERSON, 1975 modifiée) ; *Hakeliosomus hakelensis* (d'après GAYET 1993b, modifiée).

— un hyomandibulaire dont la tête est toujours double et dont l'articulation se fait avec l'autosphénotique pour le processus antérieur et le ptérotique pour le processus postérieur **(13)** (GAYET, 1993b). Chez les « Chanoidei » la tête de l'hyomandibulaire est toujours simple, comme chez *Parachanos* (TAVERNE, 1981, fig. 10), *Tharrhias* (PATTERSON, 1975, fig. 6), *Rubiesichthys* (WENZ, 1984 : 279), *Chanos* : PASLEAU, 1974, fig. 16 ; FINK et FINK, 1981, fig. 8 ; obs. pers.) et l'articulation se fait avec l'autosphénotique et le ptérotique ; chez les Kneriidae *Kneria* et *Parakneria* (LENGLET, 1974 : 70), la tête articulaire est simple et l'articulation ne se fait qu'avec le ptérotique tandis que chez *Cromeria* (AUBENTON, 1961 : 138) elle se fait avec l'autosphénotique ;
— tous les représentants du sous-ordre Gonorhynchoidei, à l'exception de *Notogoneus*, possèdent en commun la présence de plaques dentées très développées, accolées à l'entoptérygoïde **(14)**. Dans certains cas, il semble que ces plaques soient mobiles et non fixées sur cet os (GAYET, 1993b chez *Charitosomus major* ; PASLEAU, 1974 chez *Gonorhynchus gonorhynchus*), ce qui ne change rien au fait de leur présence. Ces dents sont supposées secondairement disparues chez *Notogoneus* (voir caractère 35) ;
— enfin, ils possèdent tous un opercule triangulaire que ne présentent pas les « Chanoidei » **(15)** ni les Kneriidae et les Phractolaemidae chez qui l'opercule a une forme quadrangulaire, aux angles postérieurs plus ou moins arrondis selon les genres (Fig. 6) (PATTERSON, 1975 ; TAVERNE, 1981). Le sousopercule est petit, triangulaire, et situé en position sub-horizontale, suivant le bord inférieur de l'opercule. Dans le sous-ordre Gonorhynchoidei, le bord inférieur de l'opercule est oblique (formant un angle d'au moins 45° par rapport au bord antérieur) et le sousopercule, plus développé, suit ce bord inférieur (GAYET, 1993b).

• Les Kneriidae et les Phractolaemidae ont en commun :
— une extension des ailes des ethmoïdes latéraux **(16)** (HOWES, 1985 : 301) ;

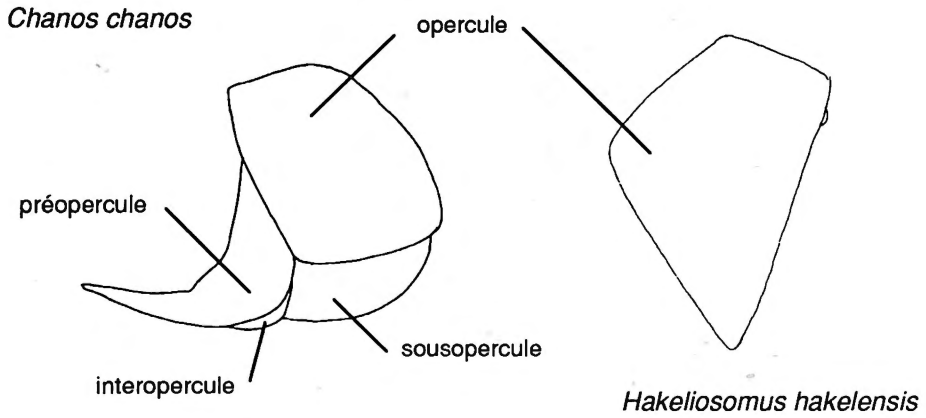

Fig. 6. — Opercule. *Chanos chanos* (d'après TAVERNE, 1981 modifiée ; *Hakeliosomus hakelensis* (d'après GAYET 1993b, modifiée).

— la mobilité du palatin **(17)**. Chez *Chanos*, l'ectoptérygoïde présente une forme trifide (GAYET, 1986, fig. 21 ; PASLEAU, 1974, fig. 16) et non bifide comme observée par FINK et FINK (1981, fig. 8). Il est en effet formé par trois branches : la branche inférieure qui vient se plaquer sur le bord antérieur du carré, la branche supéro-antérieure qui vient s'articuler sous le palatin et la branche supéro-postérieure qui se développe le long du bord supérieur du carré (avec un certain recouvrement) et s'accole au bord inférieur de l'entoptérygoïde. D'après PASLEAU (*op. cit.*) l'ectoptérygoïde peut présenter chez *Chanos* un développement extrême, la branche supéro-postérieure venant s'accoler aux bords inférieur du métaptérygoïde et antérieur du symplectique. Dans le sous-ordre des Gonorhynchoidei, plusieurs cas de figure se présentent. Chez *Judeichthys* (GAYET, 1985a, fig. 3), comme chez *Hakeliosomus* (GAYET, 1993b, fig. 8), la branche postérieure est absente ou quasi absente et on note une réduction importante de la branche supéro-antérieure qui peut se détacher du bord inférieur du palatin. Chez *Charitosomus* (*ibid.*, fig. 25) et chez *Charitopsis* (*ibid*, fig. 41), l'ectoptérygoïde possède une branche supéro-postérieure qui, bien que très développée, ne connaît cependant pas le développement de celle de *Chanos*. Chez *Gonorhynchus*, la branche inférieure est très réduite et les deux branches supérieures connaissent un développement sub-égal (GAYET, 1986, fig. 20 ; CHARDON, inédit). Dans tous les cas cependant, la branche antérieure de l'ectoptérygoïde, quel que soit son développement, vient se glisser de manière plus ou moins importante sous le palatin, interdisant de ce fait tout mouvement du palatin, contrairement à ce qui s'observe chez les Cypriniformes chez qui le palatin, libre de contact avec l'ectoptérygoïde, est articulé à l'entoptérygoïde. Seule la disposition observée chez *Charitosomus* permettrait, si articulation il y a, un mouvement du palatin. Une telle mobilité a été signalée par FINK et FINK (1981 : 304) chez *Gonorhynchus* et les formes africaines d'eau douce. En fait, d'après CHARDON (inédit), le palatin de *Gonorhynchus* est lié à l'entoptérygoïde par une large zone cartilagineuse qui

vient se positionner parallèlement à lui et ne permet pas de mouvements. Dès lors, seules les formes africaines présentent une mobilité vraie de cet os.

En dehors de ces deux caractères, les Kneriidae (LENGLET, 1974, figs. 3, 4 ; AUBENTON, 1961, fig. 4) et les Phractolaemidae (THYS VAN DEN AUDENAERDE, 1961, fig. 12) présentent en commun une réduction du mésethmoïde largement séparé des ethmoïdes latéraux **(18)**, que l'on observe aussi chez les Gonorhynchidae (CHARDON, inédit ; PERKINS, 1970, fig. 2) et que ne possèdent pas ni les autres « Chanoidei » ni les autres Gonorhynchoidei. Chez ces formes, il est, au contraire, très développé et vient au contact des ethmoïdes latéraux (GAYET, 1993b). Chez les Téléostens primitifs et chez les Cypriniformes considérés comme primitifs, le mésethmoïde, dont le développement est moindre que chez les formes fossiles du sous-ordre Gonorhynchoidei, entre largement en contact avec les ethmoïdes latéraux.

• Les représentants des Kneriidae forment un groupe monophylétique avec, selon Howes (1985 : 301) :
— un développement latéral très fort des ailes du mésethmoïde **(19)** ;
— une inclinaison ventrale du vomer **(20)** ;
— une extension rostrale **(21)**.

• Les Phractolaemidae, reliés entre eux par des apomorphies des muscles de la mâchoire (HOWES, 1985 : 299) **(22)**, posent problème quant à leurs relations avec les Gonorhynchoidei et même avec les Kneriidae. Ils partagent avec *Gonorhynchus* une division du muscle A2, avec *Grasseichthys* (Kneriidae) seul, un allongement épineux de l'interopercule, avec les Kneriidae sauf *Grasseichthys*, une division du A1 originaire en partie du carré et avec *Kneria* seul, la possibilité d'utiliser l'air atmosphérique (HOWES, 1985 : 299).

• Les Charitosomidae et les Gonorhynchidae possèdent en commun six caractères que ne possèdent pas *Judeichthys*, les Kneriidae, les Phractolaemidae et les « Chanoidei » :
— la fusion du second hypural à ce même complexe **(23)** (Fig. 3) ;
— la fusion du parhypural au complexe caudal terminal **(24)** (Fig. 3) ;
— l'allongement et le rétrécissement médian des frontaux **(25)** (moins marqué chez *Hakeliosomus*) (GAYET, 1993b) (Fig. 4) ;
— la perte du processus antérieur de l'hyomandibulaire **(26)**. Un processus antérieur à l'hyomandibulaire est connu avec un développement variable, chez *Tharrhias*, *Chanos*, *Judeichthys* (formes chez qui l'hyomandibulaire est bien préservé). Un processus semblable est présent chez *Ramallichthys* (GAYET, 1986, fig. 26), *Chanoides* (PATTERSON, 1984b, fig. 5), chez certains Cypriniformes (SAWADA, 1982, fig. 28). FINK *et al.* (1984 : 1036) signalent sa présence de façon variable chez certains Clupeomorphes, Salmonidae, Characiformes et Siluriformes. Chez tous les Gonorhynchoidei, à l'exception de *Judeichthys*, l'hyomandibulaire possède une fine plaque osseuse antérieure très développée ;
— la présence d'un interhyal ossifié **(27)**. Nous avons noté la présence d'un interhyal ossifié chez *Hakeliosomus* comme chez *Gonorhynchus*. L'observation n'a pas été possible chez les autres formes fossiles. Une telle ossification est absente chez les Kneriidae et les Phractolaemidae ainsi que chez les « Chanoidei »

(McALLISTER, 1968 : 46-47). La présence de cette ossification, difficile à déceler chez les formes fossiles, est supposée chez *Charitosomus* et chez *Charitopsis* (GAYET, 1993b) et considérée comme synapomorphie reliant les Charitosomidae aux Gonorhynchidae;

— des écailles striées particulières **(28)**.

• *Judeichthys*, et lui seul, présente, la fusion des deux premiers hypuraux **(29)**, l'ensemble s'articulant au complexe terminal. Chez *Gonorhynchus*, les deux premiers hypuraux apparaissent soudés entre eux mais ils sont fusionnés au complexe terminal.

• Les Charitosomidae présentent un processus rétroarticulaire inférieur très développé **(30)** (GAYET, 1993b) que ne possèdent pas les Gonorhynchidae.

La séparation du genre *Charitosomus* en *Hakeliosomus* et *Charitosomus* (Gayet, 1993b) modifie les relations phylogénétiques des formes libanaises entre elles telles que les avaient supposées Gayet (1993a : 261).

• *Charitosomus* et *Charitopsis* présentent :

— un sousopercule épineux **(31)** (Gayet, 1993b, fig. 26 et 40) que ne possède pas *Hakeliosomus* ;

— un processus rétroarticulaire supérieur **(32)** (*ibid.*, fig. 23 et 42) ;

— un rapport de position mésethmoïde-vomer inverse de celle des autres Gonorhynchiformes (GAYET, 1993b), c'est-à-dire que le mésethmoïde dépasse ici largement le vomer vers l'avant **(33)** (Fig. 7) ;

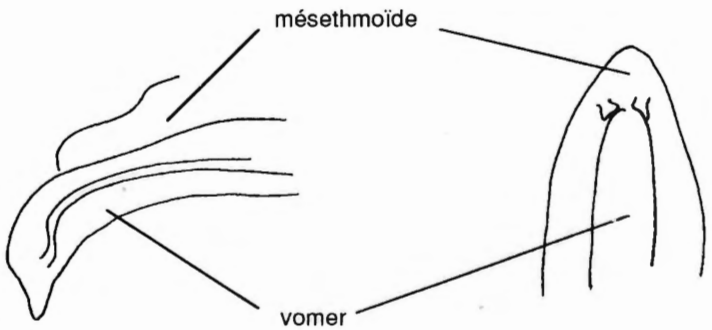

Fig. 7. — Partie antérieure du museau. *Hakeliosomus hakelensis* en vue latérale (d'après GAYET, 1993b modifiée) ; *Charitopsis spinosus* en vue ventrale (d'après GAYET 1993b, modifiée).

• *Charitopsis* se sépare de tous les autres genres par son opercule à huit épines **(34)** (GAYET, 1993a, b)

• *Charitosomus* présente un allongement excessif de la tête et du corps **(35)** (GAYET, 1993b).

• Les Gonorhynchidae (*Notogoneus* et *Gonorhynchus*) ont une tête recouverte d'écailles **(36)** alors qu'elle est nue chez les Charitosomidae, des écailles frangées sur leur bord postérieur (GRANDE, 1984, fig. II-53) **(37)** et la réduction du mésethmoïde (caractère **18** apparu parallèlement chez les Kneriidae et les Phractolaemidae).

• *Notogoneus* possède deux caractères uniques :
— un sousopercule incisé **(38)** ;
— la perte des plaques dentées endoptérygoïdiennes **(39).**

• *Gonorhynchus* est le seul à présenter une fusion des frontaux en un frontal unique **(40).**

FINK et FINK (1981 : 304) avaient relié les formes africaines d'eau douce (Kneiidae et Phractolaemidae) à *Gonorhynchus* par la réduction de l'ectoptérygoïde et la mobilité du palatin, caractère qui apparaît parallèlement chez les Cypriniformes et que nous avons limité aux seuls Kneriidae et Phractolaemidae **(17)**, ainsi que par la fusion des arcs neuraux et des parapophyses aux vertèbres, caractère que nous considérons comme une convergence chez les formes actuelles **(41).**

Problème du genre *Ramallichthys*

Ramallichthys orientalis (GAYET, 1982) du Cénomanien inférieur de Rammallah (Monts de Judée) pose plusieurs problèmes (GAYET, 1986) que l'étude phylogénétique des Gonorhynchiformes, réalisée ici, ne résout pas totalement dans l'état de nos connaissances.

Ce genre avait été considéré tout d'abord comme un Ostariophysaire *incertae sedis* (GAYET, 1982) puis en 1986 le même auteur montrait les problèmes posés par ce genre dans la mesure où la base de travail restait, en l'état, le cladogramme de FINK et FINK (1981) sur la phylogénie des Ostariophysi. Si on admettait ce cladogramme pour vrai et unique, *Ramallichthys* qui présentait des synapomorphies de Cypriniformes ne pouvait être considéré que comme un représentant de cet ordre.

En effet, *Ramallichthys* est sans conteste un Ostariophysaire puisqu'il possède les caractères proposés par FINK et FINK (1981) et acceptés (PATTERSON, 1984a ; GAYET, 1986), bien que nous réiérons notre remarque selon laquelle un super-ordre de l'importance des Ostariophysi est basé sur cinq caractères seulement dont trois ne sont que des disparitions d'os, caractères que l'on peut retrouver dans d'autres groupes non directement liés à lui (voir p. 170).

Par rapport aux Gonorhynchiformes tels que définis ici, *Ramallichthys* partage les caractères suivants :

• avec tous
(1) un prémaxillaire latéral au maxillaire ;
(2) la réduction du septum interorbitaire ;

• avec tous sauf *Aethalionopsis*
(3) la réduction des pariétaux ;
(4) l'élargissement de la troisième côte pleurale ;

• avec tous sauf *Aethalionopsis* et le groupe-*Tharrhias* :
(5) un complexe terminal (PU1 + U2 + U1 + Un + nPU1) ;

(6) la perte d'un second uroneural dépassant la vertèbre préurale 1.

Il ne possède pas, comme *Judeichthys*, le caractère **(7)** à savoir la perte des postcleithrums (mais voir p. 177).

- avec les Kneriidae-Phractolaemidae et les Gonorhynchoidei :

(9) la perte de l'épine neurale du premier arc neural ;
(10) la tendance au développement latéral des ailes du mésethmoïde ;
(11) ? ce caractère (disparition des ossifications des premiers basibranchial et pharyngobranchial), non observable chez les formes fossiles étudiées, a été supposé chez elles ; il peut donc également être supposé chez *Ramallichthys*.

- avec les Gonorhynchoidei seuls :

(12) l'angle des deux branches du préopercule supérieur à 90° ;
(13) une tête de l'hyomandibulaire double à articulation autosphénotique-ptérotique ;
(14) des plaques dentées liées (ou non ?) à l'entoptérygoïde et au basihyal.

Il ne possède pas le caractère **(15)** : opercule triangulaire.

- avec les Gonorhynchoidei et les Charitosomidae, il partage le caractère **(23)** (fusion du second hypural au complexe axial terminal), caractère que ne possède pas *Judeichthys*, mais ne possède pas les autres caractères **(24-28)**

- avec les Charitosomidae

(30) le développement marqué du processus rétroarticulaire inférieur.

Si l'on s'en tient à ces caractères Gonorhynchiformes, on constate donc que *Ramallichthys* pourrait être considéré comme le groupe-frère plésiomorphe des Gonorhynchoidei à la condition seulement de faire apparaître deux fois les caractères **(23)** (fusion du second hypural au complexe terminal) et **(30)** (présence d'un processus rétroarticulaire inférieur développé). Il resterait néanmoins le problème de la disparition du postcleithrum **(7)** qu'il conviendrait alors de faire apparaître trois fois : chez *Chanos*, chez les Kneriidae-Phractolaemidae et chez les Gonorhynchoidei.

Néanmoins, le problème des relations phylogénétiques de *Ramallichthys* reste entier si on accepte la phylogénie des Ostariophysi telle qu'elle est définie par FINK et FINK (1981). En effet, *Ramallichthys* présente une modification des éléments neuraux antérieurs (Fig. 8) qui le sépare de tous les Gonorhynchiformes et qui, si on se limite à cet ordre, apparaît comme une apomorphie de ce genre. Le fonctionnement de cette structure a été considéré comme une transmission non-webérienne à l'image de celles de *Chanos* et de *Gonorhynchus* (GAYET et CHARDON, 1987 : 39). Il est vrai que l'étude des modifications des vertèbres antérieures des Gonorhynchoidei tels que *Hakeliosomus* et *Charitosomus* (GAYET, 1993b) montre une certaine variation dans la forme principalement des deux premiers arcs neuraux et supraneuraux (Fig. 9), ressemblant à autant d'essais « avortés » pour en arriver aux formes actuelles chez qui la régularité des éléments neuraux est de mise. Néanmoins, force est de constater que l'état de modification des éléments neuraux des premières vertèbres de *Ramallichthys*, plus spécialisé que celui des Gonorhynchiformes, y compris celui de *Hakeliosomus*, représente aussi le (un ?) stade plésiomorphe des Otophysi. Considérant que l'appareil de Weber n'a pas dû se former dans son état actuel

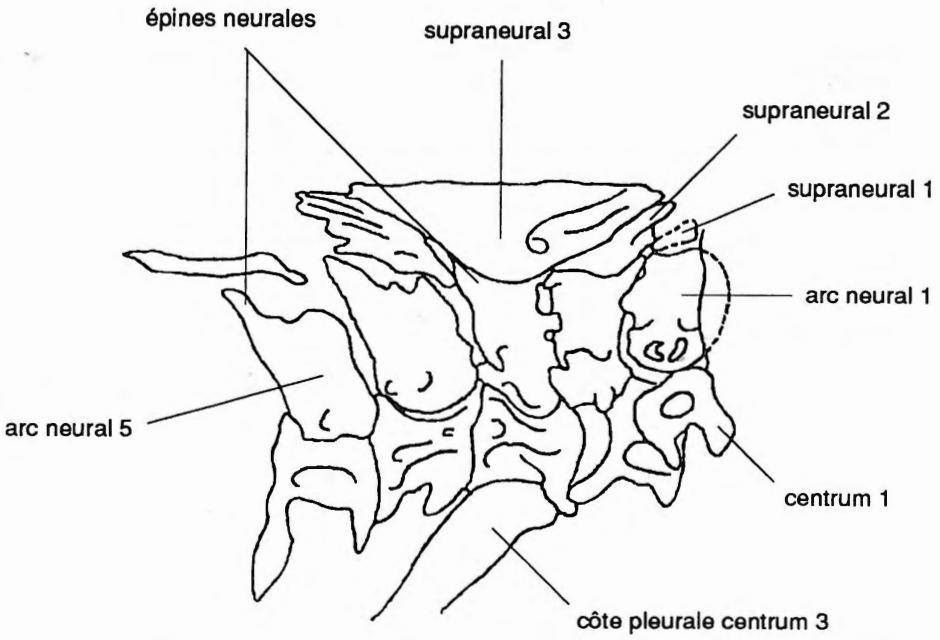

Fig. 8. — Vertèbres antérieures de *Ramallichthys orientalis* (d'après GAYET, 1986 modifiée).

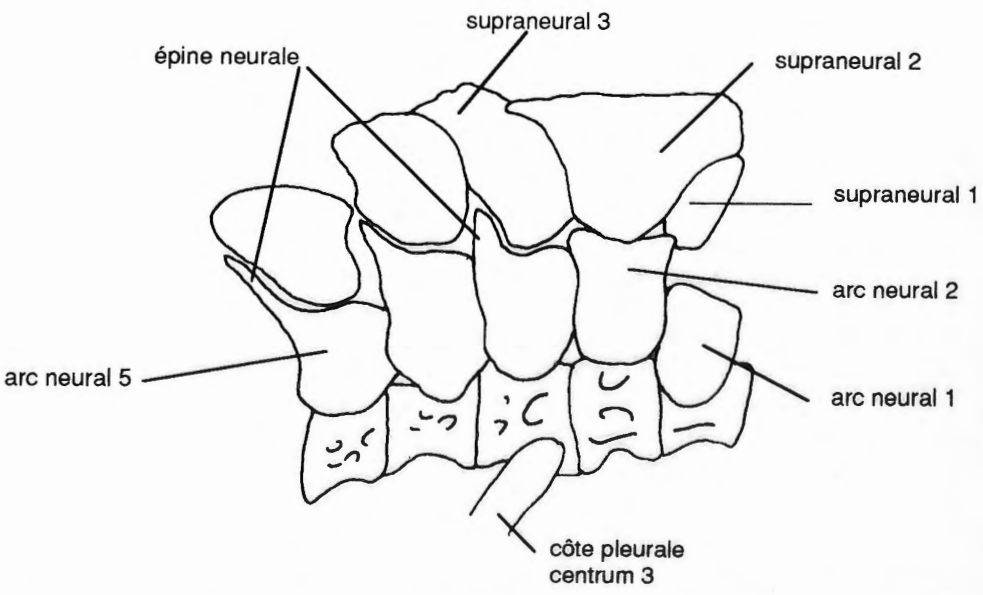

Fig. 9. — Vertèbres antérieures d'*Hakeliosomus hakelensis* (d'après GAYET 1993b, modifiée).

(c'est-à-dire tel qu'il se présente chez les différents groupes d'Otophysi actuels) mais que des états intermédiaires, fonctionnant différemment selon leurs possibilités (GAYET et CHARDON, 1987), ont existé, cela signifie que l'appareil de Weber, tel qu'il est connu actuellement ne représente pas une synapomorphie des Otophysi *sensu lato* c'est-à-dire incluant formes fossiles et actuelles. Il est inconcevable que vingt éléments différents (supraneuraux, arcs neuraux, vertèbres, parapophyses et côtes pleurales de quatre centra) sans parler des parties molles, se soient modifiés simultanément pour former un appareil de Weber parfaitement fonctionnel et identique à l'actuel, même s'il est admis que la nature fait des sauts (lesquels ne sont peut-être, dans certains cas, que le fruit de notre ignorance). Quelques fossiles sont là pour confirmer cette hypothèse : *Lusitanichthys* (GAYET 1981, 1985b), *Salminops* (Gayet 1985b, 1985c), *Chanoides* (PATTERSON 1984b), d'autres seront probablement découverts. D'ailleurs, nous répétons une remarque déjà faite (GAYET, 1986), si on considère l'appareil de Weber comme un tout indissociable au niveau des Otophysi, pourquoi le fragmenter en plusieurs synapomorphies à ce niveau comme l'ont fait FINK et FINK (1981) ?

PATTERSON (1984b : 453), critiquant GAYET (1986), décèle « an example of a familiar syndrome, the paleontologist desires to propose that Recent groups are polyphyletic, and that structures characterizing them, ..., have evolved more than once ». Or, fonder des cladogrammes uniquement sur les formes actuelles en évacuant les documents fossiles peut être confortable mais semble aberrant. Les formes fossiles ayant précédé les actuelles entretiennent avec celles-ci des relations à préciser puisque ces dernières en découlent. Il est, dès lors, simplificateur et non objectif de postuler *a priori* que toutes les formes actuelles sont directement reliées entre elles et de considérer ainsi toutes les formes fossiles comme des plésions. Ainsi, s'il est relativement facile à PATTERSON (1984a) de placer *Tharrhias* comme plésion des Chanidae, il lui est nécessaire, pour placer *Chanoides* comme plésion des Otophysi (PATTERSON, 1984b) d'éliminer certains caractères comme « non-homologous ». Il rejette ainsi le caractère « hypural 1 décroché » (synapomorphie des Characiformes **parce que** *Chanoides* ne possède pas les autres synapomorphies de cet ordre). Quant à *Lusitanichthys*, il le considère comme étant simplement un Otophyi mais non pas comme un characiforme ou un Characiphysi ; or, cela oblige à considérer (si on conserve les synapomorphies des Characiphysi et des Characiformes telles que définies) comme non-homologues trois caractères de Characiphysi (raccourcissement des trois premiers centra, articulation du vomer postérieur au mésethmoïde, articulation du prémaxillaire) et deux caractères de Characiformes (ouverture de la fosse temporale, hiatus à la partie distale du premier hypural) (GAYET, 1985b : 114-115). Ainsi également, *Salminops*, découvert depuis la publication de PATTERSON (GAYET, 1985b), possède des synapomorphies des Characiformes telles que définies par FINK et FINK (1981) mais ne possède pas toutes celles des Characiphisi ni même des Otophysi. *Ramallichthys*, dont l'étude détaillée (GAYET, 1986) n'était pas encore publiée lors de la description de *Chanoides* (PATTERSON 1984b), est considéré comme « less otophysan-like than *Chanoides* » (p. 453). Pour cela, il faut ne pas tenir compte de la présence, chez ce taxon, d'un kinethmoïde, de pré-ethmoïdes, d'un processus dorso-médian du palatin et de la tendance à la formation d'une articulation pala-

tino-entoptérygoïdienne, caractères considérés comme synapomorphies des Cypriniformes ou considérer ces caractères comme non homologues. Il est vrai qu'un kinethmoïde est également présent chez *Chanoides*, considéré par PATTERSON (1984b) comme non homologue, ainsi qu'une articulation palato-entoptérygoïdienne, et que le processus dorso-médian du palatin est au moins présent, et bien développé, chez *Hakeliosomus* et chez *Charitosomus* (GAYET, 1993b, fig. 9 et 24). Par ailleurs, on peut remarquer que plusieurs caractères rencontrés chez *Ramallichthys* et chez les Gonorhynchoidei, mais non chez les « Chanoidei » à l'exception de *Chanos*, se retrouvent chez les Cypriniformes et/ou les Characiformes, comme la formation d'un complexe axial terminal, puis la fusion du second hypural à ce complexe, la perte d'un long uroneural accolé latéralement à la vertèbre préurale 1, ou encore la réduction du nombre de postcleithra.

Mettre *Aethalionopsis* et le groupe « *Tharrhias* » comme plésion des Ostariophysi obligerait à faire apparaître trois fois (ou deux fois selon les caractères) les synapomorphies définies pour les Gonorhynchiformes, y compris la réduction des pariétaux.

En conclusion, si les Gonorhynchiformes n'étaient pas considérés comme des Ostariophysi, *Ramallichthys* serait mis presque sans problème comme groupe-frère plésiomorphe des Gonorhynchoidei, puisque seuls les caractères **(23)** : fusion du second hypural au complexe axial terminal et **(30)** : développement exagéré du processus rétroarticulaire inférieur, apparaissent parallèlement chez d'autres Gonorhynchiformes (Fig. 1). Dans ces conditions, les caractères comme la modification des éléments neuraux des premières vertèbres, d'un kinethmoïde et de pré-ethmoïdes, seraient considérés comme non homologues de ceux des Cypriniformes et pourraient être considérés comme apomorphies de *Ramallichthys*.

Mais si on maintient les Gonorhynchiformes dans les Ostariophysi, l'apparition chez *Ramallichthys* de caractères considérés comme des synapomorphies chez les Cypriniformes (et eux seuls au sein des Ostariophysi) repose, si on ne veut pas modifier les synapomorphies des Otophysi et plus particulièrement celles des Cypriniformes, le problème de la position phylogénétique de ce taxon.

Enfin, le cladogramme (Fig. 10) replacé en fonction de la stratigraphie mérite quelques remarques. On constate, en effet, qu'à l'exception de *Chanos* et des formes d'eau douce africaines, le cladogramme suit la stratigraphie. *Aethalionopsis* et le groupe-*Tharrhias* du Crétacé inférieur apparaissent comme les formes plésiomorphes ; la spécialisation des Gonorhynchoidei évolue parallèlement à la chronologie avec « apparition » dans le cladogramme des formes du Crétacé supérieur (Judeichthyidae et Charitosomidae), puis du Tertiaire (*Notogoneus*) et enfin actuelles avec les Gonorhynchidae. Le seul anachronisme se situe au niveau de *Chanos*, des Kneriidae et des Phractolaemidae. Néanmoins, il serait fort intéressant de découvrir des formes fossiles correspondant à ces lignées ; le genre *Chanos* est connu à l'état fossile mais sa mauvaise préservation ne permet pas d'étudier les caractères nécessaires à une comparaison. Il est probable que *Chanos* et les formes d'eau douces africaines ne sont que l'aboutissement de longues lignées apparues au moins au Crétacé inférieur.

Cela vient confirmer encore, s'il en était besoin, la nécessité de prendre en compte les données paléontologiques dans l'élaboration et la compréhension des cladogrammes.

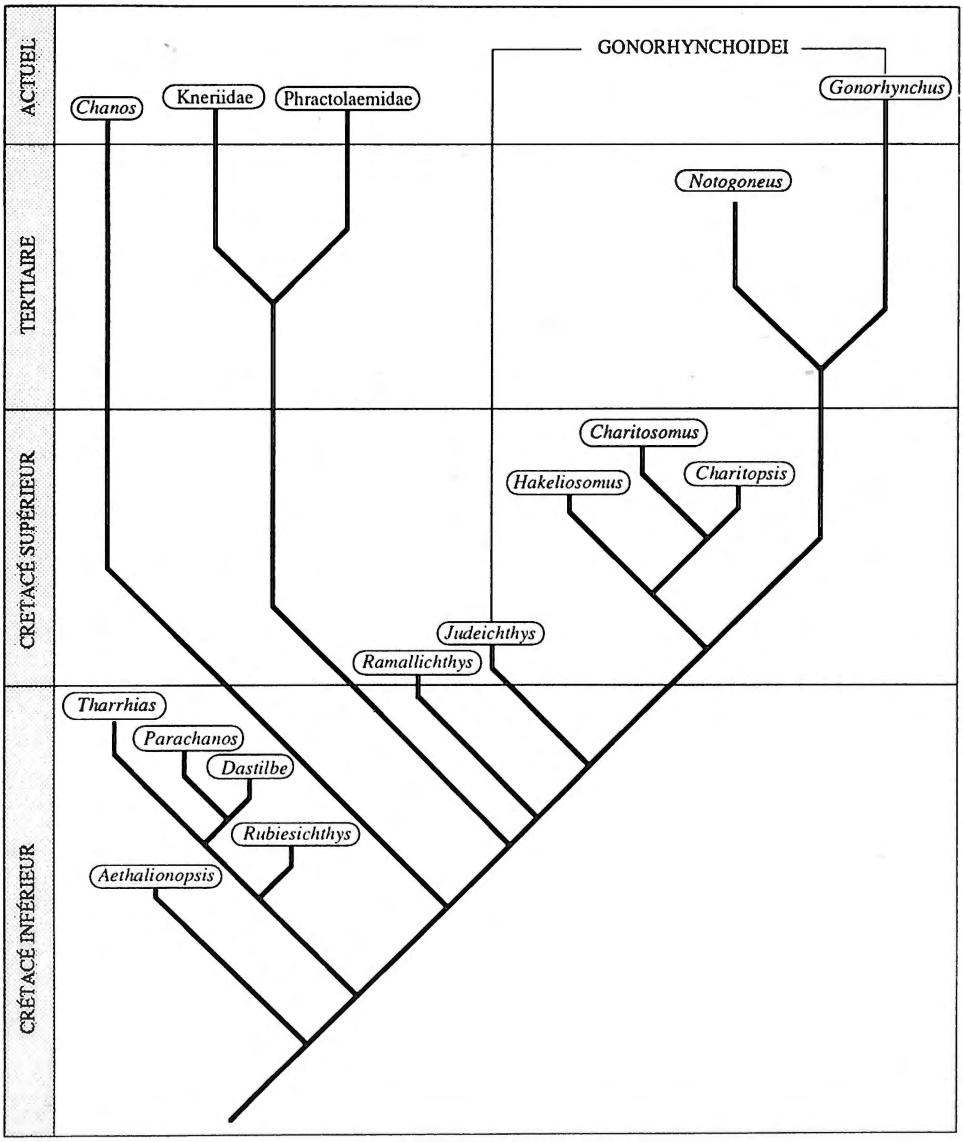

Fig. 10. — Cladogramme des Gonorhynchiformes en fonction de la stratigraphie.

RÉFÉRENCES

AUBENTON, F. D' (1961) — Morphologie du crâne de *Cromeria nilotica occidentalis* DAGET 1954. *Bull. IFAN*, **23**, sér. A (1) : 131-164.

ARAMBOURG, C. et D. SCHNEEGANS (1935) — Poissons fossiles du Bassin sédimentaire du Gabon. *Ann. Paléont.*, **24** : 139-160.

BASSANI, F. (1879) — Vorläufige Mittheilungen über die Fischfauna der Insel Lesina. *Verhandl. K. k.; Geol. Reichs.*, **8** : 161-168.

BLOT, J. (1978) — Les Apodes fossiles du Monte Bolca. *Studi e Ricerche sui giacimenti Terziari di Bolca, Verona*, **III** : 1-260.

BRITO, P. M. et S. WENZ (1990) — O endocrânio de *Tharrias* (Teleostei, Gonorhynchiformes) do Cretáceo inferior da Chapada do Araripe, Nordeste do Brasil. *Actas 1° Simp. Bacia do Araripe e Bacias Interiores do Nordeste Crato* : 375-382.

CHABANEAU, P. (1931) — Affinités morphologiques, répartition statigraphique et géographique des poissons fossiles et actuels de la famille des Gonorhynchidés. *Bull. Soc. géol. France*, **5**, 1 : 497-517, Paris.

CHARDON, M. (1968) — Anatomie comparée de l'appareil de Weber et des structures connexes chez les Siluriformes. *Ann. Mus. R. Af. centr.*, **169** : 1-277.

FINK, S. V. et W. L. FINK (1981) — Interrelationships of the ostariophysan fishes (Teleostei). *J. Linn. Soc. London*, **72** (4) : 297-353.

FINK, S. V., P. H. GREENWOOD et W. L FINK (1984) — A critique of recent work on fossil ostariophysan fishes. *Copeia* 1984 (4) : 1033-1041.

GAUDANT, J. (1981) — Contribution de la paléoichthyologie continentale à la reconstitution des paléoenvironnements cénozoïques d'Europe occidentale : approche systématique, paléoécologique, paléogéographique et paléoclimatologique. Thèse Dc d'Etat, Univ. P. et M. Curie, Paris, inédit.

GAUDANT, M. (1978) — Recherches sur l'anatomie, la systématique et la phylogénie des Cténothrissiformes et des Pattersonichthyiformes du Cénomanien du Liban (Poissons, téléostéens). *Mém. Mus. natn. Hist. nat.*, sér. C, Sciences de la Terre, **41** : 1-124.

GAYET, M. (1981) — Contribution à l'étude anatomique et systématique de l'ichthyofaune cénomanienne du Portugal. II — Les Ostariophysi. *Comun. Serv. géol. Portugal*, **67** (2) : 173-190.

GAYET, M. (1982) — Cypriniformes ou Gonorhynchiformes ? *Ramallichthys* nouveau genre du Cénomanien inférieur de Ramallah (Monts de Judée). *C. r. Acad. Sci., Paris*, **295**, 2 : 405-407.

GAYET, M. (1985a) — Gonorhynchiformes nouveau du Cénomanien inférieur marin de Ramallah (Monts de Judée) : *Judeichthys haasi* nov. gen. nov. sp. (Teleostei, Ostariophysi, Judeichthyidae nov. fam.). *Bull. Mus. natn. Hist. nat.*, 4e sér., 7, sect. C, **1** : 65-85.

GAYET, M. (1985b) — Contribution à l'étude anatomique et systématique de l'ichthyofaune cénomanienne du Portugal. Troisième partie : complément à l'étude des Ostariophysi. *Comun. Serv. géol. Portugal*, **71** (1) : 91-118.

GAYET, M. (1985c) — Rôle de l'évolution de l'appareil de Weber dans la phylogénie des Ostariophysi suggéré par un nouveau Characiformes du Cénomanien supérieur marin du Portugal. *C. r. Acad. Sci., Paris*, II, **300** (17) : 895-898.

GAYET, M. (1986) — *Ramallichthys* Gayet du Cénomanien inférieur marin de Ramallah (Judée), une introduction aux relations phylogénétiques des Ostariophysi. *Mém. Mus. natn. Hist. nat.*, nouv. sér., sér. C., Sciences de la Terre, **51** : 1-81.

GAYET, M. (1989) — Note préliminaire sur le matériel paléoichthyologique éocrétacique du Rio Bonito (sud de Bata, Guinée Equatoriale). *Bull. Mus. natn. Hist. nat.*, 4e sér., 11, sect. C **1** : 21-31.

GAYET, M. (1993a) — Nouveau genre de Gonorhynchidae du Cénomanien inférieur marin de Hakel (Liban). Implications phylogénétiques. *C. r. Acad. Sci., Paris*, II, **431** : 57-163.

GAYET, M. (1993b) — Gonorhynchiformes du Crétacé supérieur. Systématique, paléogéographie. *Doc. lab. Geol. Lyon*, **126** : 1-128.

GAYET, M. et M. CHARDON (1987) — Possible otophysic connections in some fossil and living ostariophysan fishes. *Proc. V. Congr. europ. Ichthyol. : 31-42.*

GAYET, M. et F. J. MEUNIER (1991) — Première découverte de Gymnotiformes fossiles (Pisces, Ostariophysi) dans le miocène supérieur de Bolivie. *C. r. Acad. Sci., Paris*, **313**, 2 : 471-476

GAYET, M., F. J. MEUNIER et F. KIRSCHBAUM (sous presse) — Etude phylogénétique des Gymnotiformes (Ostariophysi) actuels et fossiles, *Cybium.*

GERY, J. (1964) — Une nouvelle famille de poissons dulçaquicoles africains : les Grasseichthyidae. *C. r. Acad. Sci., Paris*, **259** (25) : 4805-4807.

GRANDE, L. (1984) — Paleontology of the Green River Formation, with a review of the fish fauna. *Bull. Geol. Surv. Wyoming*, **63**, 2nd edit. : 1-333.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN et G. S. MYERS (1966) — Phyletic studies of Teleostean fishes with a provisional classification of living forms. *Bull. Am. Mus. nat. Hist.*, **131** (4) : 341-455.

HILLS E. S. (1934) — Tertiary Fresh Water Fishes from Southern Queensland. *Mem. Queensl. Mus.*, **10** : 157-174.

HOWES, G. J. (1985) — Cranial muscles of gonorhynchiform fishes, with comments on generic relationships. *Bull. Brit. Mus. (Nat. Hist.) Zool.*, **49** (2) : 73-303.

KINDRED, J. E. (1919) — The skull of *Amiurus. Illin. Biol. Monogr.*, **5** : 3-120.

LAUDER, G. V. et K. F. LIEM (1983) — The evolution and interrelationships of the Actinopterygian fishes. *Bull. Mus. Comp. Zool.*, **150** (3) : 95-197.

LENGLET, G. (1974) — Contribution à l'étude ostéologique des Kneriidae. *Ann. Soc. R. Zool. Belgique*, **104** : 51-103.

MCALLISTER, D. E. (1968) — Evolution of branchiostegals and classification of Teleostome fishes. *Bull. Nat. Mus. Canada*, **221** : XIV + 239.

MEUNIER, F. J. et M. GAYET (1991) — Premier cas de morphogenèse réparatrice de l'endosquelette caudal d'un poisson gymnotiforme du Miocène supérieur bolivien. *Geobios*, **13** : 223-230.

MONOD, Th. (1963) — Sur quelques points de l'anatomie de *Gonorhynchus gonorhynchus* (Linné 1766). *Mém. IFAN*, **68**, Mélanges ichthyol. : 255-296.

NELSON, G. (1967) — Epibranchial organs in lower teleostean fishes. *J. Zool.*, **153** : 71-89.

OLIVERAS, A. F. DE (1978) — O gênero *Tharrias* no Cretáceo da Chapada do Araripe. *Anal. Acad. brasil. Ciênc.*, **50** (4) : 537-552.

PATTERSON, C. (1975) — The distribution of Mesozoic freshwater fishes. *Mém. Mus. natn. Hist. nat.*, série A, **88** : 156-173.

PATTERSON, C. (1984a) — Family Chanidae and other Teleostean fishes as Living fossils. *In : Living fossils,* ELDREDGE, N. and S. M. STANLEY (Eds.), Springer-Verlag, New-York : 132-139.

PATTERSON, C. (1984b) — *Chanoides*, a marine Eocene otophysan fish (Teleostei, Ostariophysi). *J. Vert. Paleont.*, **4** (3) : 430-456.

PERKINS, Ph. L. (1970) — *Notogoneus osculus* COPE, an Eocene fish from the Wyoming (Gonorhynchiformes, Gonorhynchidae). *Postilla,* **147** : 1-18.

RADOVČIČ, J. (1975) — Some new Upper Cretaceous Teleosts from Yugoslavia with special reference to localities, geology and palaeoenvironment. *Palaeont. Jugoslavia,* **17** : 1-55.

ROSEN, D. E. et P. H. GREENWOOD (1970) — Origin of the Weberian apparatus and the relationships of the ostariophysan and gonorhynchiform fishes. *Am. Mus. Novit.,* **2428** : 1-25.

SANTOS, R. DA SILVA (1947) — Uma redescriçâo de *Dastilbe elongatus*, com algumas considerações sobre o gênero *Dastilbe*. Notas prelim. *Est. Div. Geol. Min. DNPM.,* **42** : 1-7.

SAWADA, Y. (1982) — Phylogeny and zoogeography of the superfamily Cobitoidea (Cyprinoidei, Cypriniformes). *Mem. Fac. fisheries, Hokkaido University,* **28** : 63-223.

SIGNEUX, J. (1961) — Sur quelques poissons fossiles du Bassin Parisien. *Bull. Soc. géol. Fr.,* **8** : 417-423

TAVERNE, L. (1974) — Sur l'origine des téléostéens Gonorhynchiformes. *Bull. Soc. belge, Géol.,* **83** (1) : 55-60.

TAVERNE, L. (1974) — *Parachanos* ARAMBOURG et SCHNEEGANS (Pisces Gonorhynchiformes) du Crétacé inférieur du Gabon et de Guinée Equatoriale et l'origine des Téléostéens Ostariophysi. *Rev. Zool. Afr.,* **88** (3) : 683-688.

TAVERNE, L. (1981) — Ostéologie et position systématique d'*Aethalionopsis robustus* (Pisces, Teleostei) du Crétacé inférieur de Bernissart (Belgique) et considérations sur les affinités des Gonorhynchiformes. *Bull. Classe Sci.,* **68** (1981-12) : 958-982.

TAVERNE, L. (1984) — A propos de *Chanopsis lombardi* du Crétacé inférieur du Zaïre (Teleostei, Osteoglossiformes). *Rev. Zool. Afr.,* **98,** 3 : 578-590.

THYS VAN DEN AUDENAERDE, D. F. E. (1961) — Existence d'une vessie natatoire pulmonoïde chez *Phractolaemus ansorgi* Blgr. *Rev. Zool. Bot. africaine,* **59,** 3-4 : 364-366.

VON DER MARK, W. (1885) — Fische der Oberen Kreide Westfalen. *Palaeontographica,* **31** : 32-35.

WEILER (1963) — Die Fischfauna der Tertiäres im Obenheininchen Graben des Mainzes Beckens. *Abh. Senckenb. Naturf. Ges.,* **504** : 1- 75.

WENZ, S. (1984) — *Rubiesichthys gregalis* n. g., n. sp., Pisces Gonorhynchiformes, du Crétacé inférieur du Montsech (province de Lérida, Espagne). *Bull. Mus. natn. Hist. nat.,* 4e sér., **6,** sect. C (3) : 275-285.

WOODWARD, A. S. (1896) — Extinct fishes of the family Gonorhynchidae. *Proc. Zool. Soc. London* : 500-504.

WOODWARD, A. S. (1898) — Notes on some type specimens of Cretaceous fishes from Mount Lebanon in the Edinburgh Museum of Science and Art. *Ann. Mag. Nat. Hist.,* ser. 7, **2** : 405-414.

WOODWARD, A. S. (1901) — *Catalogue of the fossil fishes in the British Museum (nat. Hist.),* art IV, xxxviii + 636 pp.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 193-201 — Brussels 1993

Manuscript received on 27 July 1993

HOME RANGES AND SOCIAL BEHAVIOUR OF THE DOWNY WOODPECKER *PICOIDES PUBESCENS* IN WINTER

by

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SUMMARY

Few detailed studies have been performed on winter social behaviour of temperate-zone woodpeckers, in contrast to other resident forest birds. We collected information on individually colour-ringed Downy Woodpeckers (*Picoides pubescens*) in central Ohio, North America, during December 1989 and January 1990. Woodpeckers were generally seen with one or two conspecifics in the vicinity. Male-female associations were observed more often than expected by chance. Woodpeckers tended to space out individually within their sex class, but they tolerated members of the opposite sex. However, there were no signs of territorial defense or permanent pair bonds. Such loose social structure has not been documented in resident birds before. Our observations contradict earlier reports of individual territoriality in the Downy Woodpecker, while they are compatible with other studies on intersexual competition and niche divergence.

Key-words : Downy Woodpecker, *Picoides pubescens,* home range, territory, social coherence, pair bond.

INTRODUCTION

Resident forest birds have been the focus of a large number of studies on social behaviour in winter (*e.g.* MATTHYSEN, 1990, 1993). Several types of social structure have been described in detail, including mixed flocks, single-species flocks, and several territorial systems (see MATTHYSEN, 1993 for a review). Although woodpeckers (family Picidae) are a prominent component of most (if not all) forest communities, there are few detailed investigations on the social behaviour of non-communally breeding species (see CRAMP, 1985 for a review of European woodpeckers). The subject of this study is the Downy Woodpecker *Picoides pubescens* which is perhaps the most abundant North American woodpecker. Information on its social

organization is limited to descriptive studies based on few individuals (LAWRENCE, 1966 ; KILHAM, 1983). This species is of particular interest since studies on foraging behaviour have demonstrated that sexes separate into different foraging niches because of male dominance (GRUBB, 1982 ; PETERS and GRUBB, 1983 ; MATTHYSEN *et al.*, 1991). This view implies that male and female Downy Woodpeckers live in the same areas in winter, contradicting KILHAM's (1983) suggestion of individually defended territories. Individual territories (defended against all conspecifics of either sex) are found in many other temperate zone woodpeckers (*e.g.* BOCK, 1970 ; HOGSTAD, 1978 ; CRAMP, 1985). In an attempt to resolve this contradiction, as well as present general information on social behaviour of a temperate-zone woodpecker, we collected data on individually marked Downy Woodpeckers in two central Ohio woodlots during the winter of 1989-1990.

STUDY AREA AND METHODS

The study was conducted in two Morrow County, Ohio woodlots (plot A = 21.1 ha, plot B = 8.8 ha) isolated from other woodlands by at least 125 m, except for one or two narrow fencerows containing shrubs and trees. The habitat consisted of deciduous woodland dominated by beech (*Fagus*) and maple (*Acer*) on uplands and by a more diverse community of oaks (*Quercus*), walnut (*Juglans*), sycamore (*Platanus*) and ash (*Fraxinus*) on lowland areas.

Between 7 and 12 December, woodpeckers were trapped at feeders and marked with coloured leg-streamers. The birds were sexed by plumage differences, but could not be aged. We recorded wing length (unflattened wing chord), tail length and body mass of each bird. The four feeders in plot A and five in plot B had been continually supplied with sunflower seeds and suet for three weeks before the trapping session. All supplementary food was removed after the last day of trapping.

Over the course of the next two months, we made 36 systematic searches of the plots for Downy Woodpeckers and other bark- foraging species between 15 December 1989 and 28 January 1990. Plots were visited on alternating days, and complete searches took 3-4 hours in plot A and 5-7 hours in plot B. During most searches we found over half of the Downy Woodpeckers present in the woodlot. For each Downy Woodpecker encountered, we recorded individual identity, location, presence of conspecifics and of other bark-foraging species. Sightings were located with reference to a 50 × 50 m grid of numbered poles. We considered observations on the same individual to be statistically independent if they were separated by at least 1 hour or 200 m. Most individuals were observed only once or twice on a given day.

An exceptional cold spell with daily maximum temperatures between −20 and −10 °C and continuous snow cover lasted from 15 to 24 December. No observations were made between 23 December and 8 January. Because of the possible effects of this cold spell, some of the January results will be discussed separately. In plot A, six males and seven females were marked and later observed, and we recorded four sightings of an unmarked female, probably the same individual. In

January, five marked males and four marked females were observed in this plot, plus a single observation of the unmarked female. Thus, the total population was estimated at 14 individuals in early December and 10 in January. In plot B, six males and 14 females were marked. Seventeen of these were observed later, and 16 in January. The number of unmarked individuals in this plot was estimated from the proportion of observations of unmarked birds (Petersen index), resulting in a total estimate of 28 woodpeckers in early December and 22 in January. Because of the difference in proportion of marked birds, data on home range overlap will be discussed separately for the two plots.

A woodpecker was considered to be in conspecific company if another woodpecker was present within 50 m. An association is defined as two woodpeckers within 50 m of one another. Observations of three or four woodpeckers within 50 m of each other therefore contained three and six associations, respectively. Aggression rates were expressed as the number of observed conflicts among Downy Woodpeckers divided by the number of associations in a particular category (e.g. male- male associations).

The extent of sociality between any two individuals was quantified using a coherence index (EKMAN, 1979),

$$\text{Coherence} = \frac{N_t}{N_t + N_a + N_b}$$

where N_t is the number of observed associations of individuals A and B, and N_a and N_b the number of observations of A and B in the absence of the other individual. Coherence could be underestimated if an individual disappeared during the observation period, but most individuals with observations sufficient to estimate coherence (see below) were observed throughout the study period.

We used the RANGES IV software (KENWARD, 1990) to calculate home range sizes from minimum convex polygons containing 100 %, 90 % and 75 % of the observations. The 90 % and 75 % polygons were calculated by excluding observations furthest from the arithmetic mean of all positions. This mean position was recalculated after each excluded position. Unless otherwise stated, home range sizes and overlaps refer to 90 % polygons. Home range overlap was calculated as the proportion of the combined range of two individuals that was shared. For each bird the most similar home range was defined as the home range it overlapped most with.

Coherence and home ranges were calculated for all individuals with at least five observations. These were all the marked birds observed in January (9 in plot A, 16 in plot B) with the exception of four marked females in plot B that were infrequently observed. We chose this rather low limit of five observations in order to extract the maximum possible information on social structure from our data. Only two of the included individuals were observed less than 10 times (2 females in plot B). Within our data set, home range size (100 %, 90 % and 75 % polygons) was not correlated with the number of observations (all $r < 0.1$ and $P > 0.2$). This

was true even if plots and sexes were separated (all $r < 0.4$, $P > 0.2$). Therefore home range sizes did not appear to be biased by number of observations.

RESULTS

Sociality

Downy Woodpeckers were found in conspecific company in 63.1 % of all observations (N = 477). Among all observations of at least two Downy Woodpeckers together (N = 122), observations on three or more birds were not infrequent (28 %). Associations of two birds (N = 81) were mainly male-female (75 %), a percentage that is significantly higher than the expected 50 % if birds with an even sex ratio had associated at random ($X^2_1 = 20.7$, $P < 0.001$). This test is conservative, since any deviation in the sex ratio would lower the expected frequency of male-female associations.

Coherence

Social coherence among Downy Woodpeckers was relatively weak. Only eight pairs of individuals had a coherence larger than 0.1, with a maximum of 0.25. Seven out of these eight pairs were male-female. Only two pairs had a coherence larger than 0.15 (plot A, M1-F1, total N = 36, C = 0.24; plot B, M2-F3, total N = 16, C = 0.25). Most woodpeckers were observed in association with three to seven different individuals during the course of the study.

Conflicts

We observed 30 conflicts or aggressive displays among a total of 196 associations. Most conflicts were limited to birds being displaced from a foraging site, or at most short- distance chases. We saw nothing resembling extended territorial border fights or intruders being chased out of a defended area. Conflicts between birds of the same sex (15/66 = 23.7 %5) were more frequent than those between birds of opposite sexes (15/122 = 12.3 %; $G_1 = 3.29$, $P < 0.01$). Most of the observed male-female conflicts were won by the male (10 wins, 3 losses, 2 unknown), but this asymmetry was not significant (binomial two-tailed test, $P = 0.09$).

Home range size

Home range size did not vary between plots or sexes (two-way ANOVA on 100 %, 90 % and 75 % polygons, all $P > 0.1$; data in Table 1). Mean home range size was 6.9 ± 2.9 ha (S.D.) for the 100 % polygon, 5.0 ± 2.3 ha for the 90 % polygon and 3.3 ± 1.8 ha for the 75 % polygon (N = 21). We found no significant correlations between home range size (90 % polygons) and any morphological measurement (body mass, wing length, tail length; N = 20, all $r < 0.4$, $P > 0.1$), even when sexes were analyzed separately (all $r < 0.6$, $P > 0.1$).

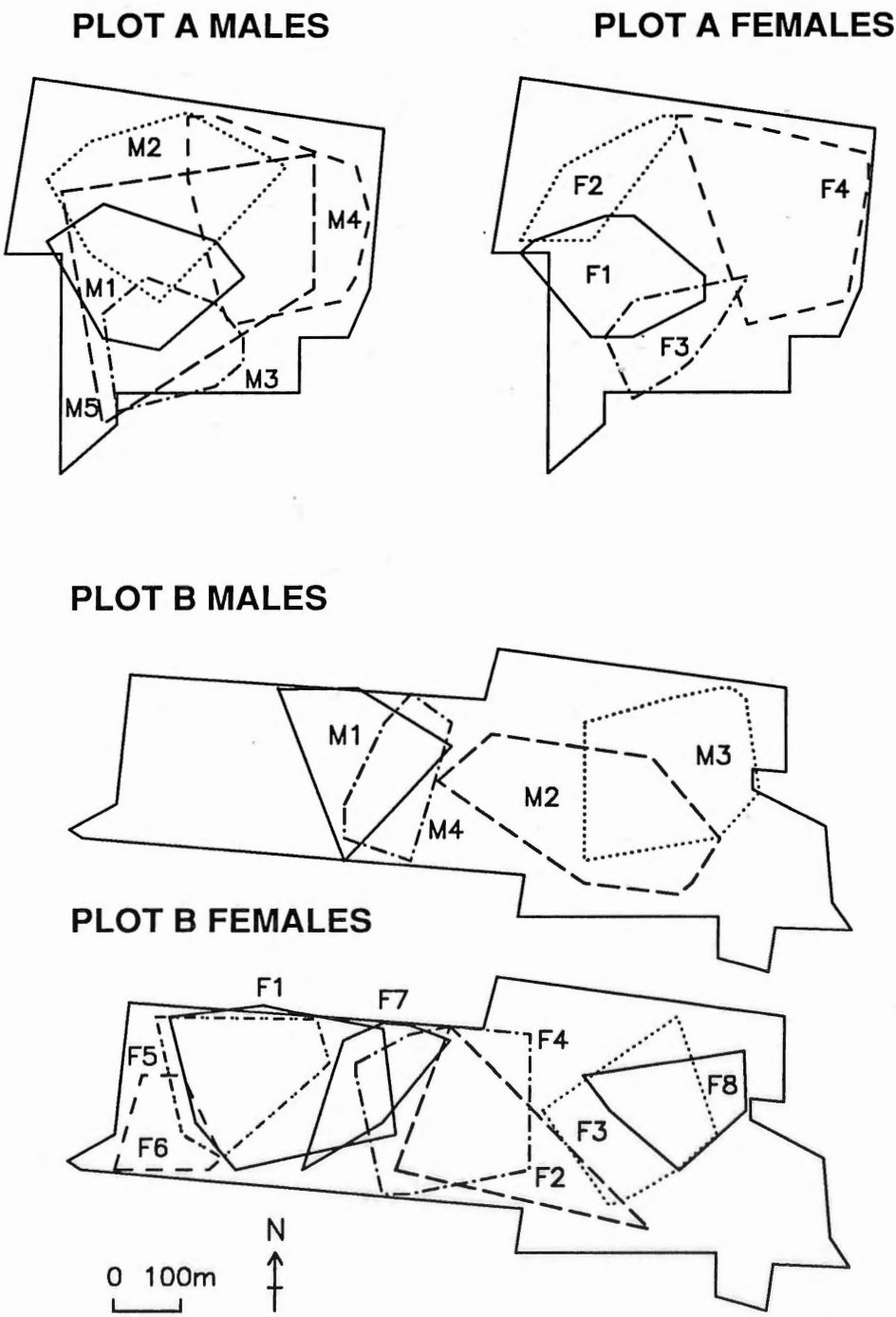

Fig. 1. — Home ranges (90 % polygons) of individually marked Downy Woodpeckers that were present throughout the study period. Not shown are four individuals that were observed fewer than five times each (all in plot B).

TABLE 1

Winter home range sizes (90 % polygons) and overlap with the most similar home range for Downy woodpeckers with at least five observations. Overlap is the percentage of their combined home range size that two individuals share, and the most similar home range is the one with the highest overlap. N = number of observations.

Individual	Home range size (ha)	N	Most similar home range	% overlap
Plot A :				
M1	4.3	31	F1	74
M2	6.0	19	M5	32
M3	3.5	24	F3	50
M4	6.8	26	F4	75
M5	10.7	14	M1	29
F1	3.6	23	M1	74
F2	2.1	16	M2	29
F3	2.2	19	M3	50
F4	6.5	21	M4	75
Plot B :				
M1	4.3	10	F7	45
M2	7.4	15	F3	36
M3	6.4	17	F3	59
M4	3.0	17	M1	35
F1	7.7	30	F5	48
F2	6.5	6	F4	47
F3	4.8	9	M3	59
F4	6.7	24	F2	47
F5	4.4	13	F1	48
F6	2.0	16	F5	9
F7	2.8	14	M1	45
F8	3.0	12	M3	47

Home range overlap

Mean overlap with the most similar home range was 48.6 ± 16.8 % (N = 21 ; range 9 to 75 % ; Table 1). In plot A, mean overlap with the most similar home range of the opposite sex was significantly greater than mean overlap with the most similar home range of the same sex (57 ± 21 % and 14 ± 14 %, Wilcoxon test, N = 9, z = 2.3, P = 0.02). With the exception of one individual with a relatively large home range (M5), home ranges in plot A can be arranged in four male-female pairs with large overlap within, but not between pairs (Fig. 1, Table 1). In plot B there was no difference between mean overlap with the most similar home range of

the opposite and the same sex (35 ± 18 % and 36 ± 13 %, Wilcoxon test, N = 12, z = 1.6, P > 0.1). There was no obvious pairwise arrangement of home ranges in plot B (Fig. 1, Table 1).

DISCUSSION

Downy Woodpeckers in our study population had relatively small home ranges (< 10 ha) in midwinter. We do not know to what extent they may have visited nearby woodlots, but since on most visits nearly all individuals were found, we believe most of the individuals resided mainly or exclusively in the study woodlots. Some additional individuals may have had a major part of their home range outside the plot and therefore have been observed infrequently. One marked female, for instance, was observed only a few times during the study but also found in an occasional visit to a woodlot near plot B. The disappearance of some individuals between early December and January could have been caused by mortality and/or emigration to other habitats associated with the unusually frigid temperatures in late December. Another possibility is that some individuals had been attracted by the supplementary food in late November and stayed for some time after the food was removed.

Downy Woodpeckers were often found in association with conspecifics (63 % of all observations). This sociality may have been the result of direct social attraction, but also a passive consequence of different individuals being attracted to the same mixed-species flock (SULLIVAN, 1984a,b). Two lines of evidence seem to suggest that Downy Woodpeckers tend to live in pairs. First, they were observed more often in male- female pairs than expected. Second, there was less aggression and more home range overlap (in one of the study plots) between members of different sexes. The lack of difference in home range overlap within and between sexes in plot B may have been due to the large number of unmarked individuals.

The high degree of association between sexes explains the widespread occurrence of sexual resource partitioning in this species, since this allows both sexes to forage together while reducing competition (PETERS and GRUBB, 1983). However, it is not clear why females did not avoid males to a larger extent, since in the absence of males they could shift to the preferred foraging niche (MATTHYSEN et al., 1991).

However, although the high frequency of male-female associations and the pairwise arrangement of male and female home ranges (in plot A only) are suggestive of winter pair bonds, these putative « pairs » do not behave as such. None of the possible male-female combinations were observed with any regularity, and there was no tendency for woodpeckers to associate with specific individuals of the opposite sex. The apparent similarity in home ranges of some males and females may have been due to a heterogeneous distribution of resources in the area or to topological constraints on positions or boundaries of home ranges. Alternatively, birds with similar home ranges may simply be former breeding partners still residing on the former breeding territory (MATTHYSEN, 1993). Out of nine

Downy Woodpeckers that were observed frequently in plot A, at least six had been present in the previous winter (CIMPRICH, pers. obs.). No such information is available for plot B. Woodpecker males and females living in the same part of the wood may well have been former mates, or future mates, but this is not clearly reflected in their behaviour.

The Downy Woodpeckers in our study area resembled most other temperate zone woodpeckers (with the exception of communal breeders, *e.g.* SHERRILL and CASE, 1980 ; STACEY and KOENIG, 1984) in lacking clear social bonds outside the breeding season. Our observations revealed high degrees of tolerance and home range overlap, especially between sexes, although birds did not behave as mated pairs. Other woodpecker species are often territorial individually or in pairs in winter (KILHAM, 1959, 1983 ; LAWRENCE, 1966 ; BOCK, 1970 ; HOGSTAD, 1978 ; CRAMP, 1985). Without presenting quantified support, Kilham (1983) suggested that most Downy Woodpeckers in New Hampshire defended individual winter territories, a description that is clearly at variance with our results. Climate, food availability and proportions of residents and migrants in the population may all cause between-population variation in social organization (DAVIES, 1976 ; PULLIAM and MILLIKAN, 1982 ; SMITH and VAN BUSKIRK, 1988 ; MATTHYSEN, 1990). The widespread occurrence of sexual niche partitioning in Downy Woodpecker populations (reviewed by PETERS and GRUBB, 1983) suggests that individual territoriality is probably uncommon in other populations of this species as well, since spatial separation in territories would remove the necessity for niche separation.

The loose social structure in this woodpecker population is quite unique among bird species. However, as Matthysen (1993) pointed out, such relatively unstructured social systems are much harder to describe in detail than obvious behaviours such as strict territoriality or highly coherent flocks. Many more bird populations on which little more is known than that individuals tend to live solitarily or in small groups, may in fact be organized in this fashion.

REFERENCES

BOCK, C.E. (1970) — The ecology and behavior of the Lewis woodpecker (*Asyndesmus lewis*). *Univ. Calif. Publ. Zool.*, **92** : 1-100.

CRAMP, S. (1985) — *Handbook of the birds of Europe, the Middle East and North Africa. Vol. 4 : Terns to Woodpeckers.* Oxford University Press, Oxford, U.K. (960 pp).

DAVIES, N.B. (1976) — Food, flocking and territorial behaviour of the Pied Wagtail (*Motacilla alba yarelli* Gould) in winter. *J. Anim. Ecol.*, **45** : 235-253.

EKMAN, J. (1979) — Coherence, composition and territories of winter social groups of the Willow Tit *Parus montanus* and the Crested Tit *P. cristatus*. *Ornis Scand.*, **10** : 56-68.

GRUBB, T.C.Jr. (1982) — Downy Woodpecker sexes select different cavity sites : an experiment using artificial snags. *Wilson Bull.*, **94** : 577-579.

HOGSTAD, O. (1978) — Sexual dimorphism in relation to winter foraging and territorial behaviour of the Three-toed Woodpecker *Picoides tridactylus* and three *Dendrocopos species*. *Ibis*, **120** : 198-203.

KENWARD, R. (1990) — *Ranges IV. Software for analysing animal location data.* Institute for Terrestrial Ecology, Wareham, U.K.

KILHAM, L. (1959). — Territorial behavior of wintering Red-headed Woodpeckers. *Wilson Bull.*, **70** : 347-358.

KILHAM, L. (1983) — *Life history studies of woodpeckers of Eastern North America.* Nuttall Ornithol. Club, Cambridge, Mass.

LAWRENCE, L. DE K. (1966) — *A comparative life-history study of four species of woodpeckers.* Ornithol. Monogr. 5, American Ornithologists' Union.

MATTHYSEN, E. (1990) — Nonbreeding social organization in *Parus.* In : *Current Ornithology Vol. 7.* POWER, D.M. (Ed.) Plenum Press, New York and London : 209-249.

MATTHYSEN, E. (1993) — Nonbreeding social organization in migratory and resident birds. In : *Current Ornithology Vol. 11.* POWER, D. M. (Ed.) Plenum Press, New York and London : 93- 141.

MATTHYSEN, E., T.C. GRUBB Jr. and D. CIMPRICH (1991) — Social control of sex-specific foraging behaviour in Downy Woodpeckers, *Picoides pubescens. Anim. Behav.*, **42** : 515-517.

PETERS, W.D. and T.C. GRUBB Jr. (1983) — An experimental analysis of sex-specific foraging in the Downy Woodpecker, *Picoides pubescens. Ecology,* **64** : 1437-1443.

PULLIAM, H.R. and G.C. MILLIKAN (1982) — Social organization in the nonreproductive season. In : *Avian Biology Vol. 6.* FARNER, D.S., J.R. KING and K.C. PARKES (Eds.) Academic Press, New York : 169-197.

SHERRILL, D.M. and V.M. CASE (1980) — Winter home ranges of four clans of the Red-cockaded Woodpecker in the Carolina Sandhills. *Wilson Bull.*, **92** : 369-375.

SMITH, D.C. and J. VAN BUSKIRK (1988) — Winter territoriality and flock cohesion in the black-capped chickadee *Parus atricapillus. Anim. Behav.*, **36** : 466-476.

STACEY, P.B. and W.D. KOENIG (1984) — Cooperative breeding in the Acorn Woodpecker. *Scientific American,* **251** : 114-121.

SULLIVAN, K.A. (1984a) — The advantages of social foraging in Downy Woodpeckers. *Anim. Behav.*, **32** : 16-22.

SULLIVAN, K.A. (1984b) — Information exploitation by Downy Woodpeckers in mixed species flocks. *Behaviour,* **91** : 294-311.

ACKNOWLEDGEMENTS

We thank Frank Adriaensen, Richard N. Connor, Jan T. Lifjeld and anonymous reviewers for critical comments on earlier drafts. This study was financed by a NATO research fellowship and a National Fund for Scientific Research (Belgium) grant to EM, and by National Science Foundation grant BSR-8717114 to TCG. EM is senior research assistant with the Belgian National Fund for Scientific Research.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 203-230 — Brussels 1993

Manuscript received on 3 August 1993

THE GENERA *LONGIDORUS* MICOLETZKY, 1922 AND *XIPHINEMA* COBB, 1913 (NEMATODA : LONGIDORIDAE) IN CAMEROON

by

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SUMMARY

Soil samples collected by the first author from the rhizosphere of a variety of food and vegetable crops in the South West, West and North West Provinces of Cameroon contained eight known longidorid species, namely, *Longidorus laevicapitatus* WILLIAMS, 1959 ; *L. pisi* EDWARD *et al.*, 1964 ; *Xiphinema elongatum* SCHUURMANS STEKHOVEN and TEUNISSEN, 1938 ; *X. ifacolum* LUC, 1961 ; *X. longicaudatum* LUC, 1961 ; *X. nigeriense* LUC, 1961 ; *X. setariae* LUC, 1958 ; and *X. vitis* HEYNS, 1974. The male, first-, second-, and third-stage juveniles of *X. nigeriense* are described for the first time. The male supplements consist of an adanal pair and a single ventromedian one. The value of the ratio of the hyaline terminal portion of the tail/tail tip width, for any given juvenile stage, was higher in *X. longicaudatum* than in *X. nigeriense*, and this ratio was used to separate their juveniles. It appears to be a reliable character for separating the juvenile stages of both species in mixed populations. A single male of *X. setariae* with a rudimentary reproductive system found in one population is the second ever recorded, the first one reported by TARJAN (1964, as *X. vulgare*). All species except *L. pisi* are first records from Cameroonian soils.

Key words : Cameroon, *Longidorus*, *Xiphinema*, nematodes, taxonomy.

INTRODUCTION

Two longidorids, *Longidorus pisi* EDWARD, MISRA and SINGH, 1964 and *Xiphinema savanicola* LUC and SOUTHEY, 1980, have previously been reported from northern Cameroon, both in association with maize (CHAVEZ and GERAERT, 1977 ; LUC and SOUTHEY, 1980). The present paper reports data on eight species of

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Longidoridae present in soil samples taken around roots of crops in the western region of Cameroon.

MATERIALS AND METHODS

Nematodes were extracted from the soil by sieving, followed by the centrifugal flotation method using sugar (CAVENESS and JENSEN, 1955 ; JENKINS, 1964), killed and fixed by pouring a hot (85 °C) solution of 4 % formaldehyde + 1 % glycerine over them, processed to anhydrous glycerine by SEINHORST's (1959) rapid method modified by DE GRISSE (1969), and permanently mounted in glycerine on aluminium double-coverslip slides. The maximum body and anal body widths in flattened specimens were corrected using GERAERT's (1961) formula. Abbreviations used in the tables include : VBW = vulval body width ; ABW = anal body width ; Od st = odontostyle ; Od ph = odontophore ; Tot st = total stylet ; Re (R) = replacement odontostyle ; and h = hyaline terminal portion of tail.

Voucher specimens. The specimens studied are deposited in the nematode collections of the Instituut voor Dierkunde, Universiteit Gent, Ledeganckstraat 35, B-9000 Gent, Belgium and the Nematology Laboratory, Department of Plant Protection, University of Dschang, Dschang, Cameroon.

SYSTEMATICS

Longidorus laevicapitatus WILLIAMS, 1959

(Tables 1 and 2, Fig. 1)

Measurements : See Tables 1 and 2.

Description : *Female*. In heat-relaxed specimens body varying from moderately to strongly ventrally arcuate, with the curvature more pronounced posteriorly, forming an incomplete figure 6. Body pores sparse ; in the neck region two dorsal and six ventral pores confined anteriorly ; lateral pores obscure. Lip region rounded, continuous with the body. Amphid large, pouch-like, symmetrically bilobed ; amphidial aperture invisible. Reproductive system with equal anterior and posterior branches. Tail dorsally convex-conoid, with a bluntly rounded terminus ; two caudal pores present.

Discussion : Our specimens fit the original description (WILLIAMS, 1959) as well as those of populations from sugarcane in Congo (MERNY, 1966), the Antilles (DALMASSO, 1967), and South Africa (JACOBS and HEYNS, 1982) except for the odontophore which is longer in ours than in those from Mauritius and Congo (43-58 µm *vs* 30 µm and 20 µm in specimens from Mauritius and Congo, respectively). All four juvenile stages were found but no male, which has been described only once from the Antilles (DALMASSO, *op. cit.*).

TABLE 1

Measurements (in µm except L = mm) of *Longidorus laevicapitatus* females of populations from okra and banana in Dschang, Cameroon.

Character	Okra population	Banana population
n	11	6
L	2.58 ± 0.3 (2.16-3.40)	2.54 ±0.2 (2.14-2.77)
VBW	52 ± 3.1 (46-55)	54 ± 3.0 (48-57)
Neck length	318 ± 34.9 (282-364)	287 ±26.5 (273-327)
Tail length	39 ± 2.6 (36-44)	39 ± 3.4 (35-42)
ABW	31 ± 1.6 (28-33)	33 ± 1.9 (29-34)
a	49.4 ± 5.0 (44.8-63.0)	47.4 ± 2.5 (44.6-50.2)
b	8.1 ± 1.2 (6.2-9.4)	9.4 ± 1.5 (7.8-11.7)
c	64.1 ± 5.0 (54.8-69.5)	65.9 ± 3.4 (61.1-70.8)
c′	1.3 ± 0.08 (1.1-1.4)	1.2 ± 0.06 (1.1-1.3)
V	48 ± 0.8 (46-49)	48 ± 1.3 (46-49)
Odontostyle	70 ± 1.8 (68-73)	70 ± 3.1 (65-73)
Odontophore	45 ± 1.9 (43-48)	50 ± 5.1 (45-58)
Total stylet	115 ± 2.1 (113-119)	120 ± 8.0 (110-131)
Guide ring	26 ± 0.8 (25-27)	24.8 ± 0.5 (24-25)
Nerve ring	146 ± 5.4 (138-152)	142 ± 11.7 (133-155)

TABLE 2

Measurements (in µm except L = mm) of *Longidorus laevicapitatus* juveniles of populations from okra and banana in Dschang, Cameroon combined.

Character	J1	J2	J3	J4
n	6	2	5	10
L	0.87 (0.83-1.02)	1.57, 1.23	1.91 (1.66-2.0)	2.17 ± 0.3 (1.82-2.81)
Tail	31 (28-33)	?, 37	37 (35-39)	40 ± 2.5 (37-43)
ABW	13.6 (12.7-14.5)	?, 18.2	26.7 (25.5-29)	28.4 ±1.7 (25.5-31)
a	35.6 (34-37)	40.3, 39.7	43.7 (37.7-51.3)	47.5 ± 2.6 (43.3-52.2)
b	5.1 (4-7.5)	?, ?,	8 (6.8-8.8)	8.4 ± 1.2 (6.9-10.4)
c	27.3 (25.8-29.6)	?, 33.2	51.2 (47.4-55.6)	54.5 ± 7.7 (46.7-63.5)
c′	2.3 (2.1-2.4)	?, 2.1	1.3-1.5	1.4 ± 0.1 (1.3-1.6)
Od st	46 (45-47)	52, 50	56 (53-60)	61 ± 1.6 (59-63)
Od ph	31 (26-37)	?, 33	42 (41-43)	41 ± 2 (39-43)
Tot st	76 (72-82)	?, 83	97 (94-100)	103 ± 3 (100-106)
R od st	50 (49-52)	65, 61	64 (62-66)	71 ± 2.1 (67-74)

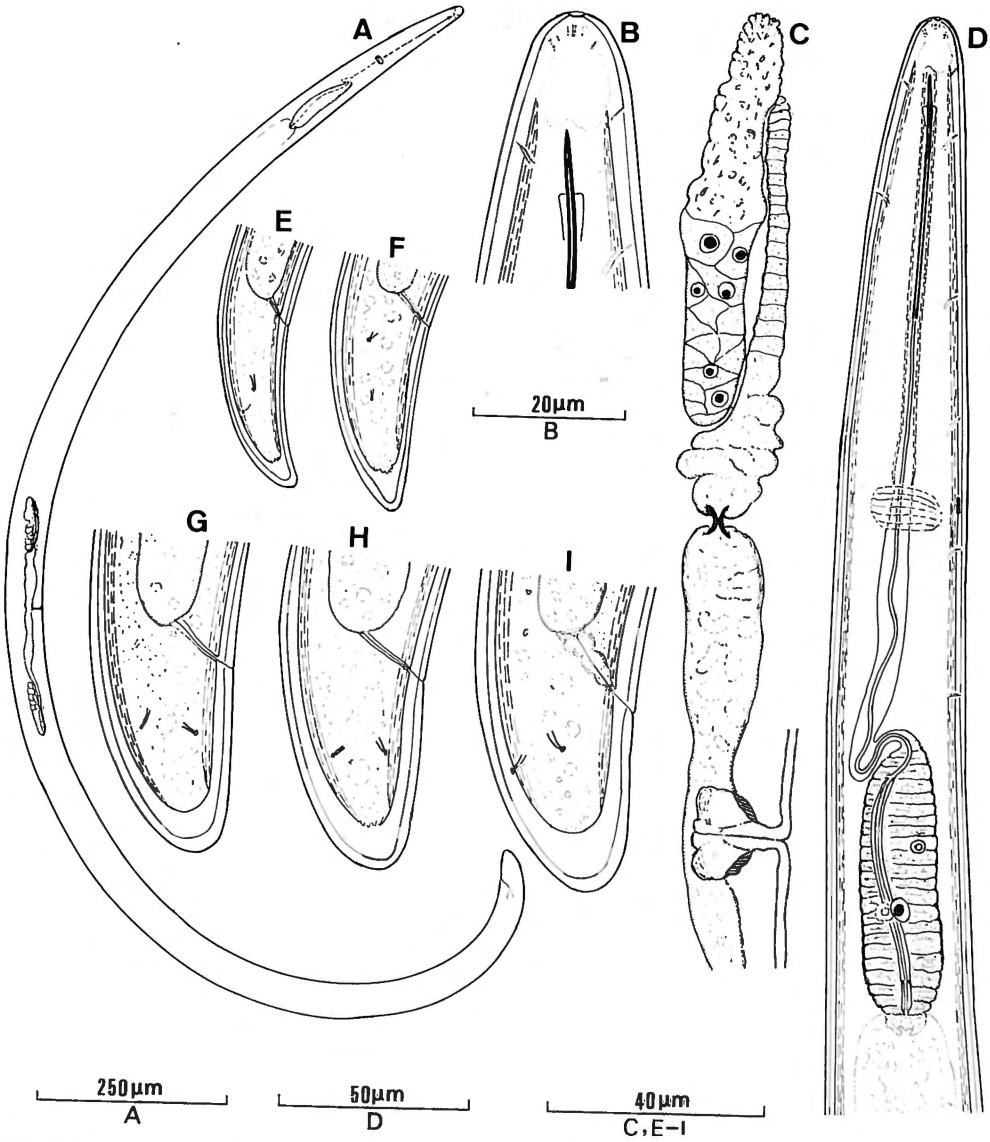

Fig. 1. — *Longidorus laevicapitatus. Female.* — A : Entire view. — B : Head region. — C : Anterior genital branch. — D : Anterior body region. — I : Tail. — E-H : Tails of juveniles. E : J1 ; F : J2 ; G : J3 ; H : J4.

Longidorus pisi EDWARD, MISRA and SINGH, 1964
(Tables 3 and 4, Fig. 2)

Measurements

TABLE 3

Measurements (in µm except L = mm) of *Longidorus pisi* females of populations from maize in Foumbot and sugarcane in Ekona, Cameroon.

Character	Maize population	Sugarcane population
n	13	8
L	3.52 ± 0.4 (2.91-3.99)	3.55 ±0.2 (3.11-3.86)
VBW	36 ± 2.9 (31-39)	36 ± 2.9 (30-39)
Neck length	306 ± 30.8 (255-345)	291 ±47.6 (245-355)
Tail length	41 ± 3 (38-47)	38 ± 3.3 (34-45)
ABW	23 ± 2 (19-25)	21 ± 1.1 (20-23)
a	98.3 ± 7.8 (83-114.5)	100 ± 7.2 (94.2-114.3)
b	11.5 ± 1.2 (10-14.6)	12.4 ± 2.2 (9.7-15.8)
c	85.3 ± 7.4 (72.8-97.4)	93.1 ± 10.2 (79.7-107.2)
c′	1.9 ± 0.1 (1.6-2.0)	1.9 ± 0.1 (1.7-2.0)
V	47 ± 1.6 (45-50)	51 ± 2 (48-53)
Odontostyle	75 ± 2.2 (72-79)	76 ± 2.4 (73-80)
Odontophore	45 ± 4.4 (39-53)	47 ± 9.2 (42-65)
Total stylet	120 ± 4.5 (113-129)	123 ± 9.4 (116-141)
Guide ring	42 ± 1.7 (39-45)	41 ± 2.3 (36-43)
Nerve ring	148 ± 5.2 (137-157)	145 ± 5 (139-150)

TABLE 4

Measurements (in µm except L = mm) of *Longidorus pisi* juveniles (J3-J4) of populations from maize in Foumbot and sugarcane in Ekona, Cameroon.

	Maize population		Sugarcane population
Character	J3	J4	J4
n	5	20	3
L	1.65 ± 0.1 (1.44-1.82)	2.41 ± 0.2 (1.95-2.89)	2.22 ± 0.2 (2.09-2.4)
Tail	39 ± 1.9 (37-42)	41 ± 4.3 (37-46)	41-43
ABW	14 ±1.4 (12.7-16.4)	18.6 ± 2.2 (15.5-22.7)	16 ± 0.9 (15.5-17)
a	68.3 ± 2.3 (64.4-70)	79.7 ± 5.3 (72-94.6)	95 ± 3.8 (92.3-99.5)

TABLE 4

	Maize population		Sugarcane population
Character	J3	J4	J4
b	7.6 ± 0.9 (6.6-9)	9.4 ± 1.3 (7.3-12.3)	8.8, 8.3 (n = 2)
c	42.6 ± 3.5 (38.9-47.9)	59 ± 3.6 (52.8-65.7)	52.3 ± 3 (50.2-55.8)
c′	2.8 ± 0.2 (2.5-2.9)	2.2 ± 0.2 (2-2.6)	2.5-2.6
Od st	51 ± 1.3 (50-53)	64 ± 1.5 (60-67)	64-65
Od ph	38, 35 (n = 2)	41 ± 3.1 (35-46)	38, 41 (n = 2)
Tot st	90, 88 (n = 2)	105 ± 3.2 (99-111)	102, 106 (n = 2)
R od st	62 ± 2.7 (59-66)	76 ± 2.9 (70-82)	67, 76 (n = 2)

Description : *Female*. Body varying from slightly to strongly ventrally curved, with most of the curvature in the posterior third when relaxed by gentle heat. Body pores completely obscure. Lateral chord 25-29 % of the midbody width. Lip region bulbous, offset from the body by a distinct constriction. Reproductive system with anterior and posterior branches more or less equally developed. Prerectum 433 ± 67 (358-517) µm long, its cells containing large, granular bodies. Tail convex-conoid, with a bluntly rounded terminus ; two caudal pores present in its posterior half.

Discussion : Compared with the type population (EDWARD *et al.*, 1964) and specimens from South Africa (JACOBS and HEYNS, 1982) and Sudan (ZEIDAN and COOMANS, 1992), ours appear wider (a = 83-114.5 *vs* 98-159 taken from all other descriptions). There were no males and only the third- and fourth-stage juveniles were found.

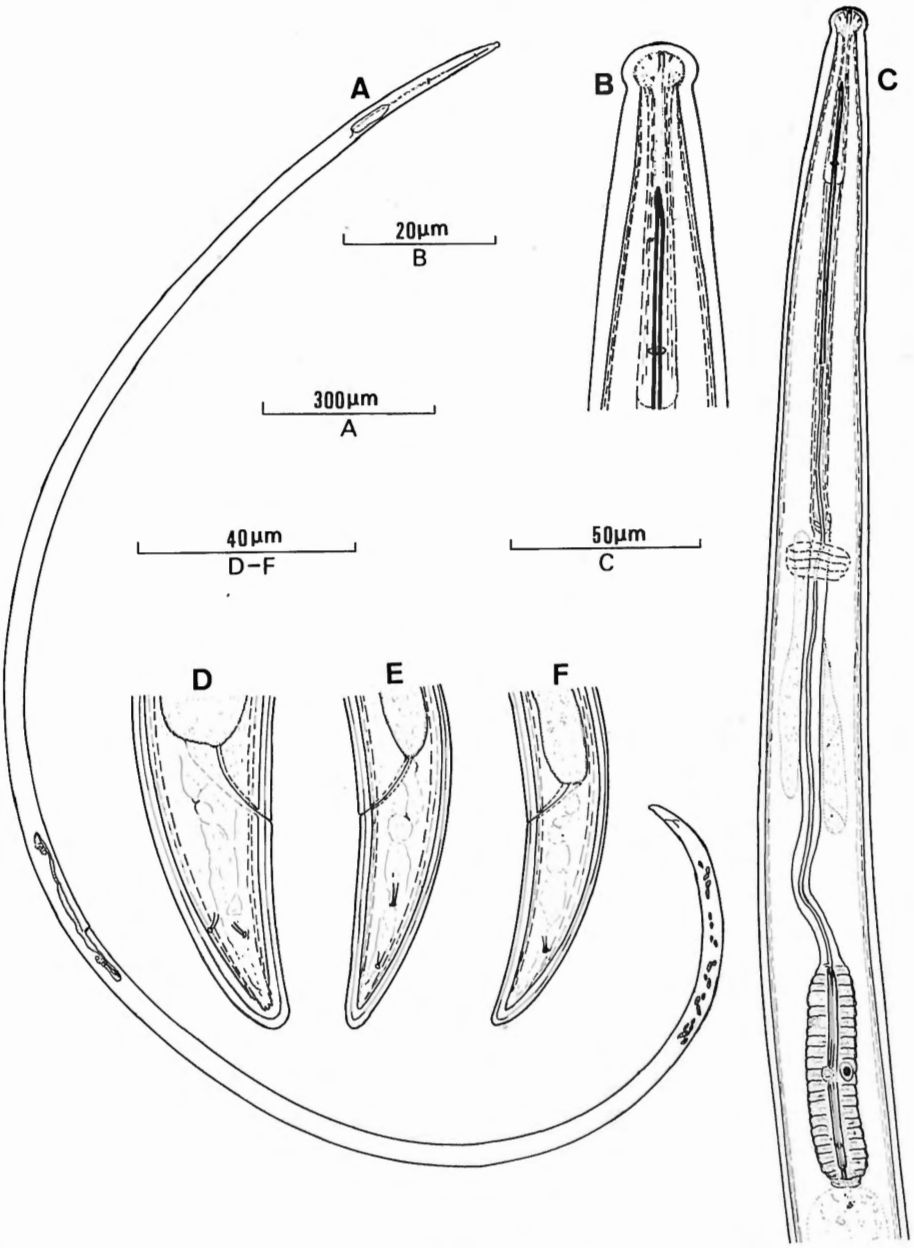

Fig. 2. — *Longidorus pisi. Female.* — A : Entire view. — B : Head region. — C : Anterior body region. — D : Tail. — E, F : Tails of juveniles. E : J4 ; F : J3.

Xiphinema elongatum SCHUURMANS STEKHOVEN and TEUNISSEN, 1938
(Tables 5 and 6, Fig. 3)

Measurements

TABLE 5

Measurements (in μm except L = mm) of *Xiphinema elongatum* females of populations from soybean in Bambui Plain and potato in Bambui Upper Farm, Cameroon.

Character	Soybean population	Potato population
n	9	8
L	2.54 ± 0.08 (2.44-2.64)	2.97 ± 0.2 (2.80-3.04)
VBW	47 ± 2.7 (42-50)	47 ± 4.5 (42-55)
Neck length	350 ± 12.9 (333-375)	408 ± 19.3 (371-431)
Tail length	54 ± 2.6 (50-59)	58 ± 2.9 (55-62)
ABW	27 ± 2.1 (25-30)	29 ± 3.5 (25-33)
a	54.5 ± 2.4 (52.5-58)	63 ± 4.9 (55.8-68.4)
b	7.2 ± 0.3 (6.8-7.7)	7.3 ± 0.2 (7-7.6)
c	47 ± 3.2 (41.4-52.8)	51.2 ± 3.5 (47.7-55.3)
c′	2 ± 0.2 (1.8-2.2)	2 ± 0.3 (1.7-2.4)
V	43 ± 0.9 (42-45)	44 ± 1.0 (43-45)
Odontostyle	83 ± 1.8 (80-86)	93 ± 1.8 (91-95)
Odontophore	56 ± 0.9 (55-57)	61 ± 2.9 (59-64)
Total stylet	139 ± 1.9 (137-141)	154 ± 2.6 (150-157)
G. ring (posterior)	75 ± 2.6 (72-79)	88 ± 2.8 (83-91)
Guiding sheath	8 ± 2.2 (4-9)	11 ± 2.1 (9-13)
Nerve ring	177 ± 5.9 (170-183)	188 ± 3.7 (185-195)

TABLE 6

Measurements (in μm except L = mm) of *Xiphinema elongatum* juveniles of populations from soybean in Bambui Plain and potato in Bambui Upper Farm, Cameroon combined.

Character	J1	J2	J3	J4
n	2	5	6	3
L	0.87, 0.97	1.34 (1.25-1.4)	1.67 (1.51-1.78)	2.02 (1.93-2.09)
Tail	53, 55	63 (58-65)	63 (57-68)	56 (50-60)
ABW	11.8, 13.6	17 (14,5-19)	21 (20-22.7)	24 (22.7-25.5)
a	41.4, 44	44.7 (40-49)	47.8 (44-50.9)	48.4 (43.9-55)
b	513.6, 4	5.2 (4.5-6.4)	5.3 (5-5.5)	6.2 (5.6-6.6)

TABLE 6

Character	J1	J2	J3	J4
c	16.4, 17.6	21.3 (20-22)	26.7 (26-26.9)	36.3 (33.3-40.8)
c′	4.5, 4	3.7 (3.4-4)	3 (2.8-3.3)	2.3 (2-2.6)
Od st	43, 45	56 (54-57)	65 (55-74)	70-72
Od ph	34, 35	43 (40-45)	47 (43-50)	50-52
Tot st	77, 80	99 (94-102)	112 (100-123)	120-122
R od st	53, 58	69 (67-72)	77 (70-84)	83 (81-84)

Description : *Female.* When heat-relaxed, body strongly ventrally arcuate, with most of the curvature in the posterior third, almost hook-like. Body pores sparse and obscure ; in the neck region one dorsal and one ventral pore occur close to the lip region, and three ventral pores occur in the pharyngeal region. Lip region broadly rounded anteriorly, offset from the body by a shallow depression. Amphidial aperture a wide transverse slit, occupying about 45 % of the head diameter. Reproductive system with equally developed anterior and posterior branches. Tail ventrally arcuate, with a bluntly pointed terminus. Three caudal pores present, the most anterior one close to anus level.

Discussion : *X: elongatum* is one of the pantropical *Xiphinema* species (cf. LUC and SOUTHEY, 1980). The stylet and body lengths and tail curvature in our populations differ from those in some published reports. Our population from soybean has a comparatively short stylet, 139 (137-141) µm long ; only one described population (from Zimbabwe, Hippo Valley) has a similarly short stylet, 141 (134-144) µm long (cf. LUC and SOUTHEY, *op. cit.*). Furthermore, the Cameroon specimens from potato are longer than any described except those from Burundi which measure 2.50-3.10 mm (COOMANS *et al.*, 1990). Finally, the first-, second-, and third-stage juvenile tails are more curved than usual (cf. LUC and SOUTHEY, *op. cit.*) except, again, in the Burundi population.

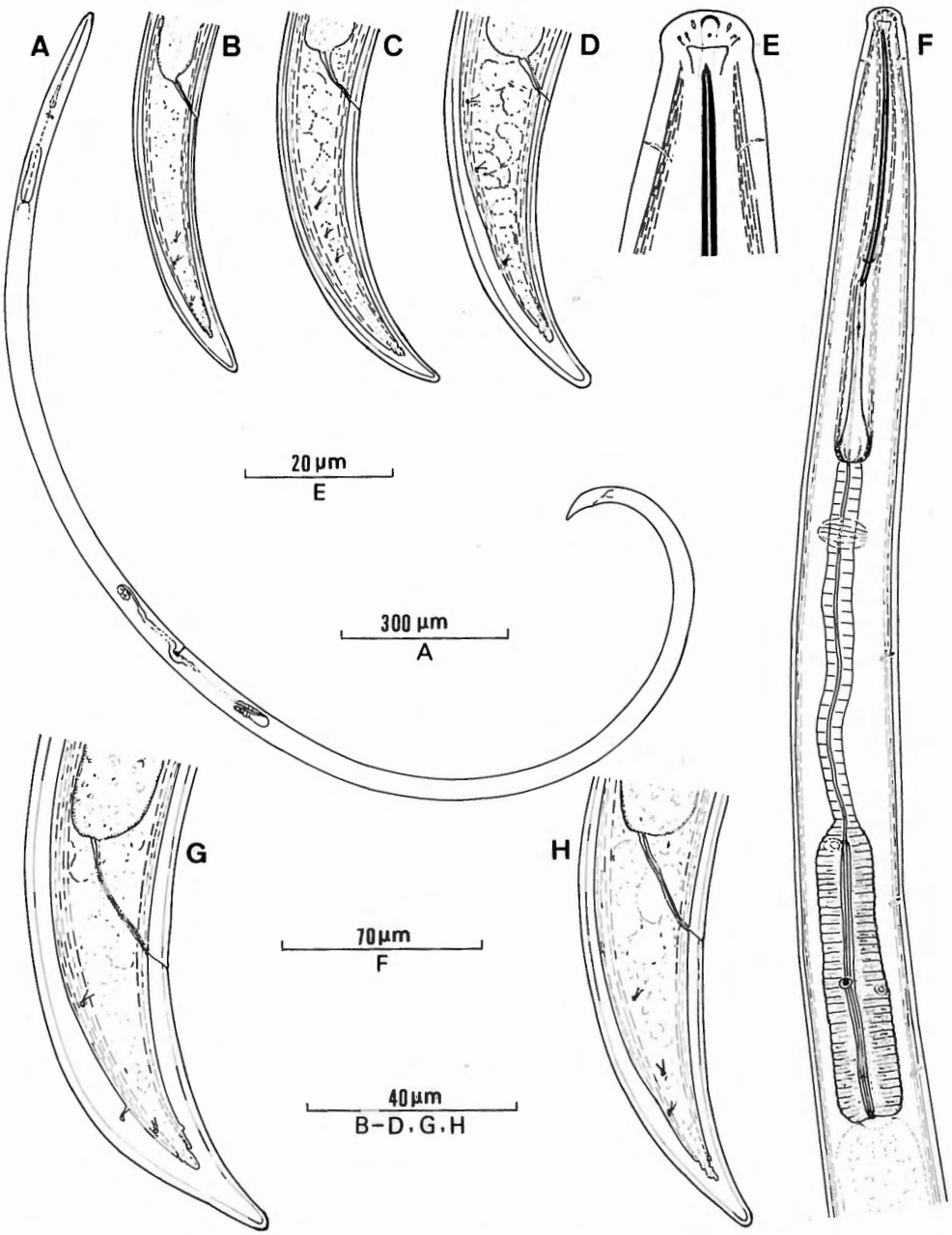

Fig. 3. — *Xiphinema elongatum. Female.* — A : Entire view. — E : Head region. — F : Anterior body region. — G : Tail. — B-D, H : Tails of juveniles. B : J1 ; C : J2 ; D : J3 ; H : J4.

Xiphinema ifacolum Luc, 1961
(Table 7, Fig. 4)

Measurements : See Table 7.

Description : *Female.* When heat-relaxed, body strongly ventrally arcuate, with most of the curvature in the posterior half, forming the shape of an incomplete figure 6. Body pores prominent ; in the neck region three dorsal pores confined anteriorly, nineteen lateral and thirteen ventral pores. Lip region rounded, barely offset from the body by a slight depression. Amphidial aperture a wide transverse slit, occupying 45 % of the head diameter. Reproductive system with equally and fully developed anterior and posterior branches ; « Z organ » present. No sperm observed. Tail short, ventrally arcuate, tapering to a bluntly pointed terminus, with a thin, terminal blind canal. Two caudal pores present, the anterior one a short distance posterior to anus level.

Discussion : *X. ifacolum* has been reported mostly from West Africa — Guinea, Ivory Coast, and Liberia (Luc, 1961 ; Lamberti *et al.*, 1987 ; Adiko, 1988), but it is also known from Brazil (Loof and Sharma, 1979) and Guyana (Luc and Coomans, 1992). The specimens from Cameroon satisfactorily fit Luc's (1961) and Loof and Sharma's (1979) descriptions except for details of the « Z organ » : the apophyses are irregularly shaped bodies in our specimens, four irregular « teeth » in Luc and Dalmasso (1975), longer and more branched in specimens from Guyana (Luc and Coomans, 1992). *X. ifacolum,* moreover, differs from all other species in the genus by the peculiar, thin, terminal, blind canal in the tail of all juvenile stages and the adult. Males were absent but all four juvenile stages were found.

TABLE 7

Measurements (in µm except L = mm) of *Xiphinema ifacolum* females and juveniles of populations from pumpkin in Massue, Cameroon.

Character	J1	J2	J3	J4	Females
n	9	8	3	2	9
L	0.83 ± 0.06 (0.76-0.93)	1.27 ± 0.06 (1.17-1.35)	1.73, 1.6 (n = 2)	2.3, 2.35	3.23 ± 0.1 (3.11-3.42)
MBW	22 ± 2.4 (19-25)	34 ± 2.4 (31-36)	39, 35 (n = 2)	45, ?	62 ± 2.8 (58-67)
Neck Length	199 ± 30.7 (155-231)	270 ± 43.9 (225-355)	339, 308 (n = 2)	354, 443	436 ± 34.8 (355-462)
Tail length	63 ± 4.2 (59-71)	71 ± 3 (68-75)	68, 67 (n = 2)	55, 56	52 ± 2.8 (48-56)
ABW	15 ± 1.5 (13.6-18.0)	21 ± 1.5 (20-23.6)	27, 24.5 (n = 2)	20, 31	34 ± 1.2 (32-36)
a	37.5 ± 3.9 (30.4-43.7)	37.3 ± 3.1 (32.5-42)	44.4, 45.7 (n = 2)	51, ?	52.2 ± 2.4 (49.4-56)
b	4 ± 0.5 (3.5-4.8)	4.8 ± 0.9 (3.3-6)	5, 5.2 (n = 2)	6.5, 5.3	7.4 ± 0.7 (6.8-8.9)
c	13.3 ± 0.4 (12.9-14)	18 ± 0.5 (16.5-19)	25. 4, 23.9 (n = 2)	41.8, 42	62.3 ± 3.6 (56.5-66.8)
c′	4.2 ± 0.2 (3.8-4.6)	3.3 ± 0.2 (3-3.7)	2.5, 2.7 (n = 2)	1.9, 1.6	1.5 ± 0.5 (1.4-1.6)
V	—	—	—	—	50 ± 1.1 (48-51)
Odontostyle	54 ± 1.1 (53-56)	69 ± 1.7 (67-72)	88 (86-91)	104, 105	120 ± 1.9 (125-131)
Odontophore	39 ± 1.6 (36-41)	48 ± 1.4 (46-50)	52 (50-54)	63, 65	71 ± 2.9 (67-75)
Tot stylet	93 ± 2.3 (90-97)	117 ± 2.7 (113-120)	140 (137-144)	167, 170	200 ± 3.7 (195-206)
R od st	68 ± 1.5 (66-70)	87 ± 4.7 (78-91)	104 (102-106)	124, ?	—
G ring (post.)	NM	NM	NM	NM	115 ± 4.5 (104-121)
G sheath	NM	NM	NM	NM	11 ± 3 (7-16)
Nerve ring	NM	NM	NM	NM	227 ± 2.4 (225-232)

NM = Not measured.

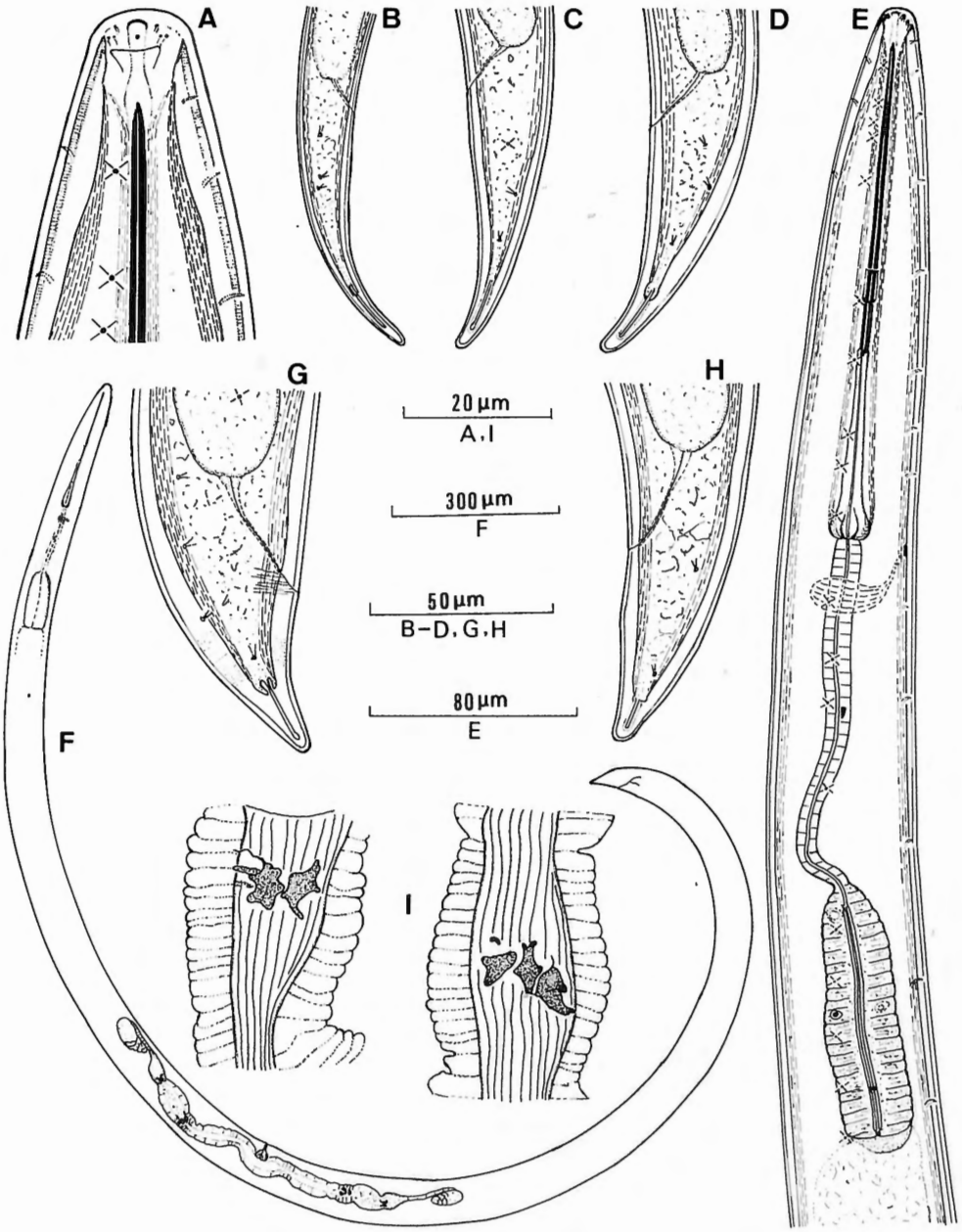

Fig. 4. — *Xiphinema ifacolum. Female.* — A : Head region. — E : Anterior body region. — G : Tail. — F : Entire view. — I : « Z organ ». — B-D, H : Tails of juveniles. B : J1 ; C : J2 ; D : J3 ; H : J4.

Xiphinema longicaudatum Luc, 1961

(Tables 8, 9 and 12, Fig. 5)

Measurements : See Tables 8, 9 and 12.

Description : *Female*. In heat-relaxed specimens, body habitus moderately ventrally arcuate, with most of the curvature in the posterior third. Body pores prominent ; in the neck region three dorsal pores confined anteriorly, twenty-two lateral and seven ventral pores. Lip region rounded, slightly offset from the body by a very shallow depression. Cephalic framework well developed. Amphidial aperture a wide, arch-shaped, transverse slit, occupying 55 % of the head diameter. Reproductive system with a fully developed posterior branch and a degenerate, short anterior branch without ovary and oviduct greatly reduced to a mass of cells ; the sphincter separating the oviduct from the uterus clearly recognizable, and the uterus itself relatively shorter and wider than the posterior one. Walls of the vagina in its expanded part composed of refractive cuticle, forming anterior and posterior pouches, interjacent tissue and sphincter muscle. Tail long, ventrally curved, with a distinct hyaline terminal portion, tapering to a bluntly pointed terminus. Two caudal pores present, the anterior one almost at anus level.

TABLE 8

Measurements (in µm except L = mm) of *Xiphinema longicaudatum* females of populations from sugarcane in Ekona and melon in Baduma, Cameroon.

Character	Sugarcane population	Melon population
n	6	2
L	2.85 ± 0.2 (2.68-3.16)	2.52, 2.39
VBW	58 ± 5.2 (53-65)	59, 57
Neck length	471 ± 47.5 (382-509)	436, 440
Tail length	201 ± 8.8 (195-211)	186, 172
ABW	29 ± 1.7 (26-30)	30, 29
a	49.7 ± 1.7 (48.3-52.7)	42.7, 41.9
b	6.2 ± 1.1 (5.2-8.3)	5.8, 5.9
c	14.1 ± 1.3 (12.7-15.8)	13.5 13.9
c'	7 ± 0.6 (6.5-8)	6.2, 5.1
V	39 ± 0.6 (38-40)	36, 37
Odontostyle	154 ± 2.4 (151-157)	148, 137
Odontophore	86 ± 3.5 (83-92)	88,79
Total stylet	240 ± 5 (235-247)	236, 216
Guide ring (posterior)	146 ± 5.6 (137-152)	140, 128
Guide sheath	15 ± 4.2 (11-20)	12, 20
Nerve ring	261 ± 29,4 (217-280)	267, ?
h	114 ± 7.3 (109-125)	131, 106
h %	58 ± 1.8 (56-60)	70, 62

TABLE 9

Measurements (in µm except L = mm) of *Xiphinema longicaudatum* juveniles of populations from sugarcane in Ekona, Cameroon.

Character	J2	J3	J4
n	6	7	3
L	1.37 ± 0.07 (1.26-1.47)	1.78 ± 0.07 (1.67-1.87)	2.34 (2.22-2.42)
a	35.8 ± 1.8 (33-38.6)	38 ± 3.3 (35-42.8)	42.4 (39-47.5)
b	4.6 ± 0.3 (4.3-5)	4.7 ± 0.3 (4-5)	5.8, 5.2 (n = 2)
c	6.9 ± 0.3 (6.4-7.2)	8.5 ± 0.6 (7.9-9.5)	10.8 (10.6-10.9)
Od st	86 ± 1.9 (84-89)	110 ± 2.8 (107-115)	130 (128-134)
Od ph	57 ± 2.3 (55-60)	66 ± 3.2 (59-68)	76, 80 (n = 2)
Tot st	142 ± 4.3 (139-149)	176 ± 3.9 (172-183)	204, 214 (n = 2)
R od st	111 ± 2.6 (109-115)	131 ± 3.7 (125-135)	155 (148-162)
Tail	199 ± 4.6 (195-205)	210 ± 11.6 (195-228)	218 (205-229)
ABW	21 ± 2.6 (18.2-25.5)	22.5 ± 2.5 (19-25.5)	29 (27.3-31.8)
c'	9.6 ± 0.9 (8-10.8)	9.3 ± 0.9 (8.3-10.5)	7.5 (6.9-8)
h	69 ± 13.2 (44-79)	86 ± 6.6 (70-95)	94 (93-96)
h %	35 ± 6.9 (21-40)	40 ± 2.5 (36-45)	43 (40-45)
h/tip θ*	35.5 ± 5.5 (29-43.5)	28.2 ± 3.8 (22-32)	31.8 (26-35)

* Width of tail at its tip.

Discussion : *X. longicaudatum* has been described only from West Africa (Luc, 1961 ; Luc and Hunt, 1978). Our specimens completely agree with both descriptions. *X. longicaudatum* was found together with *X. nigeriense* (also long-tailed) in one of our soil samples, and separation of their juveniles presented difficulty. However, we found that the value of the hyaline terminal portion of the tail/tail tip width, for any given juvenile stage, was higher in *X. longicaudatum* than in *X. nigeriense*, and this ratio was used to separate their juveniles (see Table 12). It appears to be a reliable character for separating the juvenile stages of both species in mixed populations. The tail length and hyaline terminal portion of the tail increase progressively in each juvenile stage.

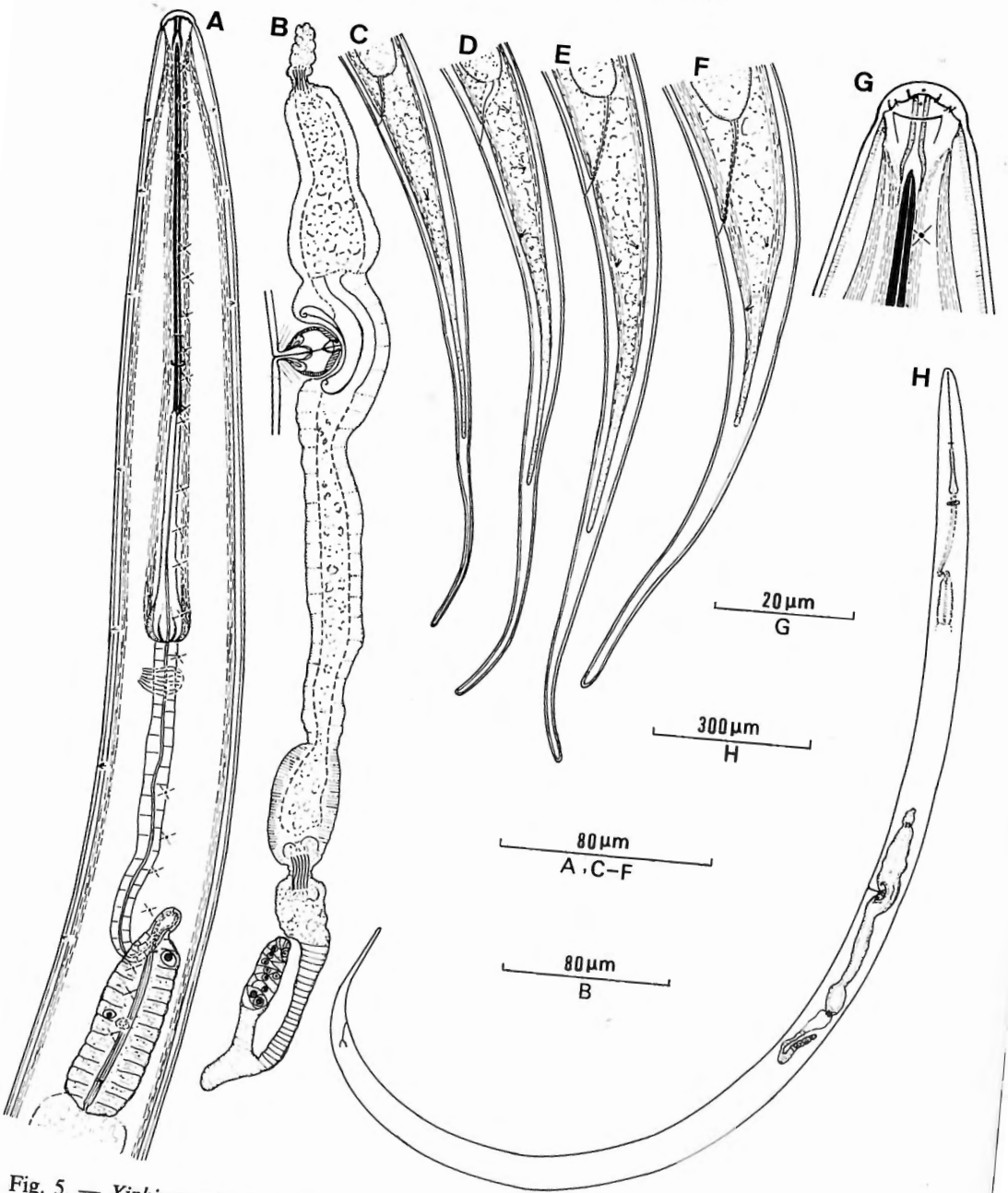

Fig. 5. — *Xiphinema longicaudatum. Female.* — A : Anterior body region. — B : Reproductive system. — F : Tail. — G : Head region. — H : Entire view. — C-E : Tails of juveniles. C : J2 ; D : J3 ; E : J4.

Xiphinema nigeriense Luc, 1961

(Tables 10, 11 and 12, Fig. 6)

Measurements : See Tables 10, 11 and 12.

Description : *Female.* When heat-relaxed, body habitus moderately ventrally arcuate, with most of the curvature in the posterior third. Body pores prominent; in the neck region three dorsal pores confined anteriorly, fourteen lateral and nine ventral pores; 10 ± 2 (8-12) and 9 ± 1.5 (7-11) ventral body pores occur in the cardia-vulva and vulva-anus regions, respectively. Lip region rounded, barely offset from the body by a very shallow depression. Cephalic framework well developed. Amphidial aperture a wide, arch-shaped, transverse slit, occupying about half of the head diameter. Reproductive system with equally developed anterior and posterior

TABLE 10

Measurements (in µm except L = mm) of *Xiphinema nigeriense* females of populations from okra in Dschang, sugarcane in Ekona and Widikum, and males from sugarcane in Widikum, Cameroon.

Character	Okra pop.	Sugarcane pop. (Ekona)	Sugarcane pop. (Widikum)	
			Females	Males
n	8	4	8	2
L	2.94 ±0.2 (2.84-3.36)	2.78 (2.51-3.0)	3.07 ± 0.3 (2.55-3.45)	?, 3.03
MBW	60 ±3.2 (55-65)	61 (57-64)	65 ±3.4 (58-69)	68, 67
Neck	411 ± 21.9 (382-445)	373 (309-436)	399 ± 26 (364-445)	355, 455
Tail	171 ± 12.8 (156-189)	143 (131-150)	167 ± 13 (153-186)	?, 168
ABW	29 ± 1.7 (27-32)	30 (27-33)	31 ± 1.6 (28-33)	45, 44
a	49.4 ± 3.3 (45.8-55)	46 (42.7-52.6)	47 ± 2.7 (44-52.3)	?, 45.2
b	7.2 ± 0.7 (5.8-8)	7.6 (6.6-9.4)	7.7 ± 1.1 (6.3-9.5)	?, 6.7
c	17.3 ± 2 (14.6-19.8)	19.5 (18.8-20)	18.6 ± 2 (15.2-20.3)	?, 18
c′	5.8 ± (5-6.9)	4.9 (4.4-5.4)	5.5 ± 0.5 (4.8-6.2)	?, 3.8
V	46 ± 1.8 (43-49)	47 (46-48)	48 ± 0.8 (46-49)	—
Od st	127 ± 3.7 (120-132)	121 (115-127)	119 ± 3.5 (114-123)	120, 120
Od ph	74 ± 3.4 (69-78)	72 (69-74)	72 ± 3 (66-75)	60, 74
Tot st	200 ± 5.6 (190-210)	193 (184-200)	191 ± 4 (185-195)	189, 194
G ring	119 ± 4.2 (113-125)	113 (105-122)	110 ± 4.4 (100-114)	110, 114
G sheath	14 ± 3 (8-16)	15 (12-17)	15 ± 1.9 (11-18)	11, 16
N ring	227 ± 5.2 (220-235)	216 (207-227)	218 ± 4.7 (212-224)	216, 222
h	87 ± 7.5 (78-94)	64 (56-68)	73 ± 4.9 (68-81)	?, 85
h %	51 ± 2.5 (48-55)	45 (39-49)	44 ± 3 (40-48)	?, 51
Spicules	—	—	—	69, 69

TABLE 11

Measurements (in μm except L = mm) of *Xiphinema nigeriense* juveniles from okra in Dschang and sugarcane in Ekona and Widikum, Cameroon combined.

Character	J1	J2	J3
n	12	14	7
L	1.09 ± 0.06 (0.94-1.14)	1.33 ± 0.08 (1.15-1.46)	1.76 ± 0.2 (1.53-1.93)
a	42.2 ± 3.2 (37.7-57)	36.9 ± 2 (32.6-39.7)	40.7 ± 3.1 (37.8-45)
b	5.1 ± 0.8 (3.7-6.7)	4.9 ± 0.5 (4.1-5.6)	5.4, 0.2 (5.2-5.6)
c	5.4 ± 0.3 (4.9-5.8)	7.9 ± 0.4 (7-8.7)	9.4 ± 0.6 (8.8-10)
Od st	57 ± 2 (55-61)	71 ± 1.3 (70-74)	91 ± 3.2 (88-94)
Od ph	41 ± 1.1 (38-42)	49 ± 2.3 (46-52)	56 ± 1.5 (55-58)
Tot st	98 ± 2.3 (95-102)	121 ± 2.8 (116-123)	147 ± 3.2 (143-150)
R od st	72 ± 1.9 (68-75)	92 ± 6.5 (87-110)	108 ± 3.2 (105-111)
Tail	200 ± 7.5 (192-212)	172 ± 9.4 (159-186)	185 ± 13,2 (170-202)
ABW	15.7 ± 1.4 (13.6-17)	19 ± 2.3 (15.5-24.5)	22 ± 3.1 (19-26.4)
c'	12.9 ± 1.1 (11.4-14.1)	9.2 ± 1 (7.3-10.6)	8.4 ± 1 (7.1-10)
h	75 ± 5.1 (66-83)	43 ± 4.4 (38-50)	61 ± 6.7 (51-70)
h %	37 ± 2.2 (34-42)	25 ± 2.4 (21-28)	32 ± 3.1 (28-35)
h/tip θ*	Not measured	12.4 ± 1.7 (10-15)	17.4 ± 1.6 (15.5-19.3)

* Width of tail at its tip.

TABLE 12

Comparison of the ratio of the hyaline terminal portion of tail (h) to tail tip width (θ) of juvenile stages of *Xiphinema longicaudatum* and *X. nigeriense* from Cameroon.

Xiphinema longicaudatum		*Xiphinema nigeriense*		
Juvenile stage	Sugarcane pop. (Ekona)	Okra pop.	Sugarcane pop. (Widikum)	Sugarcane pop. (Ekona)
J2 : n	6	2	10	2
h/tip θ	35.5 ± 5.5 (29.2-43.5)	12.8, 13.8	12 ± 1.7 (10-13.8)	15, 11
J3 : n	7	4	2	1
h/tip θ	28.2 ± 3.8 (22-32)	17.5 (15.5-19.3)	?, 17.3	15.8
J4 : n	3	—	—	—
h/tip θ	31.8 (26-35.3)	—	—	—

branches. Walls of vagina in its expanded part lined with cuticle, tissue and sphincter muscle. Tail usually long, occasionally shorter, ventrally curved, with a distinct hyaline terminal portion, tapering to a bluntly pointed terminus. Three caudal pores present, the most anterior one at anus level.

Male : Described for the first time. Supplements consist of an adanal pair and a single ventromedian one 204 and 205 µm anterior to the adanal pair. Five caudal pores present.

Discussion : *X. nigeriense* has been reported only from Nigeria (LUC, 1961 ; BOS and LOOF, 1985) ; however, compared with the type specimens, those studied by the latter authors were longer (2.75-2.96 mm *vs* 1.68-1.97 mm), had a slightly more anterior vulva (45-50 % *vs* 50-53 %), and a smaller value of the proportion of the tail occupied by the hyaline terminal portion (44-55 % *vs* 68 % in the type population). Our measurements are similar to those given by BOS and LOOF (*op. cit.*). One of us (A. C.) recently found a male of *X. nigeriense* among the paratypes, but its description has not yet been published. The first-, second-, and third-stage juveniles are described for the first time.

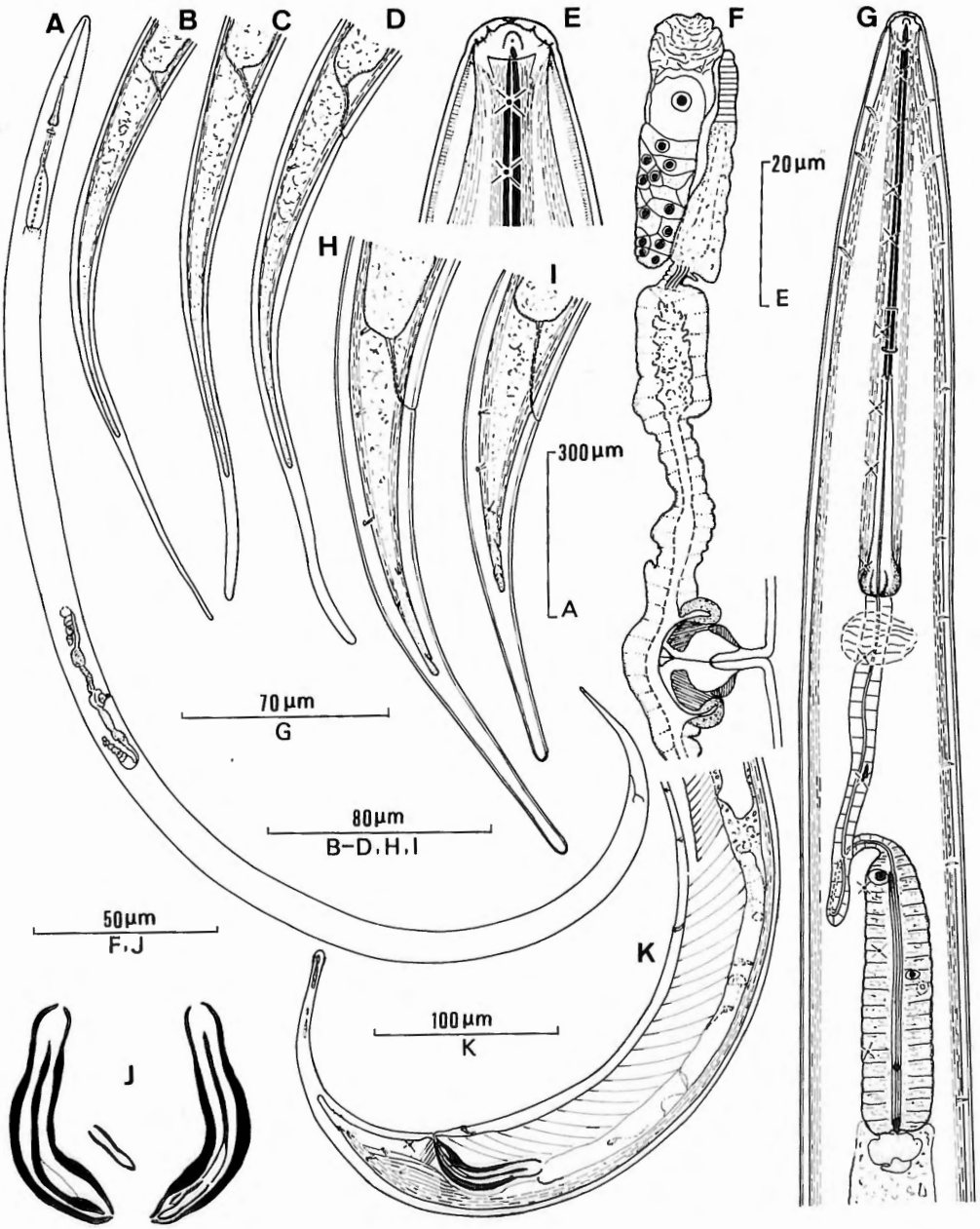

Fig. 6. — *Xiphinema nigeriense. Female.* — A : Entire view. — E : Head region. — F : Anterior genital branch. — G : Anterior body region. — H, I : Variation in tail length. — B-D : Tails of juveniles. B : J1 ; C : J2 ; D : J3. Male. — J : Spicules and lateral guiding pieces. — K : Posterior body region.

Xiphinema setariae LUC, 1958
syn. *X. vulgare* TARJAN, 1964
(Tables 13, 14 and 15, Fig. 7)

Measurements : See Tables 13, 14 and 15.

Description : *Female*. In heat-relaxed specimens body habitus J-shape. Body pores prominent ; in the neck region eleven ventral pores, ten lateral pores, occurring mostly in the anterior body region, and three dorsal pores confined anteriorly. Lip region rounded, offset from the body by a shallow depression. Amphidial aperture a wide, transverse slit, occupying about 40 % of the head diameter. Reproductive system with equally developed anterior and posterior branches. Tail dorsally convex-conoid, tapering to a bluntly pointed terminus. Usually two caudal pores, occasionally one or three, present.

TABLE 13

Measurements (in µm except L = mm) of *Xiphinema setariae* females of populations from melon in Baduma, sugarcane in Ekona and peanut (+ 1 male) in Dschang (IRA Farm), Cameroon.

Character	Melon pop.	Sugarcane pop.	Peanut population	
			Females	Males
n	10	3	4	1
L	2.49 ± 0.1 (2.33-2.63)	2.86 (2.76-2.91)	3.03 (2.85-3.24)	3.01
MBW	52 ± 2.5 (47-56)	55	56 (54-57)	55
Neck length	419 ± 17.5 (395-447)	442 (427-455)	457 (440-500)	449
Tail length	55 ± 4 (49-63)	56 (54-58)	60 (55-64)	58
ABW	30 ± 1.5 (27-32)	31-32	31-32	34
a	47.8 ± 2.6 (43-51.8)	52 (50.2-52.9)	54.5 (52.8-57.9)	54.7
b	5.9 ± 0.2 (5.7-6.5)	6.4-6.5	6.6 (6.4-6.9)	6.7
c	45.4 ± 3.4 (38.7-50.2)	51.5 (47.6-53.9)	50.5 (46.7-54)	51.9
c′	1.9 ± 0.2 (1.6-2.1)	1.7-1.8	1.8-2.0	1.7
V	36-38	37-38	37 (36-39)	—
Od style	117 ± 4.6 (105-121)	130 (129-132)	131 (126-134)	127
Od phore	66 ± 2.2 (62-69)	71	75 (71-79)	75
Tot stylet	183 ± 4.8 (173-190)	201 (200-203)	201 (202-211)	202
G ring (post.)	106 ± 4.1 (99-113)	118-120	118 (115-123)	115
G sheath	13 ± 2.9 (9-17)	12 (10-13)	15 (12-21)	13
N ring	216 ± 5.2 (205-225)	234, 226 (n = 2)	228 (215-238)	225
Spicules	—	—	—	63, 61

TABLE 14

Measurements (in μm except L = mm) of *Xiphinema setariae* females of populations from peanut in Bansoa * and Dschang ** (University Farm) and potato in Dschang, Cameroon.

Character	Peanut population *	Peanut population **	Potato population
n	3	3	4
L	3.02 (2.91-3.11)	3.04 (2.91-3.18)	2.88 (2.83-2.92)
VBW	55-57	57 (56-59)	55 (52-57)
Neck length	435 (433-438)	403 (402-404)	469 (458-475)
Tail length	51, 52 (n = 2)	55-57	52 (48-55)
ABW	30, 31 (n = 2)	29-31	31 (29-33)
a	54.2 (52.9-56.5)	53.9 (51.0-56.8)	52.4 (50.4-54.4)
b	6.9 (6.7-7.1)	7.5 (7.2-7.9)	6.2 (6.0-6.4)
c	57, 48.9 (n = 2)	54.3 (52.9-56.8)	55.8 (52.4-59.8)
c′	1.7, 2 (n = 2)	1.8-1.9	1.7 (1.5-1.9)
V	36-38	36-37	37 (34-39)
Odontostyle	123 (121-125)	130 (127-135)	130 (125-131)
Odontophore	74 (72-76)	75 (72-78)	72 (70-75)
Total stylet	197 (195-198)	205 (204-207)	202 (195-206)
G ring (post.)	115 (110-118)	122 (120-127)	124 (115-130)
G sheath	16, 14 (n = 2)	15, 21 (n = 2)	17 (10-23)
Nerve ring	231 (227-238)	235, 238 (n = 2)	230 (224-236)

TABLE 15

Measurements (in μm except L = mm) of *Xiphinema setariae* juveniles of populations fromp different hosts and localities in Cameroon combined.

Character	J2	J3	J4
n	7	11	25
L	1.18 ± 0.2 (1.02-1.46)	1.50 ± 0.1 (1.23-1.65)	2.07 ± 0.1 (1.82-2.32)
Tail	71 ± 3.9 (66-77)	70 ± 4 (64-76)	65 ± 3.4 (58-70)
ABW	16.4 ± 1.9 (13.6-19)	20.5 ± 1.6 (18-22.7)	26 ± 1.9 (21.8-30)
a	40.6 ± 1.5 (38.6-41.9)	41.3 ± 2 (39.5-44.7)	50.2 ± 4 (41.4-59.7)
b	4.4 ± 0.4 (3.9-4.9)	4.3 ± 0.3 (3.9-4.6)	5.3 ± 0.7 (4.1-6.9)
c	16.6 ± 1.8 (15.5-20)	21 ± 1.7 (19-2-23.2)	32 ± 3 (26.4-38)
c′	4.3 ± 0.4 (3.8-4.9)	3.4 ± 0.2 (3-3.6)	2.5 ± 0.2 (2.2-2.9)
Od st	69 ± 7.8 (65-85)	89 ± 2.5 (86-93)	106 ± 6 (96-120)
Od ph	47 ± 1.2 (45-48)	57 ± 1 (55-58)	62 ± 3.8 (52-67)
Tot st	116 ± 8.6 (110-133)	146 ± 2.8 (143-151)	168 ± 7.9 (154-177)
R od st	89 ± 3 (84-91)	108 ± 2.5 (105-111)	126 ± 6 (117-133)

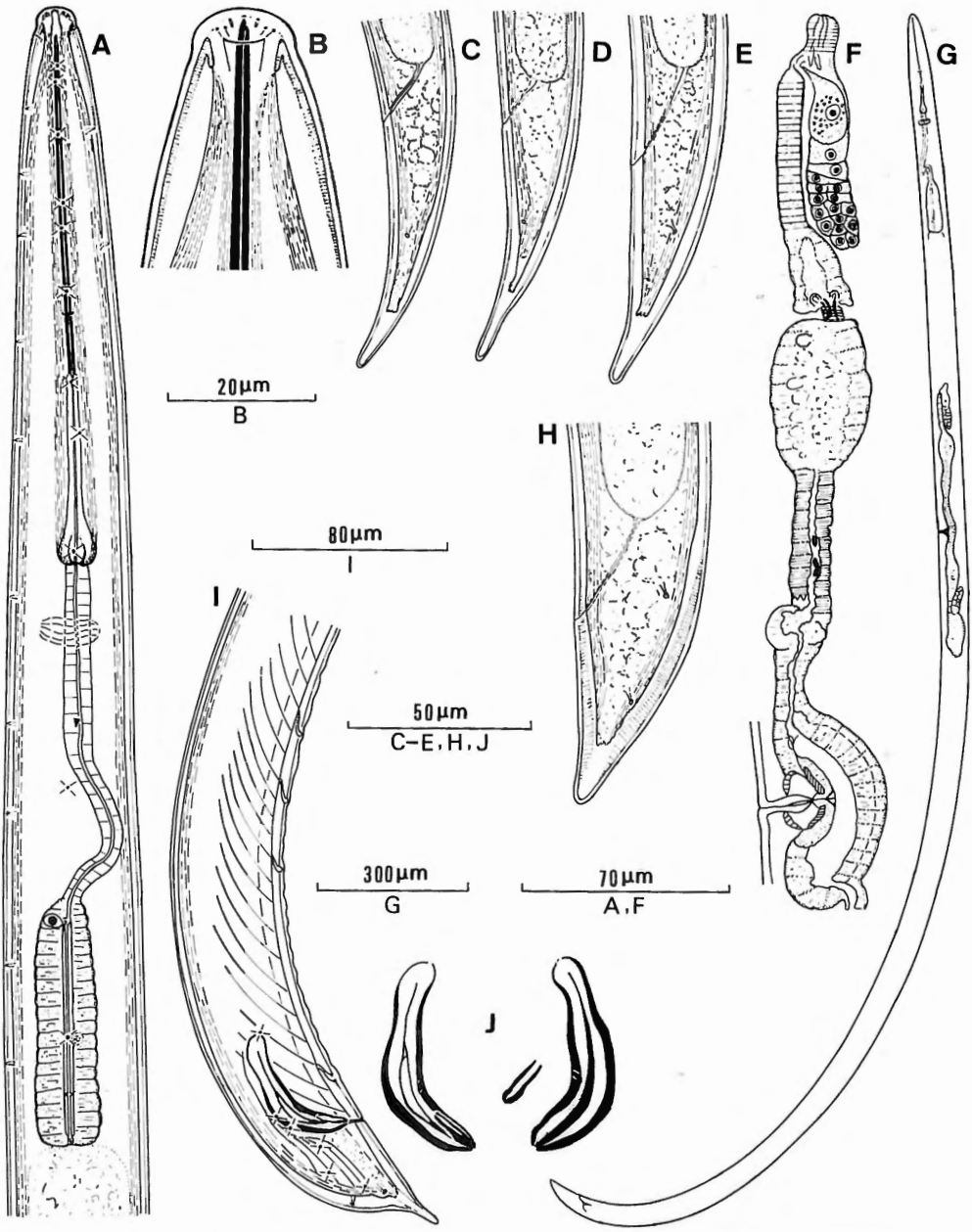

Fig. 7. — *Xiphinema setariae*. *Female*. A : Anterior body region. — B : Head region. — F : Anterior genital branch. — G : Entire view. — H : Tail. — C-E. Tails of juveniles. C : J2 ; D : J3 ; — E : J4. — Male. I : Posterior body region. — J : Spicules and lateral guiding pieces.

Male : Found for the second time. Supplements consist of an adanal pair and three single ventromedian ones. Reproductive system poorly developed. Five caudal pores present.

Discussion : *X. setariae,* another pantropical *Xiphinema* species (cf. LUC and COOMANS, 1992), differs from all others in the genus by its typical J-shape when heat-relaxed and a relatively anterior vulva ; V rarely exceeds 40 % (34-39 % in all our specimens) of body length from the anterior end. Our female specimens satisfactorily fit previous descriptions. The single male specimen we found in one of our populations is the second ever reported, the first one reported by TARJAN (1964, as *X. vulgare*). Its testes, vas deferens, and oblique muscles around the vas deferens were all indistinct indicating a rudimentary and non-functional reproductive system. The second-, third-, and fourth-stage juveniles were found.

Xiphinema vitis HEYNS, 1974

(Tables 16 and 17, Fig. 8)

Measurements

TABLE 16

Measurements (in µm except L = mm) of *Xiphinema vitis* females of populations from peanut in Balikumbat, plantain in Bali, sweet potato in Babungo, and sugarcane in Widikum, Cameroon.

Character	Peanut pop.	Plantain pop.	S. potato pop.	Sugarcane pop.
n	3	5	4	1
L	3.04 (3.0-3.07)	2.78 ± 0.1 (2.62-2.95)	2.99 ± 0.1 (2.82-3.12)	2.70
VBW	60 (58-64)	59 ± 1 (57-60)	55 ± 2.8 (51-57)	58
Neck	373 (345-391)	358 ± 5.2 (327-364)	385 ± 21.7 (382-409)	373
Tail	55-57	52 ± 3.2 (49-57)	51 ± 3.8 (46-54)	45
ABW	33 (31-34)	31-33	31 ± 1.3 (29-32)	31
a	50.5 (47-52.9)	47.5 ± 2.3 (45-50.5)	54 ± 3.5 (49.5-57.6)	46.6
b	8.2 (7.9-8.7)	8 ± 0.6 (7.4-8.8)	8 ± 0.7 (7.2-8.5)	7.2
c	54.3 (52.6-55.8)	53.5 ± 1.9 (51.8-56.5)	58.5 ± 4.9 (52-63.7)	60
c′	1.7-1.8	1.6 ± 0.1 (1.5-1.8)	1.6-1.7	1.4
V	51-52	50.5 ± 1 (49-51)	52 ± 1.2 (51-53)	51.5
Od st	109 (106-112)	110 ± 4.4 (106-115)	109 ± 3.6 (106-114)	105
Od ph	70 (69-72)	68 ± 1.5 (66-69)	70	64
Tot st	180 (175-182)	178 ± 5.3 (172-184)	179 ± 3.6 (176-184)	169
G ring	99 (96-103)	103 ± 5.6 (98-111)	105 ± 4.2 (100-109)	95
G sheath	15 (12-17)	12 ± 4.9 (5-17)	16 ± 1.4 (15-18)	15
N ring	209 (204-214)	211 ± 6.1 (206-217)	213 ± 7.5 (205-223)	205

TABLE 17

Measurements (in µm except L = mm) of *Xiphinema vitis* juveniles of populations from different hosts and localities in Cameroon combined.

Character	J1	J2	J3	J4
n	6	3	3	14
L	0.87 (0.85-0.94)	1.2 (1.18-1.26)	1.67 (1.6-1.77)	2.23 ± 0.1 (2.05-2.45)
Tail	57 (54-59)	63 (60-65)	61 (57-64)	59 ± 3.4 (54-67)
ABW	14 (13.6-14.5)	19 (17-21)	24.5 (23-26)	28 ±2.5 (21.8-31)
a	43.7 (41-45.3)	39 (36.4-42)	39.6 (37-42.3)	46.5 ± 3.8 (41-51.4)
b	3.7 (3-4)	4.7 (4.3-5.3)	6 (5.3-6.5)	6.2 ± 0.4 (5.9-7)
c	15.4 (14.7-16)	19.3 (18.4-29)	27.3 (25.4-28.9)	38 ± 3.6 (32.7-45)
c′	4 (3.9-4.2)	3.3 (2.9-3.7)	2.5 (2.4-2.7)	2 ± 0.2 (1.9-2.6)
Od st	55 (54-58)	67-69	81 (75-85)	96 ± 2 (91-100)
Od ph	40 (37-42)	46, 48 (n = 2)	54, 54 (n = 2)	62 ± 1.8 (59-65)
Tot st	95 (92-100)	115, 115 (n = 2)	129, 138 (n = 2)	159 ± 3 (154-163)
R od st	69 (67-71)	82 (80-84)	96 (92-101)	110± 3.9 (98-115)

Description : *Female.* When relaxed by gentle heat, body strongly ventrally arcuate in the posterior half, forming an incomplete figure 6. Body pores prominent ; in the neck region three dorsal pores confined anteriorly, fifteen lateral and ten ventral pores. Lip region flattened anteriorly, offset from the body by a shallow depression. Amphidial aperture a wide, transverse slit, occupying 60 % of the head diameter. Reproductive system with equally developed anterior and posterior branches. Tail dorsally convex-conoid, tapering to a bluntly rounded terminus. Three caudal pores present.

Discussion : In comparison with specimens described from South Africa (HEYNS, 1974) and Burundi (COOMANS *et al.*, 1990), (i) ours from plantain are slightly shorter (2.62-2.95 mm *vs* 2.62-3.45 mm in the original description and 2.85-3.83 mm in specimens from Burundi, and (ii) the vulva is slightly more posterior in ours (49-53 % *vs* 42-49 % and 39-49.6 % in the type and Burundi populations, respectively). No males were present, but all four juvenile stages were found.

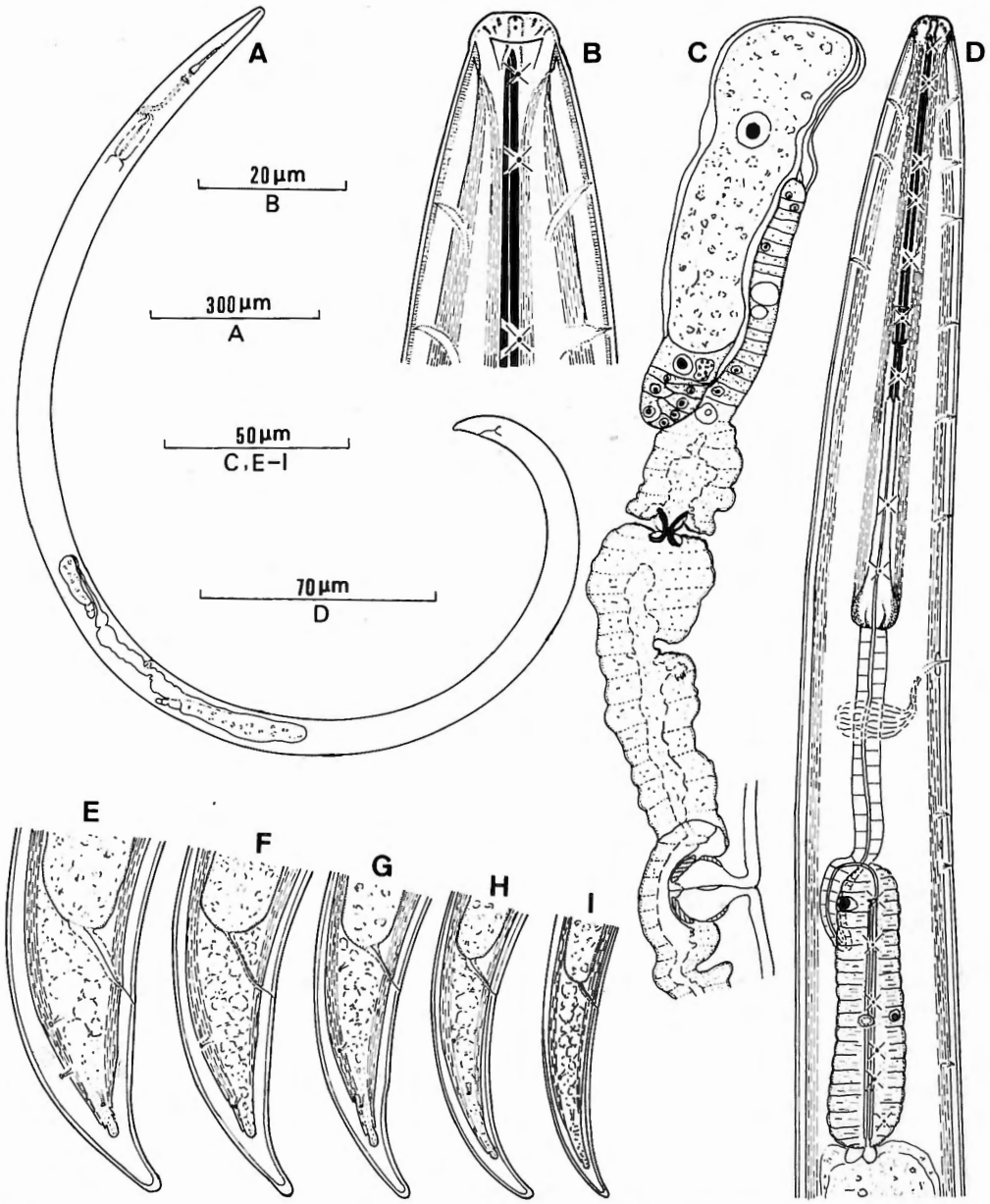

Fig. 8. — *Xiphinema vitis. Female.* — A : Entire view. — B : Head region. — C : Anterior genital branch. — D : Anterior body region. — E : Tail. — F-I : Tails of juveniles. F : J4 ; G : J3 ; H : J2 ; I : J1.

ACKNOWLEDGEMENTS

The first author expresses his gratitude to : the Belgian Administration for Development and Cooperation (ABOS/AGCD) for financial support ; Dr. J. Foko, Head of Department of Plant Protection, University of Dschang, Dschang, Cameroon, for logistical support and laboratory space ; Messrs. Zomo Sebastien (technician) and Dongho Jean-Claude (driver) of the University of Dschang, for technical assistance during sample collection in Cameroon.

REFERENCES

ADIKO, A. (1988) — Plant-parasitic nematodes associated with plantain, Musa paradisiaca (AAB), in the Ivory Coast. *Revue Nématol.*, **11** : 109-113.

BOS, W. S. and P. A. A. LOOF (1985) — Nigerian species of the genus *Xiphinema* Cobb, 1913 (Nematoda : Dorylaimida). Part I. *Nematologica*, **30** :395-418.

CAVENESS, F. E. and H. J. JENSEN (1955) — Modification of the centrifugal-flotation technique for the isolation and concentration of nematodes and their eggs from soil and plant tissue. *Proc. helminth. Soc. Wash.*, **22** : 87-89.

CHAVEZ, E. and E. GERAERT (1977) — Observations sur quelques mononchides et dorylaimides du Cameroun et du Zaire. *Revue Zool. Afr.*, **91** : 765-780.

COOMANS, A., F. M. RASHID, and M. LUC (1990) — Observations on *Xiphinema vitis* HEYNS, 1974, *X. elongatum* SCHUURMANS STEKHOVEN and TEUNISSEN, 1938, *X. fatikae* BOS and LOOF, 1984, and description of *X. fatikae eburnense* subsp. n. (Nemata : Longidoridae) from Africa. *Revue Nématol.*, **13** : 239-248.

DALMASSO, A. (1967) — Description du mâle de *Longidorus laevicapitatus* WILLIAMS, 1959 (Nematoda : Dorylaimina), parasite de la canne à sucre aux Antilles. *Annls. Épiphyt.*, **18** : 313-315.

DE GRISSE, A. (1969) — Redescription ou modifications de quelques techniques utilisées dans l'étude des nématodes phytoparasitaires. *Meded. Rijksfak. LandbWetensch. Gent*, **34** : 351-369.

EDWARD, J. C., S. L. MISRA and G. R. SINGH (1964) — *Longidorus pisi* n. sp. (Nematoda, Dorylaimoidea) associated with the rhizosphere of *Pisum sativum* from Uttar Pradesh, India. *Jap. J. app. Ent. Zool.*, **8** : 310-312.

GERAERT, E. (1961) — Corrections of measurements of nematode diameters. *Nematologica*, **6** : 258-259.

HEYNS, J. (1974) — The genus *Xiphinema* in South Africa. II. *X. elongatum* group (Nematoda : Dorylaimida). *Phytophylactica*, **8** : 67-78.

JACOBS, P. J. F. and J. HEYNS (1982) — *Longidorus* species from sugarcane in Natal (Nematoda : Longidoridae). *Phytophylactica*, **14** : 195-204.

JENKINS, W. R. (1964) — A rapid centrifugal-flotation technique for separating nematodes from soil. *Pl. Dis. Reptr.*, **48** : 692.

LAMBERTI, F., T. BLEVE-ZACHEO, D. K. TUOPAY, A. CIANCIO, and J. B. BOIBOI (1987) — Relationship between *Xiphinema ifacolum* and rice in Liberia. *Nematol. medit.*, **15** : 303-314.

LOOF, P. A. A. and R. D. SHARMA (1979) — Plant-parasitic nematodes from Bahia State, Brazil : The genus *Xiphinema* COBB, 1913 (Dorylaimida). *Nematologica*, **25** : 111-127.

LUC, M. (1958) — *Xiphinema* de l'Ouest Africain : description de cinq nouvelles espèces (Nematoda : Dorylaimidae). *Nematologica,* **3** : 57-72.

LUC, M. (1961) — *Xiphinema* de l'Ouest Africain : deuxième note (Nematoda : Dorylaimoidea) *Nematologica,* **6** : 107-122.

LUC, M. and A. COOMANS (1992) — Les nématodes phytoparasites du genre *Xiphinema* (Longidoridae) en Guyane et en Martinique. *Belg. J. Zool.,* **122** : 147-183.

LUC, M. and A. DALMASSO (1975) — Considerations on the genus *Xiphinema* COBB, 1913 (Nematoda : Longidoridae) and a « lattice » for the identification of species. *Cah. ORSTOM, sér. Biol.,* **X** : 303-327.

LUC, M. and D. J. HUNT (1978) — Redescription of *Xiphinema longicaudatum* LUC, 1961 and observations on *Xiphinema krugi* LORDELLO, 1955 (Nematoda : Longidoridae). *Nematologica,* **24** : 1-18.

LUC, M. and J. F. SOUTHEY (1980) — Study of biometrical variability in *Xiphinema insigne* LOOS, 1949, and *X. elongatum* SCHUURMANS STEKHOVEN and TEUNISSEN, 1938 ; description of *X. savanicola* n. sp. (Nematoda : Longidoridae). *Revue Nématol.,* **3** : 243-269.

MERNY G. (1966) — Nématodes d'Afrique tropicale : un nouveau *Paratylenchus* (Criconematidae), deux nouveaux *Longidorus* et observations sur *Longidorus laevicapitatus* WILLIAMS, 1959 (Dorylaimidae). *Nematologica,* **12** : 385-395.

SCHUURMANS STEKHOVEN, J. H. and R. J. H. TEUNISSEN (1938) — Nématodes libres terrestres. *Exploration du Parc national Albert, Mission de Witte,* **22** : 1-229.

SEINHORST, J. W. (1959) — A rapid method for the transfer of nematodes from fixative to anhydrous glycerine. *Nematologica,* **4** : 67-69.

TARJAN, A. C. (1964) — Two new American dagger nematodes (*Xiphinema* : Dorylaimidae) associated with citrus, and comments on the variability of *X. bakeri* WILLIAMS, 1961. *Proc. helminth. Soc. Wash.,* **31** : 65-76.

WILLIAMS, J. R. (1959) — Studies on the nematode soil fauna of sugarcane fields in Mauritius. 3. Dorylaimidae (Dorylaimoidea, Enoplida). *Mauritius Sugar Ind. Res. Inst., Occ. Paper,* **3,** 28 pp.

ZEIDAN, A. B. and A. COOMANS (1992) — Longidoridae (Nematoda : Dorylaimida) from Sudan. *Nematol. medit.,* **19** : 177-189.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 231-261 — Brussels 1993

ELECTROMYOGRAPHY AND MECHANICS OF MASTICATION IN THE SPRINGHARE, *PEDETES CAPENSIS* (Rodentia, Pedetidae)

by

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SUMMARY

In springhares, *Pedetes capensis* (FORSTER, 1778) ingestion, transport and mastication of food are cyclic events. During these cycles, the movement of the lower jaw shows no lateral component and the activity of all muscles is bilaterally symmetrical. The temporal muscles reach a peak activity during the fast-closing stage. During the reduction stages, peak activities are subsequently reached in the maxillomandibular muscles, the medial pterygoids, the masseters, the zygomaticomandibular muscles, the posterior masseters, and the lateral pterygoids in order. During fast opening, only the digastrics fire bilaterally. Magnitude and duration show some variation for the different types of food offered. The maxillomandibular muscle reaches its maximum activity whenever the animals feed on groundnut. Food that does not require biting (*i.e.* rolled oats), produces very low muscle activity.

The Rodentia include groups with a similar gross muscular morphology but considerable differences in their masticatory patterns, whereas members of different major groups show similar masticatory patterns. Although the masticatory patterns shown by *Rattus* and *Pedetes* are similar, the forces acting on their lower jaws differ. In *Pedetes* the masseter-complex is more important than in *Rattus* as the bite force at the incisors is 68 % of the estimated muscle resultant.

Keywords : mastication, jaw muscles, electromyography, biomechanics, rodents, *Pedetes*.

INTRODUCTION

Cinematography and electromyography have substantially added to our knowledge of mammalian mastication (for review see GANS *et al.*, 1978 ; HIIEMAE, 1978 ; GORNIAK, 1985). Experimental studies on rodent mastication modify the conclusion of theoretical analyses (*cf.* MAYNARD SMITH and SAVAGE, 1959) and show that masticatory mechanics differs remarkably among rodents.

Comparison of the kinematics and anatomical data on rodent mastication shows that the absence or presence of isognathy, the orientation and occlusal pat-

tern of the molar teeth, and the position of the incisors are the most important dental characteristics regulating the masticatory pattern.

Springhares, *Pedetes capensis*, are rodents that do not fit confortably into their present systematical classification. Their characteristics do not permit placement within any of the four major rodent groups (Protrogomorpha, Sciuromorpha, Myomorpha, and Hystricomorpha) (OFFERMANS and DE VREE, 1989). Their characteristics are shared with those of groups, such as the Anomaluridae, Ctenodactylidae, Dipodidae, and Theridomorpha. Despite their substantial morphological differences, the mastication pattern in *Pedetes* is similar to that of *Rattus* (OFFERMANS and DE VREE, 1990). Both masticate bilaterally : chewing the food simultaneously on both sides.

The present paper reports on the muscular activity during ingestion and mastication of springhares. These data and quantified motion analysis have been combined in a threedimensional model that permits investigation of external forces that act upon the mandible during ingestion and mastication cycles.

MATERIALS AND METHODS

Feeding movements were studied on two adult specimens (one male of 2.5 kg and one female of 2.1 kg), placed at our disposition by the Zoo of Blijdorp (Rotterdam, The Netherlands). After the experiments, the female specimen was sacrificed for analysis of the muscle pattern. Additionaly, a preserved head (State Museum, Windhoek, Namibia) and dry skulls (Mus. r. Afr. Centr., Tervuren, Belgium) could bestudied.

In six experiments, the animals were studied while ingesting and masticating rolled oats and groundnuts (peanuts). The animals were not restrained as it was found that they were easily trained to accept food in the experimental setting.

Electromyography electrodes were formed of 0.076 tefloncoated stainless steel wires (Medwire Corp.), and inserted in the muscles with 16-gauge hypodermic needles through small skin incisions under general anesthesia (40 mg Ketalar/kg and 0.04 ml Rompun/kg) (GANS and GORNIAK, 1980). Movements of the electrode tips were minimized by gluing the electrodes at the insertion site with histoacryl (Braun Melsungen AG). The electrodes were led subcutaneously to the back of the animal between the shoulder blades. The ends of the wires were soldered to an externally placed, 31-pole miniature connector (Amphenol, nr 222-22N31) that subsequently was attached to the skin with silicon rubber (Silastic 382 Medical Grade, Elastomer, Dow Corning) (DE GUELDRE and DE VREE, 1988). EMG signals were passed through Tektronix 26A2 differential preamplifiers and Honeywell Accudata 117 DC amplifiers and recorded on a Honeywell medium bandpass 96FM 14-channel tape recorder at 19 cm/sec.

Electromyography was combined with X-ray cinematography using a Siemens Tridoros X-ray flash apparatus in combination with a Siricon 2 image intensifier. Film sequences were recorded in lateral view at 50 fps with an Arriflex 16 mm camera, using Gevapan 30 negative film (80 asa). Films were projected frame by

frame on a Vanguard analyzer with a PCD projecting system. The coordinates of the markers were determined and digitized with a PCD analyzer and recorded with a IBM-AT computer.

Electromyograms were digitized with a Keithley DAS A/D converter using an IBM-AT computer. Muscle activity was described as spike number, amplitude and product of spike number times amplitude for intervals of 10 msec (two intervals per film frame). As the product of spike number times amplitude correlates best with tension (GORNIAK and GANS, 1980 ; GORNIAK *et al.*, 1982 ; DE GUELDRE and DE VREE, 1988), this value was used for further calculations. The muscle activities recorded with each electrode were averaged and the %EMG was expressed as a fraction of the maximum value observed for that electrode in any interval.

Wet muscle weights were determined on a freshly killed female specimen and a preserved head. The muscles were excised carefully, weighed, and fixed in 10 % formalin. To dissolve the connective tissue the muscles were immersed in 25 % nitric acid for five to six days and then placed in 50 % glycerol. Fiber lengths were measured on a Wild M5 dissecting microscope with an ocular micrometer. Physiological cross sectional areas were estimated by dividing the mean wet weight, used as measure of volume, by the mean fiber length (FICK, 1910 ; SCHUMACHER, 1961 ; WEIJS and DANTUMA, 1981 ; DE GUELDRE and DE VREE, 1990).

The origin and insertion of the theoretical central fibers (RAYNE and CRAWFORD, 1972) were marked on the skull and the mandible with lead markers (HIIEMAE, 1971). The working lines of the muscles were determined from the coordinates in the x, y and z planes of the points of origin and insertion. To do this the skull was mounted in a stereotactic apparatus with the teeth in full occlusion. The coordinates of these points, of the teeth and the condyles were determined relative to the sagittal and occlusal planes. The changing direction of the working lines during the ingestion and mastication cycles could be established using standardized cycles (OFFERMANS and DE VREE, 1990). The origin-insertion lengths and the moment arms of the muscles could also be derived from these data.

The magnitude of instantaneous muscular force was estimated for each muscle by multiplying the value of %EMG, a measure of the degree of activity, with the physiological cross section, a measure for maximal force (WEIJS and DANTUMA, 1981 ; DE GUELDRE and DE VREE, 1990).

RESULTS

Anatomy

The morphology of the masticatory apparatus of the springhare has been described in detail (OFFERMANS and DE VREE, 1989). Most muscles of the masseteric complex are well separated from each other. However, the superficial masseter barely can be distinguished from the deep masseter. Therefore, these muscles were threated as a single unit for the electromyographic and biomechanical study. The zygomaticomandibular and maxillomandibular muscles form a uniform mass which

is well separated from the other muscles of the masseteric complex. The temporal muscle is small and consists of a single layer, which shows no connection with the zygomaticomandibular muscle : *Pedetes* shares this characteristic with other rodents (ALLEN, 1880). The masticatory muscles are illustrated in Figure 1 and their areas of origin and insertion of are summarized in table 1.

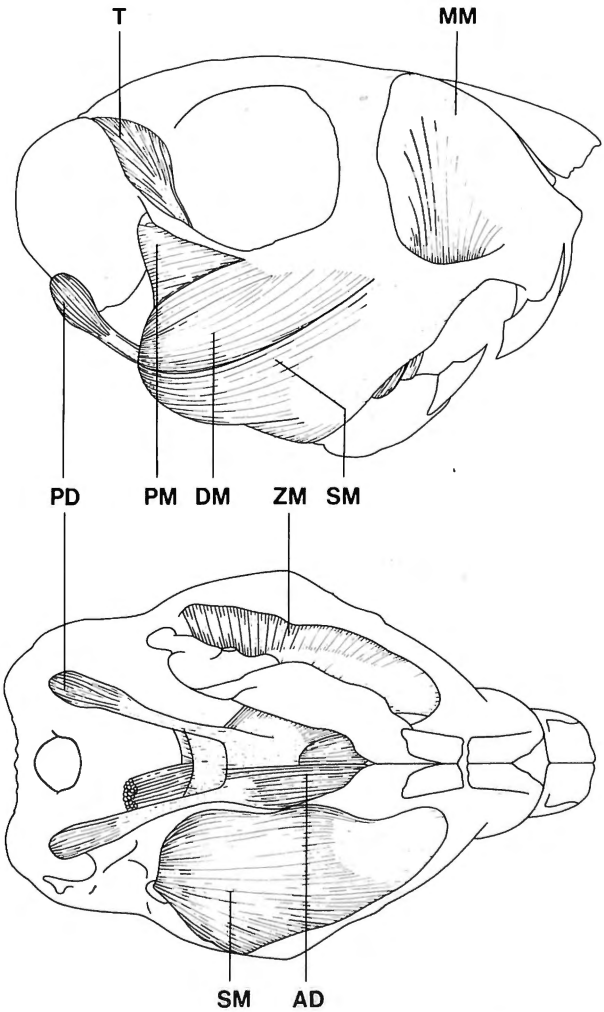

Fig. 1. — *Pedetes capensis*. Lateral and ventral view of the masticatory muscles. AD = anterior digastric muscle, DM = deep masseter, LP = lateral pterygoid muscle, MP = medial pterygoid muscle, MM = maxillomandibular muscle, PD = posterior digastric muscle, PM = posterior masseter, SM = superficial masseter, T = temporal muscle, ZM = zygomaticomandibular muscle.

TABLE 1

Areas of origin and insertion of the masticatory muscles in *Pedetes capensis*.

Muscle	Origin	Insertion
Masseter-complex		
M. masseter superficialis	aponeurosis of origin lateral surface of the zygomatic process of the maxillary bone	aponeurosis of insertion lateral and medial side of the angular process
M. Masseter profundus	medial aponeurosis of origin lateral surface of the zygoma	aponeurosis of insertion posterior edge of the angular process lateral surface of the lower jaw, dorsal to the anterior and posterior masseteric ridges
M. masseter posterior	lateral surface of the zygoma	lateral surface and posterior edge of the conylar process
M. maxillomandibularis	aponeurosis of origin maxilla and premaxilla	aponeurosis of insertion
M. zygomaticomandibularis	medial wall of the zygoma	aponeurosis of insertion
M. temporalis	temporal fossa	medial surface of the coronoid process
M. pterygoideus medialis	external aponeurosis pterygoid fossa	aponeurosis of insertion medial wall of the angular process
M. pterygoideus lateralis	lateral surface of the outer pterygoid lamina lateral surface of the maxillary bone	medial surface of the condyloid process articular capsule
M. digastricus		
Anterior part	hyoid	medioventral edge of lower jaw
Posterior part	jugular process	hyoid

Although the upper and lower toothrows lie at an acute angle with the sagittal plane, *Pedetes* is isognathic. It can keep both toothrows in occlusion during propalineal movements of the lower jaw. The upper molars slant outward from the midline and the lower ones inward at an angle of 5°. The premolars and molars are bilobed. These on the maxilla show a buccal valley. This crosses the maxillary teeth almost to the lingual margin, whereas a lingual valley crosses the mandibular teeth equally far. See FRIANT (1963), LAVOCAT and MICHOUX (1966), and WOOD (1962, 1965a) for a detailed description of dental morphology.

Movement profiles

During feeding in the springhare, two cyclic events, namely ingestion and mastication (Fig. 2) can be distinguished (OFFERMANS and DE VREE, 1990). During the ingestion cycles, the mandibular movement profile depends on the type of food ingested. During ingestion of groundnut, the lower jaw rotates with a single degree of freedom and little or no condylar translation occurs. Ingestion of rolled oats involves mandibular rotation as well as translation. During the closing stage, the jaw rotates upward and the condyle simultaneously moves backward. A marked forward translation coincides with the end of the opening stage and the beginning of the closing stage.

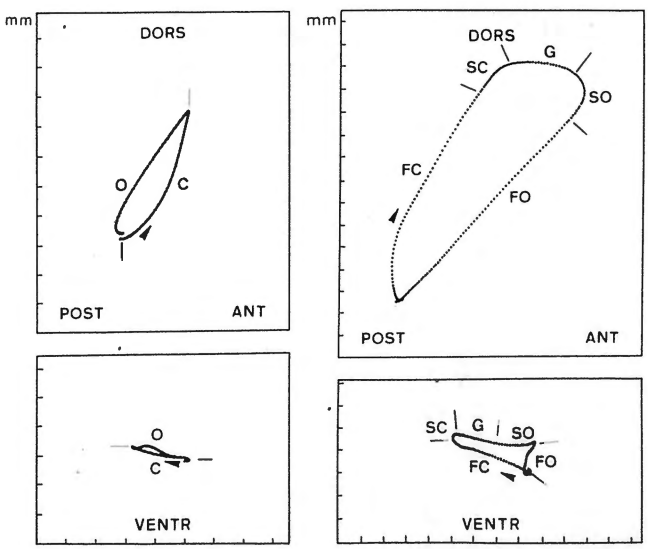

Fig. 2. — *Pedetes capensis*. Mean movement profiles of the mandibular incisor (above) and condyle (below) during ingestion (left, N = 30) and mastication (right, N = 54) of rolled oats. Data derived from cineradiographic films taken at 50 fps in lateral projection. Arrows indicate direction of movement. C = closing, FC = fast-closing stage, FO = fast-opening stage, G = grinding stage, O = opening, SC = slow-closing stage, SO = slow-opening stage.

Movement profiles during mastication are essentially the same for all food types investigated. *Pedetes* shows a bilateral, propalineal mastication cycle. This cycle can be divided into a fast- and slow-closing stage, a grinding stage, and a slow- and fast-opening stage. Fast closing of the mouth is established by an upward rotation of the jaw, accompanied by a backward translation of the condyle. The upward movement of the jaw is slowed when tooth-food-tooth contact is reached, whereas at that moment, the jaw slowly shifts forward. The forward movement of the condyles coincides with the beginning of the slow-closing stage during mastication of rolled oats. During mastication of groundnut, this forward movement starts at the end of the slow-closing stage, which results in a prolonged activity in some of the muscles during the closing stages. During the grinding stage, the lower jaw shifts forward with the molar teeth in full occlusion on both sides simultaneously. This forward movement is accompanied by a small downward rotation during the slow-opening stage. Fast opening of the jaw is a downward rotation with a single degree of freedom.

Activity in single muscles

Ingestion

The activity patterns of the masticatory muscles demonstrate a completely different ingestion for rolled oats and groundnut (Fig. 3). Rolled oats are not bitten during ingestion. Instead, the lower jaw shovels in the small food particles. Ingestion of groundnut involves biting off of small pieces. The lower incisors move more anteriorly and dorsally to grasp the food against the upper ones.

Whereas the temporal muscles fire at a level of 5 % or less, halfway into the closing stage during the ingestion of rolled oats, they are inactive during the ingestion ofgroundnut.

The maxillomandibular muscles show hardly any activity during the ingestion of rolled oats. However, during ingestion of groundnut the level of firing reaches 100 % early in the closing stage. This activity drops rapidly and ceases before the end of the stage. After the end of the closing phase, the activity increases again and reaches its maximum at the beginning of the next closing stage. The activity pattern of the zygomaticomandibular muscles resembles that of the maxillomandibular ones. During ingestion of rolled oats, they show no activity. During ingestion of groundnuts, firing starts halfway the opening stage to reach its maximum at a 50-60 % level at the beginnning of the closing stage. However, activity decreases rapidly and ceases halfway into this stage.

The activity of the masseter muscles during the ingestion of rolled oats does not exeed the 5 % level during half of the closing stage. In contrast, firing reaches the 20 % level at the beginning of the closing phase during ingestion of groundnuts. The activity slowly decreases towards the end of this stage. Firing resumes before the end of the opening stage. The posterior masseter controls condylar movement. As there is little or no condylar translation during the ingestion of groundnut, it then shows hardly any activity. During the ingestion of rolled oats, this activity (10-

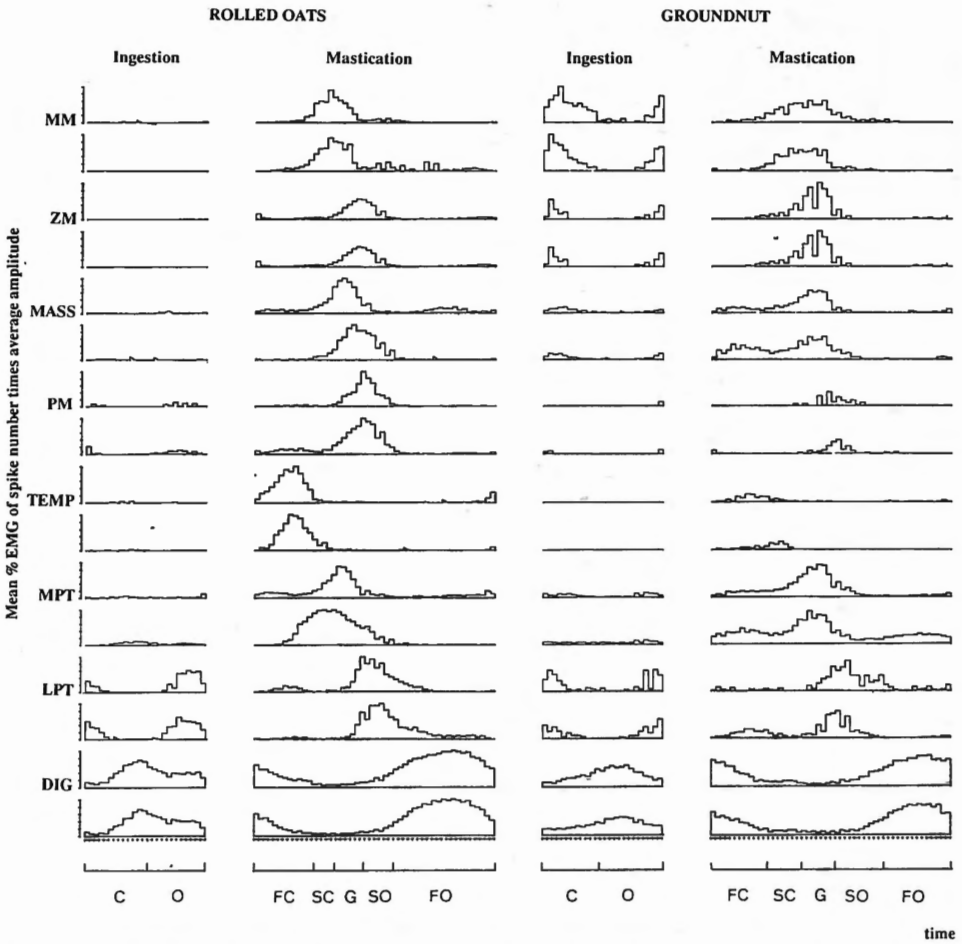

Fig. 3. — *Pedetes capensis.* Overall pattern of muscle activity during the ingestion and mastication of rolled oats and groundnut. The EMG activities are expressed as the mean % distributions of the product of spike number times amplitude. Activities of right (above) and left (below) muscle of each pair is given. C = closing stage, DIG = anterior digastric, FC = fast-closing stage, FO = fast-opening stage, G = grinding, LPT = lateral pterygoid, MASS = superficial masseter, MM = maxillomandibularis, MPT = medial pterygoid, O = opening stage, PM = posterior masster, SC = slow-closing stage, SO = slow-opening stage, TEMP = temporalis, ZM = zygomaticomandibularis.

20 % level) coincides with the forward movement of the condyle at the beginning of closing and during the opening stage.

The activity patterns of the lateral pterygoids resemble those of the posterior masseters. The former fire at a 50 % level at the beginning of the closing stage and reach a 60 % level during the opening stage. Although there is little or no condylar translation during the ingestion of groundnut, the lateral pterygoids show a similar

activity pattern during the ingestion of this type of food. For both food types the medial pterygoids show a continuous low level activity (always less than 15 %).

The digastric muscle acts to open and retract the jaw. It is mainly active during the opening stage. However, the activity starts to build up during the closing stage, increasing rapidly during its second half and reaching peak activity at the closing-opening transition. During the opening stage activity gradually diminishes. The activity pattern is essentially the same for both food types. However, ingestion of rolled oats coincides with a higher activity level (70-80 %) than ingestion of groundnut (50-60 %).

Mastication

Not only the movement patterns of the lower jaw but also the activity sequences of the masticatory muscles are similar for the different food types investigated (Fig. 3). However, they considerably differ in their activity levels and some muscles are active for different periods. The following description is based on electromyography during mastication of rolled oats. Whenever marked differences occur during mastication of groundnut, these are mentioned.

The temporales start to fire at the end of fast opening and are mainly active during fast closing. Muscle activity increases rapidly and reaches a 100 % level (only 20-30 % for groundnut) halfway into fast closing. Activity then drops to 5-10 % during slow closing and ceases.

During fast-closing, the activity of the maxillomandibular muscles is low but increases rapidly towards the end of this stage. During slow-closing, these muscles reach peak activity at a 90-95 % level. Then, firing drops rapidly. It reaches a 10-20 % level at the end of the grinding stage and continues till the end of slow-opening. During ingestion of groundnut, the activity of the maxillomandibularis only reaches 60 %. However, firing remains at this level almost till the end of the grinding stage, then drops rapidly to 10 to 20 % and decreases slowly towards the end of slow-opening. The zygomaticomandibular muscle becomes active halfway into fast-closing. Firing reaches 10 to 20 % during this stage. Activity slowly increases during slow-closing to reach a maximum during grinding at a 60 % level (100 % for groundnut). After reaching maximum activity, firing decreases rapidly.

Whenever rolled oats are masticated, firing of the masseter reaches 10 % during fast-closing. During slow-closing, muscular activity increases rapidly and reaches a 100 % level at the end of this stage. During the grinding stage, the activity drops to 5 %, and this continues during the first half of the subsequent slow-opening stage. In mastication of groundnut firing is much more active (40-50 %) during fast-closing. However, the maximum activity reached at the end of slow-closing stays below the 70 % level. In contrast to the activity pattern for rolled oats, this maximum activity is maintained during most of the grinding stage, after which firing diminishes till halfway into slow-opening.

Reduction of rolled oats involves an activity of the posterior masseter that is similar to that of the masseter muscle. However, during the reduction stages (slow-

closing, grinding and slow-opening), the activity of the posterior masseter builds up more slowly, so that it only reaches the 100 % activity level halfway through the grinding stage. This instance coincides with the forward translation of the lower jaw. During the reduction of groundnut, the posterior masseter also achieves maximal activity coincident with the forward translation of the lower jaw. However, this translation occurs during the grinding stage and the first half of slow-opening. The maximal activity (40 %) occurs at the end of grinding.

During the closing stages, the activity of the lateral pterygoids does not exceed 10 %. Activity increases during the grinding stage and the slow-opening stage, during which the mandible is shifted forward. A maximum (100 % for rolled oats, and 70 % for groundnut) is reached at the grinding slow-opening transition, after which activity diminishes rapidly. Although the medial pterygoids show some activity throughout the entire mastication cycle, firing rapidly increases prior to the forward shift of the lower jaw (the end of fast-closing for rolled oats, and the end of slow-closing for groundnut). They reach their maximum activity in the subsequent stage (100 % for rolled oats, and 90 % for groundnut), and then become inactive.

Both during the reduction of rolled oats and of groundnut, the digastric muscles are maximally active during the fast-opening stage (100 % and 80 % respectively). Firing then diminishes, to reach a minimum at the end of fast-closing. Activity stays low during the subsequent slow-closing and grinding stages, and slowly increases during slow-opening.

Activity patterns

Ingestion

Ingestion of rolled oats does not involve biting, and most muscles have low activity, the lateral pterygoids and the digastrics forming an exception. During the beginning of the closing stage, upward rotation is accompanied by forward translation of the condyle. At that moment the digastrics show low and decreasing activity, whereas that of the posterior masseters is weak, and the lateral pterygoids fire at 50 %. Early in the closing stage, the condyles reverse their movement and the posterior masseters cease firing; also the activity in the lateral pterygoids diminishes rapidly. At the same time, the masseter muscles are weakly active. However, this activity ceases halfway the closing stage. At this time the temporal muscles start to fire. Meanwhile, the medial pterygoids and digastrics are increasingly active and are most active at the closing-opening transition. During the opening stage, these muscles remain active at a reduced level. Opening of the mouth is accompanied by a forward translation of the condyles. The posterior masseters and the lateral pterygoids become increasingly active during this stage, whereas the temporal muscles become silent.

During the ingestion of groundnuts, muscle activities are much higher than during the ingestion of rolled oats. The mouth is closed and opened by rotation at the temporomandibular joint with the condyles in their most anterior position. Early in the closing stage, the muscles of the masseteric complex show a peak activity. The maxillomandibular muscles are especially active (100 %), but the zygomatico-

mandibular muscles reach 50 % of maximal activity. Although there is little or no condylar translation during the ingestion of groundnut, during this stage the posterior masseters and lateral pterygoids are highly active. The medial pterygoids are weakly active throughout the entire cycle. However, the temporal muscles are inactive. At the beginning of the cycle, the activity of the digastrics is low, but it increases toward the end of the closing stage. At the same time, the activity of the lateral pterygoids and the muscles of the masseteric complex dimishes. It ceases at the end of this stage. During the first half of the opening stage, the activity of the digastric muscles peaks. Whereas their activity diminishes during the second half of the opening stage, the activity of the muscles of the masseteric complex and the lateral pterygoids increases.

Mastication

During mastication, the condyles lie in their most forward position at maximum opening of the mouth. Fast closure of the mouth is accompanied by a backward translation of the condyles. At the beginning of fast-closing, the digastrics show a decreasing activity. The activity of the muscles of the masseteric complex is very low, except for the superficial masseters, as well as the medial pterygoids, during the mastication of groundnut. The first muscles that become highly active are the temporales which reach peak activity halfway into fast-closing. Decreasing activity in the temporales generally coincides with low level activity in the lateral pterygoids. These bursts of activity stop before the reversal of condylar translation (beginning of slow-closing for rolled oats, and near the end of slow-closing for groundnut). When tooth-food-tooth is reached (beginning of slow-closing) the upward rotation of the mandible slows and the jaw slowly shifts forward. The muscles of the masseteric complex and the medial pterygoids become increasingly active. The maxillomandibular muscles reach their activity peak during slow-closing, closely followed by subsequent activity peaks in the medial pterygoids (closely after the beginning of the forward movement of the condyles), the masseter muscles, and the zygomaticomandibular muscles. While their activity level decreases toward the end of the grinding stage, the posterior masseters and the lateral pterygoids become increasingly active, reaching peak activity halfway through the grinding stage and at the transition between the grinding and slow-open stages respectively. As a result the mandible is shifted forward, with the molar teeth in full occlusion. This motion continues during slow-opening, accompanied by a small downward rotation of the lower jaw about the temporomandibular joint. While activity in the posterior masseters and lateral pterygoids decreases, activity in the digastrics rapidly increases, to reach a maximum halfway fast-opening. During this stage, low level activity may occur in the medial pterygoids. The condyles stay in their most forward position throughout the fast-opening stage.

Physiological cross section

Physiological cross sections are customarily assumed to provide an estimate of the maximal force the muscle can produce. However, recent analyses suggest that the aggregate mass provides a better basis of comparison (GANS and DE VREE,

1987). The muscle weights, fiber lengths and physiological cross sections of the masticatory muscles are given in table 2. These data show the importance of the muscles of the masseter-complex. Both mass and physiological cross section are largest for the zygomaticomandibularis, the masseter and the maxillomandibularis. The data suggest that the increased size and complexity of the masseter-complex is at the expense of the temporal muscle, which has the smallest physiological cross section and mass of all masticatory muscles in *Pedetes*. Whereas the medial pterygoid is relatively large, the lateral pterygoids and temporal muscles have a comparable physiological cross section.

TABLE 2

Wet weights (mg), fiber lengths (mm), and physiological cross sections (g wet/cm^2) of the masticatory muscles of *Pedetes capensis*.

Muscles	Wet Weight	Fiber length		Cross section
		Mean	Range	
Maxillomandibularis	3208.6	1.43	1.21-1.68	2.244
Zygomaticomandibularis	1911.2	0.81	0.72-0.93	3.360
Masseter	4126.9	1.43	1.12-1.66	2.886
Posterior masseter	398.9	0.61	0.54-0.71	0.654
Temporalis	418.2	0.81	0.77-0.91	0.516
Lateral pterygoid	378.6	0.73	0.64-0.78	0.519
Medial pterygoid	1163.7	1.03	0.86-1.15	1.130
Digastricus	408.0	0.75	0.61-0.89	0.544

The effective force produced by the masticatory muscles not only reflects the theoretical maximum but also the three-dimensional angle of insertion, which is subject to considerable change during rotation of the jaws. Even more important (and customarily ignored) is the range of muscle shortening relative to the length-tension curve (GANS and DE VREE, 1987; WEIJS and VAN RUIJVEN, 1990). As this information is here lacking (it would cost too many specimens to generate it) we provide calculations of origin-insertion lengths, angles with the antero-posterior, vertical and transverse axes, vector components along these axes and moment arms about the horizontal, vertical and bicondylar axes. These are established for 50 jaw positions during the mastication of rolled oats and groundnut, and for 25 positions during the ingestion of both types of food. Table 3 gives these data for the different masticatory muscles at occlusion during ingestion of rolled oats. Table 4 and Figure 4 give it for the equivalent position during their mastication. The difference reflects the changed direction of action by some of the muscles.

For instance during ingestion, the lower jaw is shifted forward and the mouth is slightly more opened than during mastication. The forward component of the

TABLE 3. — *Pedetes capensis*. Origin-insertion length in mm (l), angles relative to X(a), Y(b), and Z(c) axes, vector components along the horizontal (X), vertical (Y), and transverse (Z) axes, and moment arms around the Z, Y, and X axes (MXY, MXZ and MYZ for the right and MXY, MXZ′, and MYZ′ for the left condyle) of the masticatory muscles for the lower jaw in the most closed position during the ingestion of rolled oats.

Muscle	l	d	a	b	c	x	y	z	MXY	MXZ	MYZ	MXZ′	MYZ′
Maxillomandibularis	54.53	43.84	85.36	4.76	88.95	0.08	1.00	0.02	33.14	1.96	9.55	37.05	30.45
Zygomaticomandibularis	14.63	26.87	107.75	43.35	127.96	−0.30	0.73	−0.62	10.04	14.54	8.22	32.30	38.76
Masseter muscle	24.07	25.55	32.41	57.62	88.81	0.84	0.54	0.02	24.95	1.28	2.42	38.71	37.55
Posterior masseter	6.73	4.92	37.30	96.66	126.50	0.80	−0.12	−0.59	4.47	0.83	4.63	31.20	3.02
Temporal muscle	32.47	20.95	126.01	36.14	92.65	−0.59	0.81	−0.05	0.57	0.57	0.51	39.31	39.42
Lateral pterygoid	17.69	3.39	42.99	122.29	64.92	0.73	−0.53	0.42	1.07	2.45	1.39	32.16	29.95
Medial pterygoid	22.51	26.68	68.69	28.57	71.88	0.36	0.88	0.31	6.67	6.80	14.26	23.60	23.45
Digastricus	46.68	45.01	143.30	55.81	101.74	−0.80	0.56	−0.20	20.47	11.52	2.67	27.25	34.94

TABLE 4. — *Pedetes capensis*. Origin-insertion length in mm (l), angles relative to X(a), Y(b), and Z(c) axes, vector components along the horizontal (X), vertical (Y), and transverse (Z) axes, and moment arms around the Z, Y, and X axes (MXY, MXZ and MYZ for the right and MXY, MXZ′, and MYZ′ for the left condyle) of the masticatory muscles for the lower jaw in the most closed position during the mastication of rolled oats.

Muscle	l	d	a	b	c	x	y	z	MXY	MXZ	MYZ	MXZ′	MYZ′
Maxillomandibularis	50.57	43.83	81.47	8.61	88.87	0.15	0.99	0.02	37.90	4.36	9.51	35.29	30.48
Zygomaticomandibularis	12.04	26.87	90.00	48.37	138.37	0.00	0.66	−0.75	21.00	21.00	8.64	21.00	35.21
Masseter muscle	26.62	25.54	25.62	64.40	88.92	0.90	0.43	0.02	25.48	1.25	2.48	38.74	37.49
Posterior masseter	12.22	4.92	19.72	94.70	109.11	0.94	−0.08	−0.33	4.31	0.66	4.37	37.12	5.34
Temporal muscle	28.26	20.94	119.7	29.89	93.04	−0.50	0.87	−0.05	4.47	0.00	0.55	39.77	39.38
Lateral pterygoid	22.95	3.39	31.83	114.45	70.93	0.85	−0.41	0.33	1.13	2.62	1.43	34.71	29.97
Medial pterygoid	24.11	26.68	61.51	33.95	73.12	0.48	0.83	0.29	12.96	5.13	14.25	29.04	25.50
Digastricus	43.62	45.01	144.47	57.40	102.58	−0.81	0.54	−0.22	16.49	9.99	2.18	28.65	34.90

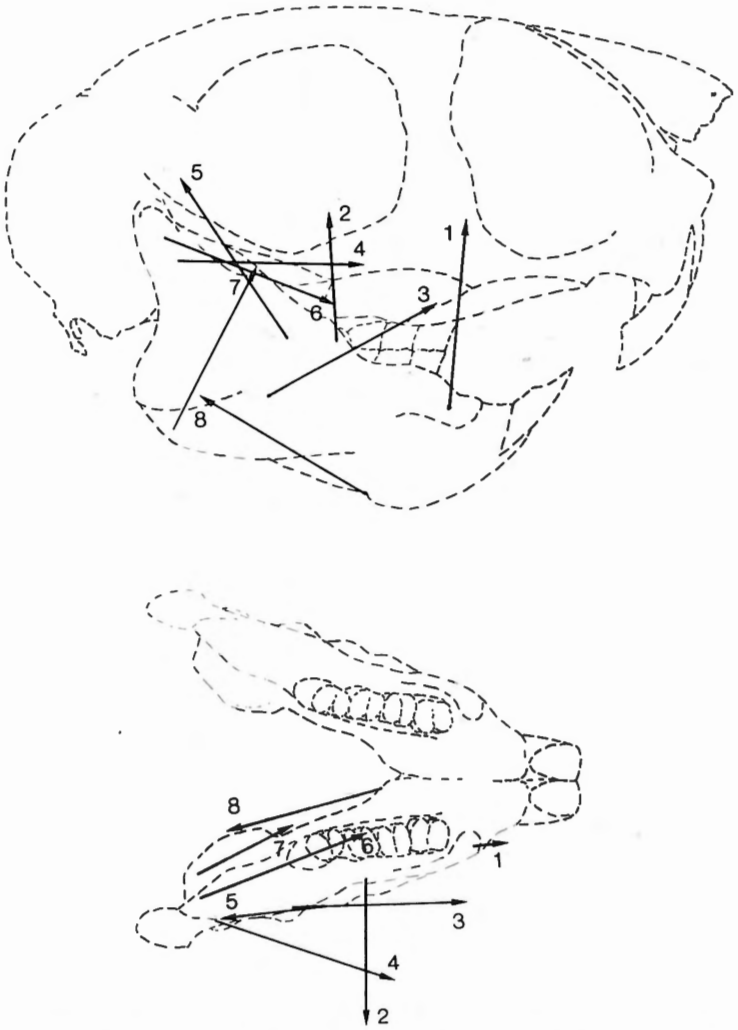

Fig. 4. — *Pedetes capensis*. Working lines of the masticatory muscles during the mastication of rolled oats with the lower jaw in the most closed position. 1 = Maxillomandibularis, 2 = Zygomaticomandibularis, 3 = Masseter, 4 = Posterior masseter, 5 = Temporalis, 6 = Lateral pterygoid, 7 = Medial pterygoid, 8 = Digastric muscle.

muscles of the masseter-complex (except for the posterior masseter) and the medial pterygoids decreases, and may even reverse to a backward component (zygomaticomandibular muscles). The vertical component on the other hand, increases, whereas the transverse component remains unchanged. The forward component of the pull of the posterior masseter and lateral pterygoids, both protractors of the lower jaw, decreases due to the forward position of the jaw, whereas their upward component increases as the mouth is more opened. Whereas the changes in the directional pull

TABLE 5. — *Pedetes capensis*. Changes in the origin-insertion length (l) and vector components along the horizontal (X), vertical (Y), and transverse (Z) axes during the different stages of groundnut ingestion. a-beginning closing stage ; b-halfway closing ; c-closing-opening transition ; d-halfway opening.

	l				x				y				z			
Muscle	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
Maxillomandibularis	57.35	55.84	54.66	56.05	0.10	0.07	0.05	0.07	1.00	1.00	1.00	1.00	0.02	0.02	0.02	0.02
Zygomaticomandibularis	15.90	15.56	15.41	15.60	−0.28	−0.35	−0.41	−0.34	0.77	0.74	0.70	0.74	−0.57	−0.58	−0.58	−0.58
Masseter muscle	24.79	23.64	22.59	23.81	0.84	0.83	0.82	0.83	0.55	0.56	0.57	0.56	0.02	0.02	0.02	0.02
Posterior masseter	5.64	5.51	5.28	5.54	0.69	0.68	0.64	0.68	−0.12	−0.13	−0.14	−0.13	−0.71	−0.73	−0.76	−0.72
Temporal muscle	33.42	33.51	33.68	33.49	−0.58	−0.60	−0.62	−0.60	0.81	0.80	0.78	0.80	−0.04	−0.04	−0.04	−0.04
Lateral pterygoid	16.46	16.44	16.31	16.44	0.68	0.68	0.67	0.68	−0.57	−0.57	−0.58	−0.57	0.46	0.46	0.46	0.46
Medial pterygoid	22.33	22.11	21.89	22.15	0.39	0.34	0.29	0.35	0.87	0.89	0.90	0.88	0.31	0.32	0.32	0.32
Digastricus	46.22	47.23	48.15	47.09	−0.77	−0.80	−0.81	−0.79	0.60	0.57	0.55	0.58	−0.21	−0.20	−0.20	−0.20

TABLE 6. — *Pedetes capensis*. Changes in the origin-insertion length (l) and vector components along the horizontal (X), vertical (Y), and transverse (Z) axes during the different stages of groundnut mastication. a-beginning fast-closing stage ; b-beginning slow-closing ; c-beginning grinding stage ; d-end grinding stage ; e-beginning fast-opening.

	l					x					y					z				
Muscle	a	b	c	d	e	a	b	c	d	e	a	b	c	d	e	a	b	c	d	e
Maxillomandibularis	59.85	54.74	53.17	52.39	55.14	0.13	0.08	0.06	0.03	0.04	0.99	1.00	1.00	1.00	1.00	0.02	0.02	0.02	0.02	0.02
Zygomaticomandibularis	16.74	14.76	14.36	14.61	15.81	−0.21	−0.31	−0.37	−0.45	−0.43	0.82	0.73	0.69	0.65	0.70	−0.54	−0.61	−0.63	−0.62	−0.57
Masseter muscle	26.19	24.05	23.01	21.68	22.37	0.84	0.84	0.84	0.82	0.81	0.54	0.54	0.54	0.57	0.59	0.02	0.02	0.02	0.02	0.02
Posterior masseter	5.38	6.57	6.53	5.77	4.87	0.66	0.78	0.78	0.70	0.55	−0.11	−0.12	−0.13	−0.15	−0.15	−0.74	−0.61	−0.61	−0.69	0.82
Temporal muscle	33.63	32.60	32.52	33.12	34.13	−0.55	−0.59	−0.61	−0.64	−0.63	0.83	0.81	0.79	0.77	0.78	−0.04	−0.05	−0.05	−0.05	−0.04
Lateral pterygoid	16.02	17.53	17.60	16.91	15.79	0.66	0.73	0.73	0.70	0.65	−0.59	−0.54	−0.54	−0.56	−0.60	0.47	0.43	0.43	0.44	0.48
Medial pterygoid	22.40	22.48	22.24	21.85	21.74	0.45	0.36	0.32	0.25	0.28	0.84	0.88	0.89	0.91	0.91	0.31	0.31	0.31	0.32	0.32
Digastricus	44.91	46.56	47.54	48.76	48.79	−0.74	−0.80	−0.82	−0.84	−0.81	0.64	0.56	0.54	0.51	0.55	−0.21	−0.20	−0.20	−0.19	−0.20

of the digastrics are relatively small, the pull of the temporal muscles shows an increased backward and decreased upward component.

During mastication, the maxillomandibular muscle acts upward, and has a small forward and inward component. The zygomaticomandibular muscle also shows a mainly upward directed pull, but has no forward component, whereas the transverse component is directed outward. In the masseter muscle, the vertical component is the largest. It also shows an upward and small inward component, as does the maxillomandibular muscle. Starting from their area of origin, the muscle fibers of both the posterior masseters and the lateral pterygoids run in a dorsocaudal direction. Therefore, the direction of their pull is forward and downward. Whereas the transverse component of the lateral pterygoids is directed inward, the posterior masseters pull outward. The gross directional pull of the temporal and digastric muscles is upward and backward, with a small outward component, whereas that of the medial pterygoid resembles that of the maxillomandibular muscle.

Tables 5 and 6 show the changes in the length of the muscles, and in the direction of their working lines for respectively ingestion of groundnut and for their mastication.

Forces

The force applied to the lower jaw during ingestion and mastication has been calculated by vectorial addition of the maximal forces estimated for the individual muscles. The instantaneous force of the muscle has been estimated by multiplying the value of % EMG with the physiological cross section (WEIJS and DANTUMA, 1981 ; DE GUELDRE and DE VREE, 1990), (Fig. 5).

During the ingestion of groundnut, the lower jaw rotates with a single degree of freedom. During the ingestion of rolled oats, this rotation is accompanied by a translation. The ingestion of oats does not involve biting, thus the resultant forces then are only 10 % of those during the ingestion of groundnut.

The ingestion cycle of rolled oats is divided into closing and opening stages. Early in the closing stage the horizontal component (X) is protractive (Fig. 5), whereas the vertical component (Y) is close to zero : hence the condyles move forward. Throughout the entire cycle, the transverse components (Z) generated by the ipsilateral, contralateral, and resultant forces are zero. Backward shift of the lower jaw is achieved by an increase of the upward and retractive components of the retracting resultants. These reach their maximum before the end of closing and decrease during opening. During the second half of the opening stage, the resultant force is protractive only.

During the ingestion of groundnut, the resultant is large and upward at the beginning of the closing stage, as well as relatively small and anteriorly directed. Both components decrease slowly, to reach their minimum at the end of the closing stage. At the start of closing, the muscles of each side generate a minor outwardly directed component, but those of the two sides cancel each other. During the first half of the opening stage, the resultant force is upward and retractive. The upward

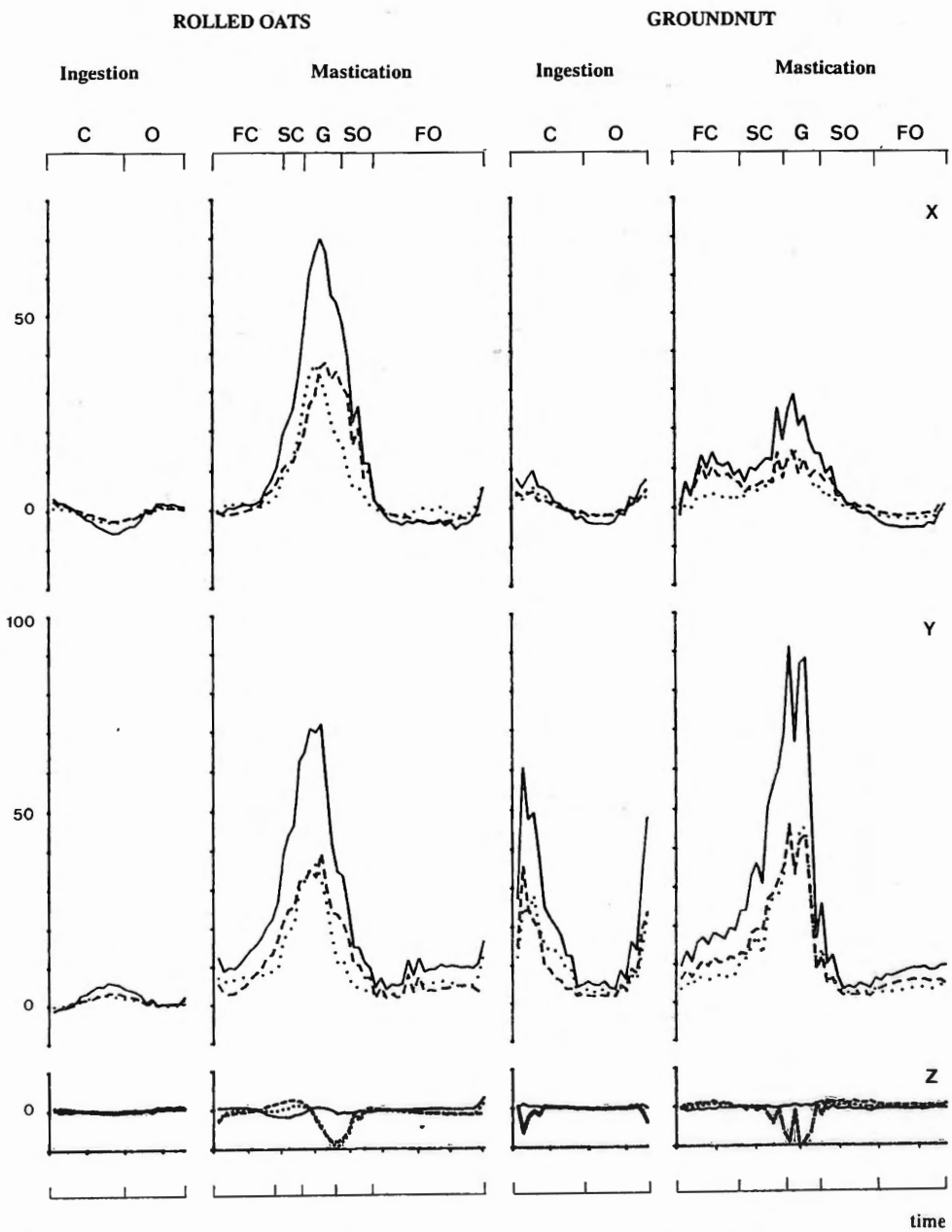

Fig. 5. — *Pedetes capensis*. Estimates of the horizontal (X), vertical (Y), and transverse (Z) components of the resultant force during ingestion and mastication of rolled oats and groundnut. Force estimates are expressed in kgf if an absolute force of 10 kgf/cm^2 is accepted. Solid lines = bilateral resultant force, dashed line = resultant of right side muscles, dotted line = resultant of left side muscles.

component increases significantly thereafter as the horizontal component becomes protractive.

The horizontal component of the resultant muscular force is protractive during the closing stages, the grinding stage and the slow-opening stage in a mastication cycle. At the start of closure, this component is absent during feeding on rolled oats. The component increases rapidly at the end of fast-closing, and reaches a maximum at the beginning of the grinding stage. The protractive component decreases rapidly toward the end of slow-opening. During the mastication of groundnut, the protractive component appears at the beginnning of fast-closing, but reaches a much lower maximum during the grinding stage. The horizontal component of the resultant force during the fast-opening stage is retractive for both food types.

The vertical component is similar for rolled oats and groundnut. It is directed upward throughout the entire cycle. During fast-closing, it is relatively low, but then increases rapidly to reach a maximum at the beginning of the grinding stage. Thereafter it decreases rapidly to reach a minimum halfway slow-opening (groundnut) or at the end of this stage (rolled oats). During the fast-opening stage, the upward component slowly increases.

During the mastication cycle, there usually is no net transverse component. However, this component is relatively large and directed outward during the grinding stage. As the forces are similar on both sides and act in opposite directions, the net effect is zero.

Torques

The changing proportions of the protractive, adductive and transverse components of the resultant force change the rotational forces about the bicondylar, vertical and horizontal axis. Figure 6 gives the moments around the three axes. Moments are calculated using the right condyle as centre of rotation, the X-axis directed to the snout, the Y-axis to the top of the skull and the Z-axis directed medially. During closing, the moment about the bicondylar axis is positive and negative during opening. In a mastication cycle, the moment increases during fast- and slow-closing, and reaches a peak value at the beginning of the grinding stage. It then decreases toward the end of slow-opening (groundnut) or halfway through this stage (rolled oats). At the end of slow-opening and during fast-opening the moment around the bicondylar axis is slightly negative. When rolled oats are ingested, the value stays close to zero throughout the entire cycle. During ingestion of groundnut, the moment peaks early in the closing stage. It then decreases, becoming negative during the opening stage.

The moment around the Y-axis is generally low in all cycles studied. During mastication, it is slightly positive in the first half of fast-closing and during fast-opening. A negative peak occurs at the end of slow-closing (rolled oats) or at the beginning of the grinding stage (groundnut). Thus, during the reduction stages (slow-closing, grinding and slow-opening), both lower jaws tend to be rotated

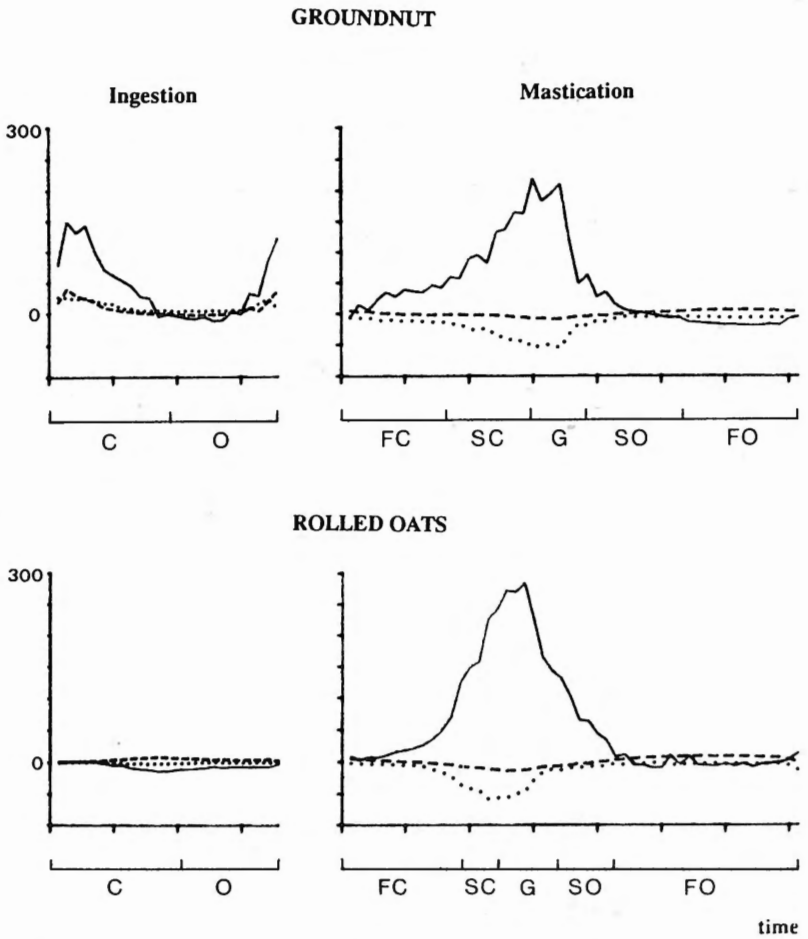

Fig. 6. — *Pedetes capensis*. Estimates of the moments around the transverse (Z, solid line), vertical (Y, dashed line), and horizontal (X, dotted line) axis, with the right condyle as the centre of rotation. Moments are expressed in kgf.m if an absolute force of 10 kgf/cm^2 is accepted.

laterally. During the ingestion of groundnut, the moment around the Y-axis is relatively large, and tends to pull the condyles medially.

The moment around the X-axis is negative in all cycles, except in the ingestion cycle of rolled oats. The positive values reflect the dominant activity of the maxillo-mandibular and zygomaticomandibular muscles and the low activity of the medial pterygoids. The peak negative values of moments around the X-axis coincide with peak negative values around the Y-axis.

TABLE 7

Pedetes capensis. Estimates of the maximal amplitude of the bite force components (Rx, Ry) at the incisor, and the components of the joint reaction forces (rx, ry) at the condyles during ingestion of rolled oats and groundnut. Reaction forces at left and right condyle are assumed to be equal. Forces are in kgf if an absolute force of 10 kgf/cm^2 is accepted.

		Rx	Ry	rx	ry
Rolled oats	Closing stage	1.74	1.00	1.09	−3.10
		2.52	0.82	1.03	−2.95
		2.82	0.92	1.24	−3.53
		3.42	1.06	1.19	−3.41
	Opening stage	3.38	0.98	1.13	−3.23
		2.78	0.82	0.92	−2.64
		2.24	0.86	0.85	−2.43
Groundnut	Closing stage	1.82	−10.42	−1.72	−4.92
		−2.00	−8.96	1.56	−4.45
		−2.52	−3.78	1.53	−4.37
		−2.32	−3.30	1.59	−4.53
	Opening stage	1.34	0.24	0.78	−2.23
		0.32	0.04	0.86	−2.46
		1.76	0.20	0.96	−2.77

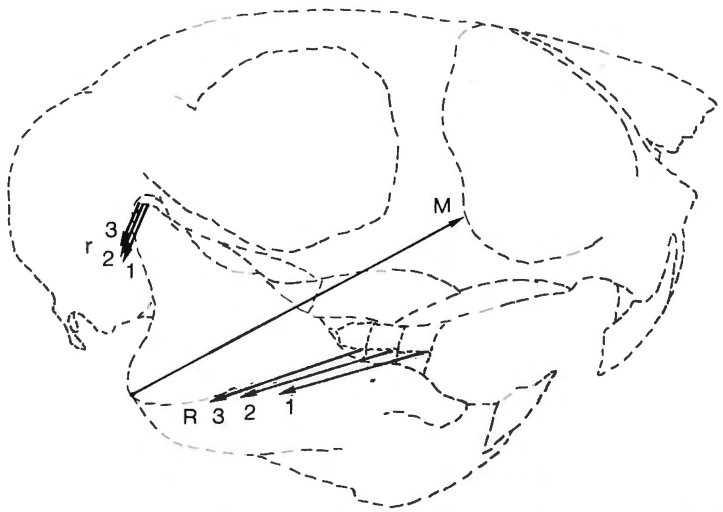

Fig. 7. — *Pedetes capensis*. Resultant muscular force (M), bite force (R), and joint reaction forces (r) for three different bite points during the mastication of rolled oats. 1 = premolar biting, 2 = first molar biting, 3 = second molar biting. Forces are in kgf if an absolute force of 10 kgf/cm^2 is accepted.

TABLE 8

Pedetes capensis. Estimates of the maximal amplitude of the bite force components (Rx, Ry) at the premolar, the first and second molar, and the components of the joint reaction forces (rx, ry) at the condyles during mastication of rolled oats and groundnut. Reaction forces at left and right bite point and condyle are assumed to be equal. Forces are in kgf if an absolute force of 10 kgf/cm^2 is accepted.

		Rx	Ry	rx	ry
Rolled oats	Premolar	−29.71	−18.23	−3.50	−10.00
		−23.70	−9.09	−2.86	−8.18
		−17.34	−6.21	−2.22	−6.33
	First molar	−30.51	−20.53	−2.70	−7.70
		−24.09	−10.21	−2.47	−7.06
		−17.60	−6.95	−1.96	−5.59
	Second molar	−31.29	−22.75	−1.92	−5.48
		−24.47	−11.29	−2.09	−5.98
		−17.85	−7.66	−1.71	−4.88
Groundnut	Premolar	−2.81	−18.20	−5.64	−16.10
		−8.82	−17.60	−5.50	−15.70
		−4.17	−23.10	−7.32	−20.90
		−5.04	−3.44	−1.69	−4.83
	First molar	−3.47	−20.1	−4.98	−14.2
		−9.47	−19.4	−4.85	−13.8
		−5.00	−25.5	−6.49	−18.6
		−5.17	−3.82	−1.56	−4.45
	Second molar	−4.09	−21.8	−4.36	−12.5
		−10.1	−21.2	−4.24	−12.1
		−5.77	−27.7	−5.72	−16.3
		−5.30	−4.18	−1.43	−4.09

Statics

Instantaneous, static reaction forces were calculated at both condyles and the incisors for ingestion cycles, and at both condyles and left and right molars for mastication cycles since *Pedetes* chews at both toothrows simultaneously. Reaction forces were assumed to be equally large at both sides and transverse reaction force components could not be calculated. Reaction forces were calculated for lower jaw positions close to the close-open transition (ingestion cycles) and for the end of slow-closing, grinding and the beginning of slow-opening (mastication cycles), whenever the lower jaw may assumed to be in static condition. The results are given in table 7 (ingestion), and table 8 and Figure 7 (mastication).

During an ingestion cycle, the reaction forces at the incisors are directed vertically, but have a small backward component. Closer to the closing-opening transition, the downward component decreases, whereas the backward component increases to the magnitude of the vertical component. At the condyles, the reaction forces then show a downward component and a smaller forward one. At the beginning of the opening stage, both the vertical and horizontal components of there action forces at the incisors are positive, which seems to have little meaning. As there is no tooth-food-tooth contact, and the lower jaw is accelerating, the forces cannot be calculated assuming static relationships. Also during the ingestion of rolled oats, the calculated reaction forces have little meaning, as tooth-food-tooth contact and therefore a semi-static condition is never established.

At the end of the slow-closing stage of a mastication cycle, the reaction forces at the molar teeth are especially directed downward, but show a considerable backward component. Whenever rolled oats are masticated, the horizontal component may even become dominant. When groundnut is reduced, the horizontal component stays relatively low, whereas the vertical component is large. For groundnut the reaction forces at the condyles are much higher during the grinding stage, than they are during the mastication of rolled oats. For both food types the reaction forces at the condyles are directed downward and backward.

DISCUSSION

General

The incisors of rodents and lagomorphs enable them to reduce a great variety of foods. They are open-rooted and grow throughout life to meet the constant wear of their tips. This incisive specialisation has divided the masticatory apparatus into two separate regions. Gnawing requires a more anterior position of the lower jaw than does mastication. The increased importance of the incisive function has led to an anterior displacement of the masseteric complex, which became the most important muscle group (WOOD, 1955, 1965b, 1985 ; TURNBULL, 1970). Furthermore, the anteriorly open glenoid fossa permits anteroposterior movements. The Rodentia are a highly specialized group (BECHT, 1953 ; SCHUMACHER, 1961 ; TURNBULL, 1970). However, the different lines appear to have evolved in parallel under the influence of similar selective pressures (WOOD, 1959). Although the morphology of their masticatory musculature represents variations of but a few basic patterns, the mechanics of chewing differs remarkably among rodents. In a comparative survey, OFFERMANS and DE VREE (1990) show that dental characteristics greatly influence the movement pattern of the lower jaw. The absence or presence of isognathy, the orientation of the molar teeth, the occlusal pattern, and the position of the incisors in relation to the molars are the most important dental characteristics influencing the movement pattern.

Muscle activities in the Rodentia

Muscle activities in Rodentia have been studied on three members of the Myomorpha (*Rattus,* WEIJS and DANTUMA, 1975 ; *Mesocricetus,* GORNIAK, 1977 ; *Tachyoryctes,* MEIRTE, 1986), and one member of the Hystricomorpha (*Cavia* : DE VREE, 1979 ; BYRD, 1981). The activity of the masseter of *Aplodontia rufa* has been briefly discussed (DRUZINSKY, 1985).

In the Myomorpha, movement of the lower jaw during the grinding stage ranges from purely propalineal (*Rattus* ; WEIJS, 1975) over oblique (*Tachyoryctes*) to purely transverse (*Mesocricetus*). As in *Pedetes*, the masticatory muscles in *Rattus* fire symmetrically. In *Tachyoryctes* and *Mesocricetus*, the shift of the lower jaw toward the balancing side is brought about by the asymmetrical or asynchronous activity of some of the masticatory muscles. Muscle activity is also asymmetric in the hystricognathous, hystricomorphous *Cavia*, whereas the masseter muscles of the primitive *Aplodontia* also fire asymmetrically.

Although the presence of the transverse component in the movement pattern of the lower jaw and the symmetry and synchronization of the muscular activity are correlated, a lot of variation occurs in the sequence of activity. In *Pedetes*, the temporal muscle reaches a peak value halfway into fast-closing, and activity ceases at the end of this stage. During the reduction stages, peak activities are subsequently reached by the maxillomandibular muscles, the medial pterygoids, the masseter muscles (slow-closing), the zygomaticomandibular muscles, the posterior masseters and the lateral pterygoids (grinding stage). This momentum conserving mechanism of successive but overlapping contractions of different muscle groups (KALLEN and GANS, 1972) is also found in *Rattus*. However, none of the muscles reaches peak activity during fast-closing. The temporales are the first muscles to reach a peak activity at the beginning of the reduction stages, followed by the infra-orbital part of the zygomaticomandibular muscle, and the masseters. Both the lateral and medial pterygoids reach a maximum level, shortly after the masseters.

Variable activity is also found in rodents in which the masticatory pattern shows a lateral component. In *Mesocricetus*, the lateral translation at the top of the orbit is produced by retrusor (temporal muscle) activity on the balancing side and protrusor (superficial masseter and medial pterygoid) activity on the working side. Furthermore, the working side anterior digastric and lateral pterygoid fire before those of the balancing side. They thus produce an additional force which drives the lower jaw to the balancing side. During the downstroke, the lower jaw is returned to the midline by the continued activity of the lateral pterygoid of the balancing side. In *Tachyoryctes* and *Cavia*, which chew unilaterally with alternating cycles, the tip of the lower jaw is shifted laterally towards the working side whenever the mouth is maximally opened. The translation of the mandible toward the balancing side in *Tachyoryctes*, is not accomplished by the temporales (which fire symmetrically), but by the asymmetrical activity of the masseters and zygomaticomandibular muscles. During the opening stages, the excursion of the mandible toward the balancing side reflects mainly activity of the working side lateral pterygoid. In *Cavia*, activity in the temporales is asymmetric during the closing stage. Lateral

translation is produced by the balancing side temporal muscle and the working side lateral pterygoid. Simultaneously, the protrusors fire asymmetrically producing a closing force with a significant anteromedial translation. Initially, the mandible returns to midline by asymmetric activity of the digastrics at the start of opening, but this movement is reversed at the end of this stage by the unilateral firing of the lateral pterygoid at the working side.

The search for patterns in the muscular activity of masticating mammals is an ongoing activity. Mammalian mastication has been studied in American opossum (CROMPTON *et al.*, 1977), tenrec (ORON and CROMPTON, 1985), shrews (DÖTSCH and DANTUMA, 1989, bats (*Myotis* : KALLEN and GANS, 1972 ; *Pteropus* : DE GUELDRE and DE VREE, 1988), rabbits (WEIJS and DANTUMA, 1981 ; WEIJS *et al.*, 1989 ; SCHWARTZ *et al.*, 1989), miniature pigs (HERRING, 1976 ; HERRING and SCAPINO, 1973 ; HERRING *et al.*, 1979), pygmy goats (DE VREE and GANS, 1976), cats (GORNIAK and GANS, 1980), dogs (DESSEM, 1989), macaques (MCNAMARA, 1974 ; LUSCHEI and GOODWIN, 1974 ; BYRD and GARTHWAITE, 1981 ; MILLER *et al.*, 1982 ; HYLANDER *et al.*, 1987) and man (AHLGREN, 1966 ; MÖLLER, 1966 ; HANNAM *et al.*, 1977 ; HANNAM and WOOD, 1981 ; STOHLER, 1986 ; WIDMALM *et al.*, 1987). Trends in the currently available data (HIIEMAE, 1978 ; GORNIAK, 1985) are confused by diversity, raising questions about the reality of a generalized sequence of muscular activity. Certainly, no generalized muscle activity pattern is obvious in the Rodentia. This is not surprising. After all, rodents display considerable variation in masticatory pattern in spite of similarity in gross muscular morphology, whereas other rodents belonging to different major groups show similar masticatory patterns.

Biomechanics

GORNIAK (1985, p. 334) commented that understanding the differences in the muscular activity of mammals requires establishment of the time that the muscle is active during its three-dimensional movement pattern, of that portion which is active at the time, of the time at which activity starts and stops relative to the activity of the other muscles, and of the magnitude of the activity relative to movement, food placement, and action of the other muscles. An important question to add to this series is : what is the effect of the activity of a muscle on mandibular movement, and what is the total effect of all muscles ?

The effect of the muscles on the mandible has been studied mainly by static, anatomical analysis of jaw mechanics on representatives of different taxa (KÜHLHORN, 1938 ; ARENDSEN DE WOLFF-EXALTO, 1951 ; BECHT, 1953 ; MAYNARD SMITH and SAVAGE, 1959 ; SCHUMACHER, 1961 ; SCHUMACHER and REHMER, 1962 ; CROMPTON, 1963 ; SCAPINO, 1965 ; TURNBULL, 1970 ; GREAVES, 1978, 1982, 1988). Such studies generally assume that the masticatory muscles simultaneously contract maximally or to the same extent. Furthermore, the components of the resultant force are subject to considerable changes during the jaw movements. Although several biomechanical studies include either mandibular displacements or changing muscular activities (CARLSOÖ, 1952 ; LEMIRE-BELMONT, 1966 ; AHLGREN, 1966 ;

AHLGREN and ÖWALL, 1970 ; HIIEMAE, 1971 ; GASPARD, 1972 ; BARBENEL, 1972 ; HERRING and HERRING, 1974 ; HYLANDER, 1975, 1978 ; BARON and DEBUSSY, 1979, 1980 ; HERRING, 1985), few have combined anatomical data with quantified movement analysis and electromyography (BARBENEL, 1974 ; WEIJS and DANTUMA, 1975, 1981 ; WEIJS *et al.*, 1987 ; OTTEN, 1987 ; DE GUELDRE and DE VREE, 1990).

The three-dimensional model here used to study the jaw mechanics of *Pedetes* is essentially similar to that used in the biomechanical studies on the rat and the rabbit (WEIJS and DANTUMA, 1975, 1981 ; WEIJS *et al.*, 1987) and *Pteropus* (DE GUELDRE and DE VREE, 1990). It estimates the resultant force at any interval of the chewing cycle. In *Pteropus*, the estimated resultant force of the masticatory muscles has a small anterior component early in the opening stage, but this is generally directed posteriorly. During the entire cycle, the resultant force remains close to the midsagittal plane. Rabbits show a resultant force with substantial vertical and forward components. The transverse component is initially directed toward the working side, but decreases to the end of the closing stage. During reduction, it is directed toward the balancing side.

Both *Rattus* and *Pedetes* chew bilaterally, and the resultant muscular force is generally directed upward and forward. Whereas in *Pedetes* the mandibular symphysis is immovable, the mandibular symphysis in *Rattus* allows independent adjustment of the two mandibular sides. As a result, the lower jaw in *Pedetes* stays close to the midsagittal plane, whereas that of *Rattus* incorporates a transverse component that is close to zero during the closing stage. During the reduction stages, the muscles tend to turn the lower border of the mandible inward and press the rami against each other in the symphysis.

Rattus and *Pedetes* chew bilaterally and both require an upward and protractive resultant force during reduction. Muscle (sequence) activity however, shows a lot of differences. Partially, this can be explained by the differences in the relative mass of the masticatory muscles. In *Rattus*, the masseteric complex accounts for 56.6 % of the masticatory muscles, whereas it accounts for 87.5 % in *Pedetes*. Consequently, the relative weight of the temporal muscle is 23.8 % in *Rattus* and 2.9 % in *Pedetes*. However, the proportional differences of the masticatory muscles are accompanied by differences in the components of their working lines (Table 9). In *Rattus*, the temporal muscle is divided in an anterior part with a dominant vertical component and a posterior part with a large retractive component. The temporal muscle of *Pedetes* consists of a single layer the fibers of which lie mainly vertically but do slope forward. Most masticatory muscles are directed more vertically in *Pedetes* than in *Rattus*. The zygomaticomandibular muscle shows no or few anteroposteriorly directed fibers. The masseteric complex on the other hand, shows a distinct posterior part in *Pedetes* that should generate substantial protraction.

These differences in proportion and direction of the working lines of the masticatory muscles, require that the muscles be activated differently in order to produce similar masticatory patterns. Although the overall resultant force shows an upward and protractive component in both species, it derives from quite different

TABLE 9

Comparison of the vector components along the horizontal (X), vertical (Y),and transverse (Z) axes of the masticatory muscles of *Pedetes* and *Rattus* halfway the grinding stage.

	Rattus			*Pedetes*		
	x	y	z	x	y	z
Superficial masseter	0.94	0.28	0.19			
Ant deep masseter	0.57	0.82	−0.05	0.90	0.43	0.02
Post deep masseter	0.64	0.67	−0.37			
Posterior masseter				0.94	−0.08	−0.33
Maxillomandibularis	0.45	0.89	−0.09	0.15	0.99	0.02
Zygomaticomandibularis				0.00	0.66	−0.75
Medial pterygoid	0.52	0.71	0.49	0.48	0.83	0.29
Lateral pterygoid	0.68	−0.25	0.69	0.85	−0.41	0.33
Ant temporalis	−0.24	0.97	0.07	−0.50	0.87	−0.05
Post temporalis	−0.88	0.41	0.24			

forces. In the rat, the resultant force traverses (in sagittal projection) the middle of the molar row and the temporomandibular joint remains unloaded. In *Pedetes*, reaction forces occur at the joint, and the bite force is smaller than the resultant force. *Pedetes* is similar to rabbits and rats, in having reaction forces with vertical and large posterior components. As expected, the reaction force increases as the bite point moves posteriorly, as also noted earlier (GOSEN, 1974; PRUIM *et al.*, 1980; WEIJS *et al.* 1987; DE GUELDRE and DE VREE, 1990).

During biting, *Pedetes* produces relative smaller reaction forces at the temporomandibular joint than *Rattus* in which the incisors counteract the forward component of the resultant, whereas the vertical component is resisted mainly in the temporomandibular joint. *Pedetes* directs the resultant force more vertically during biting. At the incisors, the bite force shows a large vertical component, reaching 68 % of the resultant force applied by the muscles.

Muscle activity differs substantially among those mammals thus far studied. Differences in the proportions and direction of the working lines of their muscles can explain these differences in forms with a similar masticatory pattern. Furthermore, the jaw apparatus has more muscles than degrees of freedom for movement. Therefore, the same force can be generated by different combinations of jaw muscle forces (WEIJS and VAN RUIJVEN, 1990). Variation in muscle activity results in a different masticatory pattern in forms with a similar muscle configuration. Three-dimensional models including data on movement patterns and muscle activity may explain the effects of this variation on the forces which act on the lower jaw (KOOLSTRA and VAN EIJDEN, 1992; VAN EIJDEN *et al.*, 1990). However, these models are scarce and not available for closely related forms.

AKNOWLEDGEMENTS

We thank the Zoo of Blijdorp (Rotterdam, The Netherlands) and the Zoo of Antwerp (Belgium) for providing specimens of *Pedetes*. We also thank Mr. J.R. Pallett for providing the preserved specimen, Dr. C. Gans for comments on an earlier draft of the manuscript, Mrs J. Fret for the technical assistance and Mr. A. Cuylits for preparation of the illustrations. Supported by IWONL-grant 840095 (to M.O.) and FKFO-grants 2.9005.84 and 2.9005.90 (to F.D.V.).

REFERENCES

AHLGREN, J. (1966) — Mechanisms of mastication. A quantitative cinematographic and electromyographic study of masticatory movements in children, with special reference to the occlusion of the teeth. *Acta Odont. Scand.*, **24** (44) : 1-109.

AHLGREN, J. and B. ÖWALL (1970) — Muscular activity and chewing force : A polygraphic study of human mandibular movements. *Archs. oral Biol.*, **15** : 271-280.

ALLEN, H. (1880) — On the temporal and masseter muscles of mammals. *Proc. Acad. Natl. Sci. Philad.*, 1880 : 385-396.

ARENDSEN DE WOLFF-EXALTO, E. (1951) — On differences in the lower jaw of animalivorous and herbivorous mammals (I and II). *Proc. Kon. Ned. Akad. Wet. Amst.*, **54** : 237-246, 405-410.

BARBENEL, J.C. (1972) — The biomechanics of the temporomandibular joint. A theoretical study. *J. Biomech.*, **5** : 251-256.

BARBENEL, J.C. (1974) — The mechanics of the temporomandibular joint — a theoretical and electromyographical study. *J. oral Rehab.*, **1** : 19-27.

BARON, P. and T. DEBUSSY (1979) — A biomechanical functional analysis of the masticatory muscles in man. *Archs. oral Biol.*, **24** : 547-553.

BARON, P. and T. DEBUSSY (1980) — Biomechanical analysis of the main masticatory muscles in the rabbit. *J. Biol. Buccale*, **8** : 265-281.

BECHT, G. (1953) — Comparative biologic-anatomical researches on mastication in some mammals (I and II). *Proc. Kon. Ned. Akad. Wet. (C)*, **56** : 508-527.

BYRD, K.E. (1981) — Mandibular movement and muscle activity during mastication in the guinea pig (*Cavia porcellus*). *J. Morphol.*, **170** : 147-169.

BYRD, K.E. and C.R. GARTHWAITE (1981) — Contour analysis of masticatory jaw movements and muscle activity in *Macaca mulatta*. *Am. J. phys. Anthr.*, **54** : 391-399.

CARLSÖO, S. (1952) — Nervous coordination and mechanical function of the mandibular elevators. An electromyographic study of the activity, and an anatomic analysis of the muscles. *Acta Odont. Scand.*, **10** : 5-132.

CROMPTON, A.W. (1963) — On the lower jaw of *Diarthrognathus* and the origin of the mammalian lower jaw. *Proc. zool. Soc. London*, **140** : 697-753.

CROMPTON, A.W., A.J. THEXTON, G. PARKER and K. HIIEMAE (1977) — The activity of the jaw and hyoid musculature in the Virginian Opossum, *Didelphis virginiana*. *In : The biology ofthe marsupials*. STONEHOUSE, B., and G. GILMORE (eds). New York, Macmillan Press Ltd. : 287-305.

DE GUELDRE, G. and F. DE VREE (1988) — Quantitative electromyography of the masticatory muscles of *Pteropus giganteus* (Megachiroptera). *J. Morphol.*, **196** : 73-106.

DE GUELDRE, G. and F. DE VREE (1990) — Biomechanics of the masticatory apparatus of *Pteropus giganteus* (Megachiroptera). *J. Zool., London,* **220** : 311-332.

DESSEM, D. (1989) — Interactions between jaw-muscle recruitment and jaw-joint forces in *Canis familiaris*. *J. Anat.*, **164** : 101-121.

DE VREE, F. (1979) — Electromyography of the masticatory muscles in guinea pigs. *Am. Zool.*, **19** : 1012 (Abstract).

DE VREE, F. and C. GANS (1976) — Mastication in pygmy goats, *Capra hircus*. *Ann. Soc. r. Zool. Belg.*, **105** : 255-306.

DÖTSCH, C. and R. DANTUMA (1989) — Electromyography and masticatory behavior in shrews (Insectivora). *Progr. Zool.*, **35** : 146-147.

DRUZINSKY, R.E. (1985) — Anatomy and EMG of the masseter of *Aplodontia rufa*. *In* : DUNKER, H.-R., and G. FLEISHER (eds) : *Vertebrate Morphology*, Gustav Fischer Verlag, Stuttgart, New York, *Progr. Zool.*, **30** : 281-283.

FICK, R. (1910) — *Handbuch der Anatomie und Mechanik derGelenke*. G. Fischer, Jena.

FRIANT, M. (1963) — Considérations sur les dents jugales d'un rongeur africain, le *Pedetes*. *Bull. Group. Int. Rech. Sci. stomat.*, **6** : 363-366.

GANS, C. and F. DE VREE (1987) — Functional bases of fiber length and angulation in muscle. *J. Morphol.*, **192** : 63-85.

GANS, C. and G.C. GORNIAK (1980) — Electromyograms are repeatable : Precautions and limitations. *Science*, **210** : 795-797.

GANS, C., F. DE VREE and G.C. GORNIAK (1978) — Analysis of mammalian masticatory mechanisms : Progress and problems. *Zbl. Vet. Med. C., Anat. Histol. Embryol.*, **7** : 226-244.

GASPARD, M. (1972) — Anatomie comparative et fonctionnelle de la musculature masticatrice chez les carnivores. II. Anatomie fonctionnelle. *Mem. Mus. Nat. Hist. nat., Zool.*, **68** : 112-207.

GORNIAK, G.C. (1977) — Feeding in golden hamsters, *Mesocricetus auratus*. *J. Morphol.*, **154** : 427-458.

GORNIAK, G.C. (1985) — Trends in the actions of mammalian masticatory muscles. *Am. Zool.*, **25** : 331-337.

GORNIAK, G.C. and C. GANS (1980) — Quantitative assay of electromyograms during mastication in domestic cats (*Felis catus*). *J. Morphol.*, **163** : 253-281.

GORNIAK, G.C., H. ROSENBERG and C. GANS (1982) — Motoractivity during mastication in the tuatara, *Sphenodon punctatus* (Reptilia : Rhynocephalia). *J. Morphol.*, **171** : 321-353.

GOSEN, A.J. (1974) — Mandibular leverage and occlusion. *J. Prosth. Dent.*, **31** : 369-353.

GREAVES, W.S. (1978) — The jaw lever system in ungulates : a new model. *J. Zool., Lond.*, **184** : 271-285.

GREAVES, W.S. (1982) — A mechanical limitation on the position of the jaw muscles of mammals : the one-third rule. *J. Mammal.*, **63** : 261-266.

GREAVES, W.S. (1988) — The maximum average bite force for a given jaw length. *J. Zool., Lond.*, **214** : 295-306.

HANNAM, A.G., R.E. DE COU, J.D. SCOTT and W.W. WOOD (1977) — The relationship between dental occlusion, muscle activity and associated jaw movement in man. *Archs. oral Biol.*, **22** : 25-32.

HANNAM, A.G. and W.W. WOOD (1981) — Medial pterygoid muscle activity during the close and compressive phases of human mastication. *Am. J. phys. Anthr.*, **55** : 359-367.

HERRING, S.W. (1976) — The dynamics of mastication in pigs. *Archs. oral Biol.*, **21** : 473-480.

HERRING, S.W. (1985) — Postnatal development of masticatory muscle function. *Progr. Zool.*, **30** : 213-215.

HERRING, S.W. and R. SCAPINO (1973) — Physiology of feeding in miniature pigs. *J. Morphol.*, **141** : 427-460.

HERRING, S.W. and S.E. HERRING (1974) — The superficial masseter and gape in mammals. *Am. Nat.*, **108** : 561-576.

HERRING, S.W., A.F. GRIMM and B.R. GRIMM (1979) — Functional heterogeneity in a multipinnate muscle. *Am. J. Anat.*, **154** : 563-576.

HIIEMAE, K.M. (1971) — The structure and function of the jaw muscles in the rat (*Rattus norvegicus* L.). III. The mechanics of the muscles. *Zool. J. Linn. Soc.*, **50** : 111-132.

HIIEMAE, K.M. (1978) — Mammalian mastication : A review of the activity of the jaw muscles and movement they produce inchewing. *In* : P.M. BUTLER and K. JOSEY (eds) *Studies of the Development, Structure and Function of Teeth.* London, Academic Press, pp. 360-398.

HYLANDER, W.L. (1975) — The human mandible : Lever or link ? *Am. J. Phys. Anthr.*, **43** : 227-242.

HYLANDER, W.L. (1978) — Incisal bite force direction in humans and the functional significance of mandibular translation. *Am. J. Phys. Anthr.*, **48** : 1-8.

HYLANDER, W.L., K.R. JOHNSON and A.W. CROMPTON (1987) — Loading patterns and jaw movements during mastication in *Macaca fascicularis* : A bone-strain, electromyographic, and cineradiographic analysis. *Am. J. phys. Anthr.*, **72** : 287-314.

KALLEN, F.C. and C. GANS (1972) — Mastication in the little brown bat, *Myotis lucifugus*. *J. Morphol.*, **136** : 385-420.

KOOLSTRA, J.H. and T.M.G.J. VAN EIJDEN (1992) — Application and validation of a three-dimensional mathematical model of the human masticatory system *in vivo*. *J. Biomechanics*, **25** : 175-187.

KÜHLHORN, F. (1938) — Anpassungserscheinungen am Kauapparat bei ernährungsbiologisch verschiedenen Säugetieren. *Zool. Anz.*, **121** : 1-17.

LAVOCAT, R. and J. MICHOUX (1966) — Interprétation de la structure dentaire des rongeurs africains de la famille des Pedetidae. *C. R. Acad. Sci., Paris*, **262D** : 1677-1679.

LEMIRE-BELMONT, L. (1966) — L'appareil masticateur des Lagomorphes. *D.E.S. Sci. Nat. Fac. Sci. Paris*, 65 pp.

LUSCHEI, E.S. and G.M. GOODWIN (1974) — Patterns of mandibular movement and jaw muscle activity in the monkey. *J. Neurophysiol.*, **37** : 954-966.

MAYNARD SMITH, J. and R.J.G. SAVAGE (1959) — The mechanics of mammalian jaws. *School Sci. Rev.*, **141** : 289-301.

MCNAMARA, J.A., Jr. (1974) — An electromyographic study of mastication in the rhesus monkey (*Macaca mulatta*). *Anat. Rec.*, 193 : 389-402.

MEIRTE, D. (1986) — *Functioneel morfologische studie van het kauwen bij de Afrikaanse molrat Tachyoryctes splendens (Rüppell)*. Unpublished Ph. D. dissert., Univ. Antwerp, 333 pp.

MILLER, A.J., K. VARGERVIK and G. CHIERICI (1982) — Electromyographic analysis of the functional components of the lateral pterygoid muscle in the rhesus monkey (*Macaca mulatta*). *Archs. oral Biol.*, **27** : 475-480.

MÖLLER, E. (1966) — The chewing apparatus. An electromyographic study of the action of the muscles of mastication and its correlation with facial morphology. *Acta Physiol. Scand.* **69** : 1-229.

OFFERMANS, M. and F. DE VREE (1989) — Morphology of the masticatory apparatus in the springhare, *Pedetes capensis* (Forster, 1778). *J. Mammal.*, **70** : 701-711.

OFFERMANS, M. and F. DE VREE (1990) — Mastication in springhares, *Pedetes capensis* : A cineradiographic study. *J. Morphol.*, **205** : 353-367.

PRUIM, G.J., H.J. DE JONGH and J.J. TEN BOSCH (1980) — Forces acting on the mandible during bilateral static bite force levels. *J. Biomech.*, **13** : 755-763.

ORON, U. and A.W. CROMPTON (1985) — A cineradiographic and electromyographic study of mastication in *Tenrec ecaudatus*. *J. Morphol.*, **185** : 155-182.

OTTEN, E. (1987) — A myocybernetic model of the jaw system in the rat. *J. Neurosci. Meth.*, **21** : 287-302.

RAYNE, J. and G.N.C. CRAWFORD (1972) — The relationship between fiber length, muscle excursion and jaw movements in the rat. *Archs. oral Biol.*, **17** : 859-872.

SCAPINO, R. (1965) — The third joint of the canine jaw. *J. Morphol.*, **116** : 23-50.

SCHUMACHER, G.H. (1961) — *Funktionelle Morphologie der Kaumuskulatur*. Gustav Fisher Verlag, Jena : 262 pp.

SCHUMACHER, G.H. and S. Rehmer (1962) — Morphologische und Funktionelle Untersuchungen an der Kaumuskulatur von *Oryctolagus* und *Lepus*. *Gegenb. Morphol. Jb.*, **100** : 678-705.

SCHWARTZ, G., S. ENOMOTO, C. VALIQUETTE and J.P. LUND (1989) — Mastication in the rabbit : a description of movement and muscle activity. *J. Neurophysiol.*, **62** : 273-287.

STOHLER, C.S. (1986) — A comparative electromyographic and kinesiographic study of deliberate and habitual mastication in man. *Archs. oral Biol.*, **31** : 669-678.

TURNBULL, W.D. (1970) — Mammalian masticatory apparatus. *Fieldiana Geology, Chicago Mus. Nat. Hist.*, **18** : 147-356.

VAN EIJDEN, T.M.G.J., P. BRUGMAN, W.A. WEIJS and J. OOSTING (1990) — Coactivation of jaw muscles : recruitment order and level as a function of bite force direction and magnitude. *J. Biomechanics*, **23** : 475-485.

WEIJS, W.A. (1975) — Mandibular movements of the albino rat during feeding. *J. Morphol.*, **145** : 107-124.

WEIJS, W.A. and R. DANTUMA (1975) — Electromyography and mechanics of mastication in the albino rat. *J. Morphol.*, **146** :1-34.

WEIJS, W.A. and R. DANTUMA (1981) — Functional anatomy of the masticatory apparatus in the rabbit (*Oryctolagus cuniculus* L.). *Neth. J. Zool.*, **31** : 99-147.

WEIJS, W.A. and L.J Van Ruijven (1990) — Models of masticatory mechanisms : their reliability, resolving power and usefulness in functional morphology. *Neth. J. Zool.*, **40** : 136-152.

WEIJS, W.A., P. BRUGMAN and E.M. KLOK (1987) — The growth of the skull and jaw muscles and its functional consequences in the New Zealand rabbit (*Oryctolagus cuniculus*). *J. Morphol.*, **194** : 143-161.

WEIJS, W.A., P. BRUGMAN and C.A. Grimbergen (1989) — Jaw movements and muscle activity during mastication in growing rabbits. *Anat. Rec.*, **224** : 407-416.

WOOD, A.E. (1955) — A revised classification of the rodents. *J. Mammal.*, **36** : 165-187.

WIDMALM, S.E., J.H. LILLIE and M.M. ASH (1987) — Anatomical and electromyographic studies of the lateral pterygoid muscle. *J. oral Rehab.*, **14** : 429-446.

WOOD, A.E. (1959) — Are there rodent suborders? *Syst. Zool.*, **7** : 169-173.

WOOD, A.E. (1962) — The juvenile tooth patterns of certain African rodents. *J. Mammal.*, **43** : 310-322.

WOOD, A.E. (1965a) — Unworn teeth and relationships of the African rodent *Pedetes*. *J. Mammal.*, **46** : 419-423.

WOOD, A.E. (1965b) — Grades and clades among rodents. *Evolution*, **19** : 115-130.

WOOD, A.E. (1985) — The relationship, origin and dispersal of the hystricognathous rodents. *In* : LUCKETT, W.P. and J.-L. HARTENBERGER (eds) : *Evolutionary relationships among rodents*, NATO ASI Series A, Life Sciences Vol. 92, Plenum Press, New York : 475-513.

Belg. J. Zool. — Volume 123 (1993) — issue 2 — pages 263-282 — Brussels 1993

Manuscript received on 18 January 1993

A POINT OF VIEW

POSITIONAL INFORMATION LIMITS THE SELF-EXPLAINING ENDEAVOUR IN MORPHOGENETIC THEORY (IN THE SENSE OF TURING)

Towards the understanding of the functioning of biological forms (1)

by

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ABSTRACT

The notion of 'positional information' with respect to morphogenetic theories is critically examined. We analyzed the significance of positional information in the original paper by TURING (1952) on morphogenesis through reaction-diffusion mechanisms. It is concluded that positional information is necessary to understand the emergence of biological forms, and hence limits the self-explaining endeavour of these forms. Moreover, it is suggested that positional information is necessary to understand some of the essential functions of biological forms, namely the functions of insulation and transport.

Key words : positional information, morphogenesis, biological functioning, reaction-diffusion models.

(1) The present article was accepted for publication in *Fundamenta Scientiae* on October 5, 1990, and was scheduled for volume 11 (1990) of this journal. However, due to economic difficulties of their editor, the journal didn't appear until the present. Meanwhile, in continuation of the former article two papers of the first author are published, respectively in *Acta Biotheoretica,* **39** : 47-62 (1991) and *Communication and Cognition,* **25** : 277-294 (1992).

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INTRODUCTION

In 1952 TURING presented a paper on « The Chemical Basis of Morphogenesis » having the purpose of « discussing a mechanism by which the genes of a zygote might determine the anatomical structure of the resulting organism ». The paper, which appeared at about the same time that WATSON and CRICK (1953) postulated the double stranded helix model for the DNA molecule, acquired a comparable status in morphogenetic theory as the DNA model did in molecular biology. TURING provided a mechanism for pattern formation based on a model of two morphogens (in later studies expanded to three morphogens) reacting with each other and diffusing through a certain configuration of cells. These models were epithetically called reaction-diffusion models and were further elaborated by many other authors. They became especially famous after PRIGOGINE's (1967) comprehensive theory on color pattern formation in a special class of chemical reactions as discovered by BELOUSOV and ZHABOTINSKY (WINFREE, 1974). Biological applications of reaction-diffusion theory were successfully elaborated in the case of the formation and reorganization of tentacular structures in the coelenterate *Hydra* (GIERER and MEINHARDT, 1972), or in the case of the generation of color patterns resembling the patterns in the coats of various mammals or reptiles (COCHO *et al.*, 1987[a,b]).

However, from the onset, morphogenetic theory was burdened with the apparently insoluble question of the nature of the so-called 'morphogens'. They are called « presumably chemical » by TURING, although they were « not intended to have any very exact meaning ». The most restrictive interpretation was offered by HARRISON (1987), who formulated the nature of morphogens as « autocatalytic substances producing themselves only by themselves », although these substances might be rather diffusible cells than molecules. In fact, already HÖRSTADIUS (1939, 1950) had pointed towards the involvement of chemical agents in the formation of embryological axes, as was inferred from experimental studies in echinoderm eggs. A full biochemical isolation and characterization of a substance with morphogenetic potential has been achieved very recently (THALLER and EICHELE, 1987, 1990). On the other hand, several authors stressed the need for structural constraints in morphogenesis (cfr. WADDINGTON 1968, 1969, 1970, 1972), which idea was crystallized in WOLPERT's (1969) notion of 'positional information'.

The purpose of this paper is to analyze the disputed notion (cfr. HARRISON, 1987) of 'positional information' and to reveal its significance in morphogenetic theory. We will emphasize its significance in the original paper by TURING (1952), as well as in later studies. We will pay special attention to one remarkable issue of 'positional information', namely the gravitational field of the earth, for the effect of gravity upon dorso-ventral polarization in amphibian eggs has long been a matter of debate for embryologists (reviewed in ALLAERTS, 1991). An ontological description of 'positional information' is inferred from HARRISON's (1987) essentialists definition of the morphogen nature, that results from the denudation of morphogenetic theory into the so-called 'kinetic preconception'.

Further we will show by some examples that the notion of 'positional information' is to be interpreted in its broadest sense not only to account for the com-

plexity observed among biological forms, but also to explain the functioning of these forms. To allow an integration of the concept of functioning of biological forms into morphogenetic theory, an integration that reaches beyond the level of intuitive perception, we will link up with THOM's (1974) ontology of the « logos of living beings », appearing as a « quasi-universality of certain functions and certain morphologies ». The latter position is believed to be helpful towards an understanding of the functioning of biological forms, as well as to a better understanding of the emergence of these forms, which is the final aim of morphogenetic theory.

A KINETIC THEORY OF MORPHOGENESIS

Recently, JI (1988) proposed a completion of the Watson-Crick model of genetic information, and called this the 'Prigoginian' form of genetic information. The latter concept refers to the so-called 'dissipative structures' of PRIGOGINE (PRIGOGINE, 1967 ; GLANSDORFF and PRIGOGINE, 1971 ; NICOLIS and PRIGOGINE, 1977), which according to JI (1988) would represent the translation of the one-dimensional information encoded in the DNA, into a spatial information field as this genetic information is expressed in the living cell. The idea underlying this concept refers to the kinetic conception of morphogenesis in ontogeny, for the first time explicitly formulated by TURING (1952). The model presented is also designated as a reaction-diffusion model (HARRISON, 1987).

The Turingian concept of morphogenesis

TURING (1952) demonstrated the principle of morphogenesis using the configuration of a ring of similar cells (Fig.1a). It was shown that a given set of chemical reactions producing the morphogenetic substances X and Y, and the ability of these substances to diffuse from one cell to another, could be sufficient to produce inhomogeneity within the initially homogeneous ring of cells. Small departures from the equilibrium concentration could, after a lapse of time, for the above conditions, result in large concentration differences and the breakdown of homogeneity. If the substances X and Y were endowed with the ability to influence the cell morphology, this would also result in the formation of a certain morphological pattern. Mathematically, these patterns can be described by stationary waves if the dominant terms of the roots of the differential equations, describing the generation of the morphogenetic substances, are real. If the roots concerned are complex, however, the generation of travelling waves is the result. It is noteworthy that according to TURING the wavelengths not only depend on the chemical data, but also depend on the dimension of the ring of cells. Nevertheless, TURING defined some kind of 'chemical wavelength' as being « the limit to which the wavelengths tend when the rings are made successively larger » (TURING, 1952 ; p. 51). The mathematical construction of a 'chemical' wavelength afterwards became popular, for instance in the paper of HARRISON (1987) (see below).

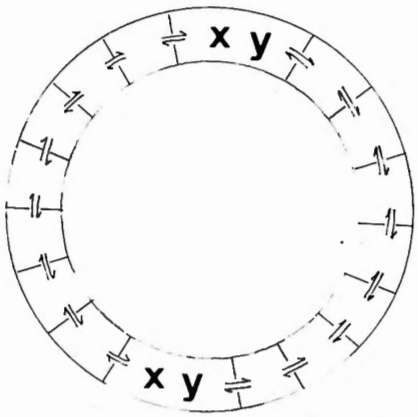
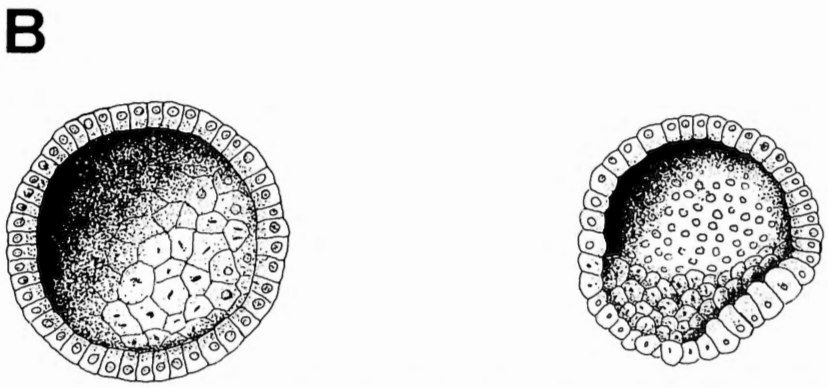


Fig. 1A. — Scheme representing the constellation used by Turing (1952) to explain pattern formation by a reaction-diffusion mechanism : a homogeneous ring of cells, containing the morphogenetic substances X and Y, that are able to diffuse from cell to cell.



B. — Early stages of gastrulation in the blastula of *Amphioxus* (after BALINSKY, 1981) : polarization in the initially homogeneous hollow sphere indicates the formation of the gastrulation axis.

TURING further demonstrated that other configurations could be also used as a model for morphogenesis, as for instance the hollow sphere of continuous tissue (cfr. the blastula) (Fig.1b). TURING suggested that the events resulting in gastrulation of the blastula could be described by using a similar analysis of reaction-diffusion on the sphere with only two morphogens, where « any small asymmetry of the zygote may be sufficient to provide the 'disturbance' which determines the axis (of the gastrulation) » (TURING, 1952 ; p. 71).

Harrison's Classification of Morphogenetic Theories

HARRISON (1987) envisages three main divisions of physico-chemical theory that are of interest to explain the self-organization of living organisms, namely the 'preconceptions' of structure, equilibrium and kinetics. These preconceptions all represent a 'phylum' of morphogenetic theories. Among the three phyla HARRISON considers the theory related to the 'kinetic preconception' as being most appropriate in explaining living self-organization, although the importance of the other phyla of theories is not clearly circumscribed.

The **structural theory** (cfr. LEHNINGER, 1970a) relates the generation of a certain morphology to the assembly of smaller parts into a larger entity (**self-assembly theory**). HARRISON considers the latter theory, designated as the preconception of molecular biology, to be only successful to explain pattern and form on the « spatial scale of viruses ». To the same phylum of morphogenetic theories HARRISON counts also the theories that provide explanations of cellular and multicellular organization through the cytoskeleton (HARRISON, 1987 ; p. 370).

On the other hand, **equilibrium theory**, which attributes form to the minimization of free energy, a preconception dating back to THOMPSON (THOMPSON, 1917), is considered to be definitely incomplete for living organisms are « intrinsically out of equilibrium in thousands of ways » (HARRISON, 1987 ; p. 371). Nevertheless, the latter phylum of morphogenetic theories is not totally neglected for some theories, such as that of STEINBERG (1970) on the assembly of cells by differential adhesion, are possibly of interest. Within this context, attention should also be paid to the contribution by THOM (1974), not mentioned by HARRISON, who integrated THOMPSON's preconception of minimization of free energy, into a more general topological theory of morphogenesis, taking advantage of the theory of catastrophes in mathematics.

HARRISON is most interested in **kinetic theory**, envisaging the generation of pattern and form by movement away from equilibrium, for the other theories apparently do not satisfy. He concludes that « most physical scientists adopt the kinetic preconception, because they see nothing else in all our philosophies » (p. 370) to « envisage living organisms non-vitalistically » (p. 370). « What else could do it ? », he exclaims (p. 370). With regard to the biologists, HARRISON correlates their « distaste for mathematical explanations » to a deep, philosophically inspired, « reluctance to adopt the kinetic preconception » (p. 369). It would be far beyond the scope of this paper to treat POPPER's (POPPER and ECCLES, 1977) elaborate argument on the emergence of living self-organization, as an answer to HARRISON's query for a non-vitalistical explanation. In our opinion however, there is no philosophical reason for not considering the constructiveness of each of the three phyla of physico-chemical theory mentioned by HARRISON. A well known example of theories that account for integration of structural and kinetic preconceptions is found in BISSELL *et al.* (1982). BISSELL *et al.* (1982) and also GOODWIN and TRAINOR (1985) attribute an important role to the cytoskeleton and extracellular matrix on the one hand, and to diffusible and/or ionic components inside and outside the cells on the other hand, in directing gene expression.

THE SIGNIFICANCE OF 'POSITIONAL INFORMATION' IN MORPHOGENETIC THEORY

The concept of 'positional information' related to morphogenetic theory was first proposed by WOLPERT (1969). According to WOLPERT (1969), positional information is to be specified as the information represented by the position of cells with respect to one or more points in a system (constituting a co-ordinate system) (see below). The specification of positional information in general precedes and is independent of molecular differentiation. We will further expand this concept to account for all types of information from outside the cell, that precede and are independent of molecular differentiation. These may include other cells, a geometrical configuration, a certain field of forces, a certain temperature distribution, and so on. The significance of an expansion of WOLPERT's concept will be clarified by the subsequent analysis of HARRISON's (1987) criticism of 'Wolpertization'. In the late papers of WOLPERT (e.g. WOLPERT, 1992) positional information is defined as the coordinate position within the biological structure, which can be read of from the chemical or molecular concentration gradients within the structure. These gradients of molecular substances would in turn be encoded by the genes of the individual cells of the structure. To our opinion it may be instructive to distinguish between secondary mediators, i.e. molecules that affect gene transcription in a concentration-dependent manner, and so-called pre-existing vector fields, such as the gravitational field or the intra-uterine environment (ALLAERTS, 1991). The latter distinction is related to the distinction between pattern formation and axis formation, as previously mentioned (ALLAERTS, 1991).

Harrison's crusade against 'Wolpertization'

As we mentioned before, HARRISON's (1987) preoccupation with the 'kinetic preconception' is inspired by a dissatisfaction concerning other physico-chemical explanations. This preoccupation incites the author to elaborate an essentialist view of reaction-diffusion theory. Therefore, the « essential nature of a morphogen » (HARRISON, 1987 ; p. 372) has to be carved out of the semantics of the word morphogen, and in the first place, has to be discarded from connotations like 'diffusibility' or 'diffusion-driven instability' (MURRAY, 1982). HARRISON imputes the latter connotations to WOLPERT's (1969) concept of morphogenesis, where « an essentially passive signaller of information » is grafted « on a pre-existing pattern ». And HARRISON specifies : « Reaction-diffusion theory treats a different problem [than WOLPERT does] : it treats the origin of the distinction between source and surroundings » (HARRISON, 1987 p. 372). By putting forward the latter proposition, HARRISON has recourse to a distinctly metaphysical position. His reluctance to adopt the possibility of a « pre-existing pattern » ensues a reluctance towards any kind of 'positional information', giving rise to the metaphysical position mentioned. The key to the understanding of this « deep, philosophically inspired reluctance » (cfr. HARRISON's criticism against the biologists), is provided by the original paper of TURING (1952) itself, as we will demonstrate below.

The deep, irreconcilable contrasts between HARRISON's and WOLPERT's notions of morphogenesis, lead to the former's crusade against 'Wolpertization'. WOLPERT indeed has significantly contributed to the development of morphogenetic theory, and also has contributed to the discovery of some of the molecular cornerstones for morphogenesis, which are needed in modern molecular biology. One of these candidates for a molecular morphogen is *retinoic acid*, which has been shown to be able to induce a second polarization region in the developing wing of the chicken embryo, resulting in a doubled wing structure (THALLER and EICHELE, 1987, 1990). We borrowed the martial phraseology from HARRISON himself : « closely allied forces fighting on the same side, which is that of the kinetic preconception » (HARRISON, 1987 ; p. 371), and « of the two British tribes, I consider 'morphogen' to belong to the language of the Turingians, not the Wolpertians » (p. 375). However, « the warriors in the cause of kinetic theory » (p. 383), i.e. those who are of a like-mind to HARRISON, are not averse to the « popularity of positional information theory » (p. 375), which makes an alliance with the « Wolpertization of British developmental biology » as a first step « towards acceptance of the kinetic preconception » (p. 375). These statements indicate a certain pragmatism that would mitigate the seclusion resulting from HARRISON's metaphysical position, but this pragmatism is probably necessary to make the concept of 'chemical wavelength' work (see below).

Living Self-Organization, 'Chemical Wavelength' and Teratogenesis

To account for the self-organizing ability of living organisms, HARRISON (1987) inclines towards the definition of a morphogen as an auto-catalyzing substance. This latter substance needs not necessarily to be a chemical substance, for the cells themselves might be regarded as « a diffusible species, such as mesenchyme cells » (HARRISON, 1987 ; p. 374). To make the self-organizing system work, one also needs to extrapolate TURING's (1952) notion of 'chemical wavelength', to let this « chemical wavelength grow in proportion to the size of the system » (HARRISON ; 1987 ; p. 375), to make it independent from the system size. It is important to note that HARRISON's concept of 'chemical wavelength' is no longer a mathematical construction as it was in TURING's (1952) paper, but now became a true physico-chemical concept : therefore reacting chemicals ('reactants') in the reaction-diffusion processes are assumed to have constant concentrations, but it is accepted that these concentrations might vary between different positions within the morphogenetic region (HARRISON, 1987 ; p. 375). It is not clear whether HARRISON here admits the existence of a pattern preceding morphological differentiation.

An interesting implication of HARRISON's use of the notion of 'chemical wavelength' results from experimental studies on teratogenesis in response to the disturbance of normal development. Reaction-diffusion theory is hence able to account for malformations, such as, for instance, those observed in insect embryos that develop two abdomens after being damaged at what should have been the anterior end. However, these experiments either answer a question that differs from the question as to what are the determinant causes of a normal development, or

they would lead, among others, to the trivial explanation that the absence of damage is a determinant cause of normal development.

It is also noteworthy that HARRISON thinks of mesenchyme cells and not of neoplastic cells as examples of a 'diffusible species'. It is a tempting idea that reaction-diffusion theory might provide new insights into the problem of metastasis in tumorigenesis, but so far this idea has only a speculative value.

A View on the Origin of Positional Information in Morphogenetic Theory : the Egg of Columbus ?

According to TURING (1952) or WOLPERT (1969), an essential feature of the departure from homogeneity is the loss of symmetry, or the reduction of symmetry to a 'lower degree'. This means polarization. Examples are easily found in which the breakdown of homogeneity depends in some manner on 'positional information'. An experimental example of the influence of positional information on the development of cell polarity is given by ZIOMEK and JOHNSON (1980). In the latter study it was demonstrated that the development of surface polarity of the 8-cell blastomere depends upon intercellular contact. After polarization, intercellular features follow such as the flattening of the cells (compaction) and the formation of specialized junctions. 'Positional information' received by the developing cell considered in this case is to be interpreted as the close presence of the other cells.

Also, in TURING's most simple model, positional information is offered by the geometrical constraint of a ring-like configuration of cells and, in the advanced model, by the hollow sphere or blastula. The question is therefore shifted to an earlier situation, as to what causes the emergence of polarization in the 'most primitive cell', not to be confused with the zygote. This represents a variant of the well-known question expressed by the riddle of the hen and the egg : which of them was first ?

According to TURING, the question has even to be shifted to an earlier event in the evolution of living organization, namely to the emergence of left-handedness or right-handedness, i.e. to the origin of asymmetry in biomolecules. It is commonly accepted that once a choice was made between left-handed and right-handed stereoisomers, this preference was maintained throughout evolution, because of the template relationship between polynucleotide and polypeptide molecules (the template theory, cfr. LEHNINGER (1970b). The choice of one of the two possible stereoisomers would be purely determined by chance.

Similarly, TURING provides an effort to assign the emergence of polarization in living organisms to 'random disturbances'. In a paragraph « definitely devoted to trained mathematicians », TURING (1952 ; p. 40) states that the laws of physics and the distribution of (mature) living organisms have apparently not the same symmetry. Leaving the technical aspect concerning the type of symmetry out of consideration, one can easily follow TURING, when he says that « men are more often found standing on their feet than on their hands » and « this may be corrected by taking gravity into account in the laws » (TURING, 1952 ; p. 45). This sentence is immediately followed by the extraordinary idea, that « it will be more convenient,

if, for the sake of argument, it is imagined that some species has been reared in the absence of gravity ». Indeed, gravitational force is one type of 'positional information' which is no longer mentioned in TURING's paper, but, on the contrary, 'random disturbances' are considered as the source of breakdown of homogeneity, as TURING concluded in the abstract of his paper.

One can summarize TURING's solution to the riddle of the hen and the egg by the following phrase : *The egg was laid without a hen, but there had to be no gravitational force !* However, we are now able to leave the meaning of this phrase behind, for it recently became clear that TURING indeed might have forgotten an important issue. Recent experiments have revealed the important role played by gravity upon the development of the dorso-ventral axis in the embryo of *Xenopus* (GERHART *et al.*, 1981 ; UBBELS and BROM, 1984). Experimental support for the role of gravity upon dorso-ventral polarization was achieved using rotation and centrifugation experiments in monospermic *Xenopus* eggs (GERHART *et al.*, 1981) as well as in fertilization experiments of these eggs during spaceflight (UBBELS and BROM, 1984). However, various experimental studies in mammals (ALDEN, 1945 ; SMITH, 1980) have indicated that gravity in itself was not the responsible agent for directing axis formation in the mammalian embryo, but that an assumed gravitational axis could be perceived by the developing embryo within the uterus (reviewed in ALLAERTS, 1991). Recently, it was also suggested that an enhanced cell proliferation and diminished cell differentiation might result from the absence of a 'normal' gravitational field, as the latter effects were invoked to explain a diminished maturation of lymphocytes (COGOLI *et al.*, 1984) and a weaker immune response in astronauts after a prolonged stay outside the earth's atmosphere (BATKAI *et al.*, 1988). Though speculative, these ideas might emphasize the importance of a 'normal' gravitational field upon different aspects of the ontogenesis of living organisms (ALLAERTS, 1991).

POSITIONAL INFORMATION AND THE FUNCTIONING OF BIOLOGICAL FORMS

In the previous paragraph, we treated various examples of 'positional information' considered as structural constraints in morphogenesis through reaction-diffusion models. The above idea allows environmental factors to play a role in developmental processes, a phenomenon well known to result in the interaction between phenotype and genotype. The notion of positional information is also related to GOODWIN's (1987) concept of 'morphogenetic fields', which are defined as « fields in which electrical, mechanical and chemical properties are combined in a particular manner, resulting in a spatio-temporal system (...) with the capacity to perform the mechanical work that underlies morphogenesis » (GOODWIN, 1987 ; p. 337). GOODWIN states that « these fields can generate ordered spatial heterogeneities that can influence gene activities, resulting in so-called harmonic patterns, but, in turn, gene products can also influence the morphogenetic fields » (GOODWIN, 1987 ; p. 337). However, WOLPERT's (1969) remark concerning the notion of 'positional information', as « preceding and being independent of molecular differentiation »,

is not devoid of importance, as we just stressed the fact that certain fields of physical forces (e.g. gravity) entirely independent from and preceding living organization, are able to influence morphogenesis.

To answer the question whether an ontological definition of 'positional information' in terms of a physico-chemical reality can be provided, we first have to offer a general specification of the notion of 'information' as provided by THOM (1974). It will thereafter be shown that THOM's conceptualization of 'information', applied to the notion of 'positional information', offers interesting perspectives to account for the 'functioning' of biological forms. The possibility of an ontological definition of the functioning of biological forms is discussed in the light of THOM's (1974) definition of « logos of living beings ». An example is provided in which reaction-diffusion theory not only accounts for pattern formation in biological forms, but also explains some typical biological functions. Moreover, the idea presented here will shed some light on the paradox mentioned by GOODWIN (1987) concerning the « stability of nature » and « natural forms ».

The 'nature' of positional information

Essentially 'positional information' has to be regarded as 'information'. With regard to living organization, according to JI (1988), it is an essential feature « for the living cell to possess the ability to transmit (genetic) information in time (e.g. from parents to progeny) as well as in space (from nucleus to extracellular space) » (JI, 1988 ; p. 239). The concept of 'transmission of information' is also the subject of communication theory (cfr. the Shannon-Weaver concept of information) (PIERCE, 1980) of which, according to JI (1988), one of the most fundamental aspects is that « the amount of information carried by a given message is determined not by the intrinsic properties of the message itself but by the property of the message source called the 'entropy of the source' » (p. 239). However, THOM (1974) cautions against the equation of the concept of information with its homologue in communication theory (in the sense of Shannon-Weaver), for this might result in the omission of information source and destination, and retain only an interest in the properties of the communication channel. Moreover, THOM objects to the probabilistic definition of information (in the case of biological forms), identifying information and 'néguentropie', for « the thermodynamic equivalent of spatial forms generally is not known or even not defined... » (THOM, 1974 ; p. 187). However, the probabilistic notion of information does have some value, according to THOM, for it conceals a relationship « connecting the rarity of the initial conditions of an instable process with the topological complexity of the resulting situation » (THOM, 1974 ; p. 188).

Concerning the information conveyed by living organisms, THOM states that the living organism itself is the 'locutor' of the information, or, « the natural morphology has to be considered as a message emitted by a fictive source toward the observer, e.g. the scientist » (THOM, 1974 ; p. 184). Quite differently formulated but essentially the same idea is expressed by GOODWIN (1987), stating that organisms should be understood as « instances of a particular state of organization of matter

that is inevitable because it is possible, and the conditions for its appearance exist on Earth » (GOODWIN, 1987 ; p. 331).

From the latter statements we can infer an 'ontological' definition of 'positional information to living organization' as the spatio-temporal system consisting of physico-chemical properties of either inanimate or animate (other living organizations) nature, that provide the conditions for the appearance of the living organization. The content of such a general definition of course suffers from vagueness, but the definition does not exclude the possibility of a minimal number of conditions for the appearance of a certain morphology. As a consequence, since the complete set of possible physico-chemical properties is in itself no longer a physico-chemical property strictu sensu, the above definition of 'positional information' limits the self-explaining endeavour of living organisms regarded purely as physico-chemical systems (cfr. HARRISON, 1987). To explain living self-organization, it therefore seems necessary to consider a physico-chemical system plus information which does not depend on the physico-chemical system. The latter statement recalls an analogy to Gödel's argument on the consistency of (mathematical) formal systems (as a reaction to the Hilbert program) (HOFSTADTER, 1979), and therefore can be considered as a kind of Gödelian argument applied to the biological sciences.

Interaction between form and function in morphogenesis : some examples

Before we proceed onto the nature of biological functions, we will first cite some examples of reaction-diffusion models applied to the genesis and functioning of biological forms. The first example is a well known application of morphogenetic theory, namely the generation of color patterns as in the coat of mammals or reptiles (COCHO *et al.*, 1987[a,b]) ; the second example is related to molecular diffusion phenomena in biological materials (WEINBAUM *et al.*, 1988 ; WEN *et al.*, 1988 ; ALLAERTS *et al.*, 1990).

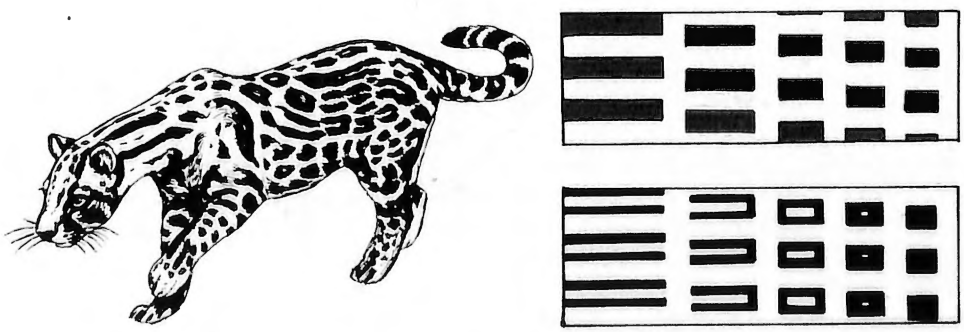


Fig. 2. — This figure should be seen as an exercise : the aim of the exercise is to produce a pattern of spots and stripes resembling the coat pattern of the ocelot (left), by increasing the number of geometrical gradients in a field of black and white rectangles. The right panels give some examples of these gradients (Idea borrowed from COCHO *et al.* 1987[b]).

Concerning the first example, it was demonstrated that a minimal number of 'structural and dynamical constraints' (cfr. WADDINGTON, 1968, 1969, 1970, 1972) were indeed sufficient to produce patterns such as the stripes and patches in the fur of mammals and in the integuments of reptiles and fishes (COCHO *et al.*, 1987[a,b]). The structural and dynamical constraints concerned were differential cell adhesion on the one hand (i.e. short range interactions between cells, due to the macromolecules present at the cell surface) and, on the other hand, the diffusion of chemicals (representing the long range interactions). With regard to the coat patterns of mammals, however, the following remarks can be made. If reaction-diffusion models are able to reproduce some handsome patterns, these patterns still are not identical to the real patterns present in the furs of living ocelots, jaguars, ... mentioned by COCHO *et al.* (1987[b]) (Fig. 2). Moreover, these reproductions of patterns apparently lack the dimensions necessary for the understanding of their functioning as well as their genesis and stability. It is not anymore mentioned that these color patterns are formed by many millions of hairs, and that the specific regions of these hairs producing the coloured pattern, vary from one species to another from somewhere at the hair root to somewhere at the hair tip. This feature is nevertheless important with respect to the stability of the pattern, for wearing of the hairs would damage them and destroy the pattern. (Therefore, the fur also consists of coarse protective hairs, as well as the thin hairs that produce the basic color tints). To account for the generation of the above patterns, information is needed concerning the regulation of the successive time periods of the hair growth cycle, for moulting of the fur results in a periodical renewal of all coat patterns, as well as of the successive periods of pigment deposit that cause the banded patterns of the individual hairs and finally the color patterns of the coat. An example of the interaction between diffusion processes and anatomical constraints in the renewal of coat patterns at moulting is illustrated in ALLAERTS and VANDEVELDE (1984).

We previously stressed the need for 'positional information' to understand the genesis of biological forms (ALLAERTS, 1991), and, the present example also illustrates the need for 'positional information' to understand the functioning of these forms. The color patterns reproduced by COCHO *et al.* (1987[a,b]) only represent a geometrical aspect of the complex forms underlying the pattern. The most important function of a pattern of patches and stripes is to make the animal less visible in a certain environment, called 'mimicry'. 'Positional information' has been necessary to produce that pattern, for the geographical constraints imposed on the mechanisms of natural selection make part of the conditions for the appearance of that type of organization. To understand the functioning of the mammalian fur however, as, for instance, the fur's insulation, these color patterns probably represent one of the least important features. Indeed, it has been shown that for a wide range of mammalian furs with colors from white to black, the emissivity, i.e. a physical parameter that determines the magnitude of heat radiation, is almost equal to unity in all cases (HAMMEL, 1956). Hence, color patterns are rather unimportant features to heat radiation. Ironically, an equivalent of reaction-diffusion theory might offer the tools for understanding some of the insulation properties of mammalian furs, for the heat transfer processes are described in terms of conduction

(diffusion)-convection-radiation (HUTCHINSON and BROWN, 1969). As schematically represented in Fig. 3A the heat transfer processes depend on both environmental parameters and structural elements of the integument. The latter example illustrates the relevance of 'positional information' to understand insulation phenomena in

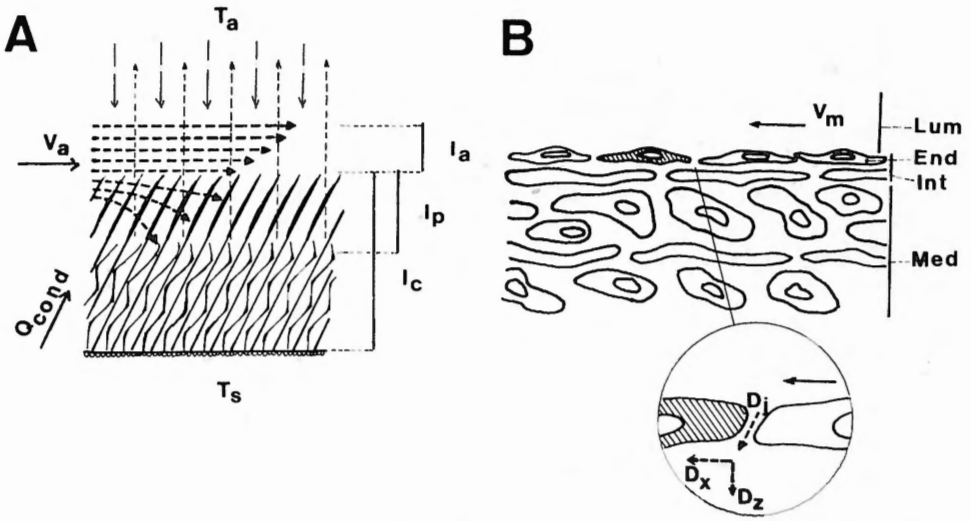


Fig. 3. — A. — Scheme representing the main constituents of a mammal's coat (skin, protective hairs and wool hairs), the main environmental factors affecting thermal insulation (T_a, V_a) and the main components of the insulating barrier (I_a, I_p, I_c). A 'gestalt switch' enables one to see the insulating phenomenon in a different way, by describing the transport processes (conduction, irradiance and air transport) rather than the insulating barrier [sum of components I_a, I_p and $(I_c - I_p)$].

I_a : (thermal) insulation of air cushion ; I_p : 'penetrance' of the fur (after HUTCHINSON and BROWN, 1969) ; I_c : total insulation of the coat ; T_a : radiating (absolute) temperature of the air ; T_s : radiating temperature of the skin ; Q_{cond} : conductive heat transfer across the fur ; V_a : velocity of air motion outside the fur ; —·—→ irradiance from environment ; ----→ irradiance from fur ; ----→transport of air, outside and inside the fur.

B. — Scheme of transport phenomena occurring in a blood vessel wall (modified after WEN *et al.*, 1988). A simplified anatomical reconstruction of the vessel wall indicates the following parts : Lum : lumen ; End : endothelium ; Int : intima (inner layer of vessel wall) ; Med : media (outer layer of vessel wall). The main components of the latter two parts are the smooth muscle cells and elastic laminae. Some endothelial cells are currently undergoing mitosis (hatched), resulting in the formation of a leakage site with respect to the neighbouring endothelial cells that form 'normal' junctions with each other (WEINBAUM *et al.*, 1988 ; WEN *et al.*, 1988). An 'environmental' factor imposed on the molecular transport across the vessel wall is the fluid motion in the vessel lumen (V_m). The diffusion process is characterized by the 'effective' diffusion coefficients of the intra-endothelial cleft (D_j) and of the subendothelial medium in lateral (D_x) and normal direction (D_z). These effective diffusion coefficients are function of the molecular species and local 'microviscosity' of the medium. Hence, reaction-diffusion theory here accounts for diffusional motion and molecular adhesion effects.

biological materials, for indeed this can be considered as a boundary-condition problem in reaction-diffusion theory.

Examples are easily found within other domains of the biological sciences, where equivalents of reaction-diffusion theory offer the appropriate tools for the understanding of the functioning of certain morphologies. We recently used diffusion theory to treat the problem of the transport of a certain hormonal signal through a tissue-like configuration of cells obtained from the pituitary gland (ALLAERTS *et al.*, 1990). Moreover, reaction-diffusion theory has some value in quantification of cell functioning, such as hormone secretion, at the level of individual cells (ALLAERTS *et al.*, 1988). Other examples have recently been described, using a combination of diffusion and forced flow to study the permeability of blood vessels to macromolecules (Fig. 3B), resulting in a renewed theory on the genesis and functioning of the blood-brain barrier (WEINBAUM *et al.*, 1988 ; WEN *et al.*, 1988). Transport functions within living organisms are indeed the subject of growing interest. One special example, the transport of neoplastic cells through an organ at metastasis, is only one of the challenging problems facing the medical enterprise of today.

Can the 'functioning' of biological forms be defined in ontological terms ?

Essentially, the two following functions can be recognized in the examples presented above : that is 'insulation' in the first example and 'transport' in the second example. These are not merely arbitrary and independent examples, for the function of 'insulation' also implies 'insulation against transport', and 'transport' implies 'movement across an insulating barrier'. Both functions are related just as 'movement' is related to 'inertia'. The only difference with the latter duality, is that it requires the presence of a medium of matter. The nature of the substance being transported might be 'heat' (i.e. in the case of thermal insulation), or a chemical substance (i.e. in the case of insulation against molecular diffusion). In both cases the mathematical formulation of the transport process is approximately the same, i.e. the transport processes are described by the same differential equations. Therefore, the standard work of CARSLAW and JAEGER on « Heat conduction in solids » (1959) is also a standard work for physicists investigating molecular diffusion. The importance of 'insulation' for living organization is not only known by cellular biologists (cfr. the role of the cell membrane), but is also reflected in the following passage from Vladimir Nabokov's « Pnin » :
« I do not know if it has ever been noted before that one of the main characteristics of life is discreetness. Unless a film of flesh envelops us, we die. Man exists only insofar as he is separated from his surroundings ».

The above idea of insulation or discreetness found its way into physiology and cellular biology, as for instance the notion of compartmentalization was considered as an important feature in tissue homeostasis (ABBOTT, 1988), and compartmentalization of the extracellular matrix was proposed to play an important role in directing gene expression at the cellular level (BISSELL *et al.*, 1982).

If insulation and transport are two major aspects of the functioning of biological forms, can we then define them in ontological terms ? According to THOM, the « logos of living organisms » appears as a « quasi-universality of certain functions and certain morphologies » (THOM, 1974 ; p. 207). One might feel somewhat uneasy with the Platonic definition of a « morphology that in the time tends towards a stable and invariant limit form » (THOM, 1974 ; p. 13), a definition used by THOM to designate the concept of « asymptotic chreode », which was introduced to extend the notion of chreode first formulated by WADDINGTON (1940). In the terminology of THOM (1974), a morphology is represented by the closed environment of catastrophes (discontinuities) in the product space of 'Space box' (**B**) x 'time' (**T**). The chreode then is postulated to account for the isomorphism between morphologies, for the open environment (**U**) on **BxT** supporting a morphogenetic field (**F**) can be depicted by the relation $\mathbf{G:BxT \rightarrow V}$ upon the abstract space (**V**) with same dimensions as **U**, in which a standard closed environment of catastrophes (**J**) is provided. In that case the morphogenetic field is called a chreode (THOM, 1974 ; p. 13). A Platonic element in Thom's concept of morphology, is that he defines the isomorphism of the closed environment **K** of catastrophes as being the inverse image $\mathbf{G^{-1}}$ of the standard environment **J** or $\mathbf{K = G^{-1}}$ **(J)**. Or, the observed 'form' (**K**) is the inverse image of a standard (ideal) (!) form (**J**), just as the inverse images appearing on the wall of Plato's cave.

It is important to mention that in the terminology of THOM, the concepts of form (morphology) and function are closely related. Though THOM unfortunately choose a bone as an example of a 'stable limit form', the above definition of « logos of living organisms » indicate that the stability resides in the entity that appears either as 'form' or as 'function'.

The latter idea is also found in the paper of GOODWIN (1987) on « The Stability of Nature », where the author expresses astonishment concerning the morphological stability of ciliate protozoa of the genus *Tetrahymena*, but however all are distinguishable with respect to macromolecular composition. This example and others make GOODWIN conclude that similarity of form does not necessarily depend upon similarity of molecular composition, just as the « characteristic spiral motion of a liquid flowing down a plughole does not depend on whether the liquid has molecular composition H_20 or C_6H_6 or C_2H_5OH » (GOODWIN, 1987 ; p. 326).

Indeed, as was emphasized by THOM, the stability of form cannot be explained in terms of the composing elementary particles, but resides in an entity, designated as 'algebraico-geometric', « endowed with the property of structural stability with regard to the incessant perturbations affecting it » (THOM, 1974 ; p. 205). THOM here refers to the metaphor of Heraclitus, regarding the universe as the πάντα ῥέι, the universal motion depicted as a stream of water. The metaphor resurges in morphogenetic theory in the formulation of EDELMAN (1984) as « the stream flowing over a rock which is below the freezing point : accumulation of ice at first disturbs the stream only in minor ways, but eventually splits it into two branches ». The functioning accompanies the form, just as the bed and the rock guide the stream of water (cfr. EDELMAN), or the plughole guides the spiral motion of water flowing down through it (cfr. GOODWIN). A 'Gestalt switch' is necessary to separate

form and functioning, or in abstract 'Thomistic' terms, to separate 'signifying' and 'signified/signification' (THOM, 1974 ; p. 197) (see Appendix).

Concerning the functions mentioned above, namely 'insulation' and 'transport', it is now clear that they can only be described in terms of 'insulation/transport within/through a certain environment', i.e. they can only be described in terms of 'positional information'. We may conclude that positional information not only is necessary to understand the emergence of biological forms, but also to understand the functioning of biological forms.

ACKNOWLEDGEMENTS

Prof. D. Thys van den Audenaerde of the Royal Museum of Central Africa of Tervuren (Belgium) proposed the study of the genesis and functioning of mammalian coat patterns already a decade ago, thereby drawing our attention to the study of diffusion phenomena in biological materials. However, it was due to the enthusiasm of Prof. C. Denef at the University of Leuven (Belgium) that we successfully handled some reaction-diffusion problems related to transport phenomena in endocrine tissues. To the inspiratory influence of both of them we are much indebted. We also wish to acknowledge Mr. John Evans for correcting the spelling of our manuscript and Ms. Mouche Bareau and Ms. Annelies de Vries for her typographical assistance.

The I.W.O.N.L.-institute and the fund for 'Geconcerteerde Onderzoeksakties' supported the former author with a fellowship and research grant.

REFERENCES

ABBOTT, N.J. (1988) — The milieu is the message. *Nature*, **332** : 490-491.

ALDEN, R.H. (1945) — Implantation of the rat egg. 1. Experimental alteration of uterine polarity. *J. Exp. Zool.*, **100** : 229-235.

ALLAERTS, W. and C. VANDEVELDE (1984) — Topographical succession of moulting in the juvenile domestic rabbit (*Oryctolagus cuniculus*). *Annls. Soc. r. zool. Belg.*, **114** : 303-315.

ALLAERTS, W., A. WOUTERS, D. VAN DER MASSEN, A. PERSOONS and C. DENEF (1988) — A diffusion-adsorption model for the computation of the amount of hormone around a secreting cell, detected by the reverse hemolytic plaque assay. *J. Theor. Biol.*, **131** : 441-459.

ALLAERTS, W., Y. ENGELBORGHS, P. VAN OOSTVELDT and C. DENEF (1990) — Evidence that folliculo-stellate cells do not impede the permeability of intercellular spaces to molecular diffusion in three-dimensional aggregate cell cultures of rat anterior pituitary. *Endocrinology*, **127** : 1517-1525.

ALLAERTS, W. (1991) — On the role of gravity and positional information in embryological axis formation and tissue compartmentalization. *Acta Biotheoretica*, **39** : 47-62

BALINSKY, B.I. (1981) — *An Introduction to Embryology*. W.B. Saunders, Philadelphia.

BATKAI, L., M. TALAS, I. STOGER, K. NAGY, L. HIROS, I. KONSTANTINOVA, M. RYKOVA, I. MOZGOVAYA, O. GUSEVA and V. KOZHARINOV (1988) — *In vitro* interferon production by human lymphocytes during spaceflight. *Physiologist*, **31** (1) (*Suppl.*) : 50-51.

BISSELL, M.J., H.G. HALL and G. PARRY (1982) — How does the extracellular matrix direct gene expression ? *J. Theor. Biol.*, **99** : 31-68.

CARSLAW, H.S. and J.C. JAEGER (1959) — *Conduction of heat in solids.* Clarendon Press, Oxford, (2nd ed.).

COCHO, G., R. PEREZ-PASCUAL and J.L. RIUS (1987[a]) — Discrete systems, cell-cell interactions and color pattern of animals. 1. Conflicting dynamics and pattern formation. *J. Theor. Biol.*, **125** : 419-435.

COCHO, G., R. PEREZ-PASCUAL, J.L. RIUS and F. SOTO (1987[b]) — Discrete systems, cell-cell interactions and color pattern of animals. 2. Clonal theory and cellular automata. *J. Theor. Biol.*, **125** : 437-447.

COGOLI, A., A. TSCHOPP and P. FUCHS-BISLIN (1984) — Cell sensitivity to gravity. *Science*, **225** : 228-230.

EDELMAN, G.M. (1984) — Cell-adhesion molecules : a molecular basis for animal form. *Sci. Am.*, **250** (4) : 80-91.

GERHART, J., G. UBBELS, S. BLACK, K. HARA and M. KIRSCHNER (1981) — A reinvestigation of the role of the grey crescent in axis formation in *Xenopus laevis*. *Nature*, **292** : 511-516.

GIERER, A. and H. MEINHARDT (1972) — A theory of biological pattern formation. *Kybernetik*, **12** : 30-39.

GLANSDORFF, R. and I. PRIGOGINE (1971) — *Thermodynamic theory of structure, stability and fluctuations.* Wiley and Sons, Interscience, New York.

GOODWIN, B.C. (1987) — The stability of nature. *Speculations in Science and Technology*, **10** : 325-338.

GOODWIN, B.C. and L.E.H. TRAINOR (1985) — Tip and whorl morphogenesis in *Acetabularia* by Calcium-regulated strain fields. *J. Theor. Biol.*, **117** : 79-106.

HAMMEL, H.T. (1956) — Infrared emissivities of some arctic fauna. *J. Mammal.*, **37** : 375-378.

HARRISON, L.G. (1987) — What is the status of reaction-diffusion theory thirty-four years after Turing ? *J. Theor. Biol.*, **125** : 369-384.

HOFSTADTER, D. (1979) — *Gödel, Escher, Bach : an eternal golden braid.* Basic Books, New York.

HÖRSTADIUS, S. (1939) — The mechanics of sea urchin development studied by operative methods. *Biol. Rev.*, **14** : 132.

HÖRSTADIUS, S. (1950) — Transplantation experiments to elucidate interactions and regulations within the gradient system of the developing sea urchin egg. *J. Exp. Zool.*, **113** : 245-276.

HUTCHINSON, J.C.D. and G.D. BROWN (1969) — Penetrance of cattle coats by radiation. *J. Appl. Physiol.*, **26** : 454-464.

JI, S. (1988) — Watson-Crick and Prigoginian forms of genetic information, (Letter to the Editor). *J. Theor. Biol.*, **130** : 239-245.

LEHNINGER, A.L. (1970a) — *Biochemistry.* Chapter 36. *The molecular basis of morphogenesis.* Worth Publishers, Inc., New York, (2nd ed.).

LEHNINGER, A.L. (1970b) — *Biochemistry.* Chapter 37. *The origin of life.* Worth Publishers, Inc., New York, (2nd ed.).

MURRAY, J.D. (1982) — Parameter space for Turing instability in reaction-diffusion mechanisms : a comparison of models. *J. Theor. Biol.*, **98** : 143-163.

NICOLIS, G and I. PRIGOGINE (1977) — *Self-organization in nonequilibrium systems.* Wiley-Interscience, New York.

PIERCE, J.R. (1980) — *An introduction to information theory.* Dover, New York, (2nd revised ed.).

POPPER, K.R. and J.C. ECCLES (1977) — *The self and its brain. An argument for interactionism.* Springer-Verlag, Berlin, Heidelberg.

PRIGOGINE, I. (1967) — In : *Fast Reactions and Primary Processes in Chemical Kinetics* (Claesson, S., Ed.). Almqvist and Wiksell, Stockholm, Interscience, New York, p. 371.

SMITH, L.J. (1980) — Embryonic axis orientation in the mouse and its correlation with blastocyst relationships to the uterus. *J. Embryol. Exp. Morph.*, **55** : 257-277.

STEINBERG, M.S. (1970) — Does differential adhesion govern self-assembly processes in histogenesis ? Equilibrium configurations and the emergence of a hierarchy among populations of embryonic cells. *J. Exp. Zool.*, **173** : 395-434.

THALLER, CH. and G. EICHELE (1987) — Identification and spatial distribution of retinoids in the developing chick limb bud. *Nature*, **327** : 625-628.

THALLER, CH. and G. EICHELE (1990) — Isolation of 3,4-didehydroretinoic acid, a novel morphogenetic signal in the chick wing bud. *Nature*, **345** : 815-819.

THOM, R. (1974) — *Modèles mathématiques de la morphogenèse. Recueil de textes sur la théorie des catastrophes et ses applications.* Inédit, Union Générale d'Editions (collection 10/18), Paris VI, (319 pp).

THOMPSON, D'ARCY W. (1917) — *On growth and form.* Cambridge University Press, Cambridge.

TURING, A.M. (1952) — The Chemical basis of morphogenesis. *Phil. Trans. Roy. Soc. (London). B. Biol. Sc.*, **237** : 37-72.

UBBELS, G.A. and T.G. BROM (1984) — Cytoskeleton and gravity at work in the establishment of dorso-ventral polarity in the egg of *Xenopus laevis. Adv. Space Res.*, **4** : 9-18.

WADDINGTON, C.H. (1940) — *Introduction to modern genetic.* Allen and Unwin, New York.

WADDINGTON, C.H. (1968) — *Towards a Theoretical Biology, Prolegomena.* University Press, Edinburgh.

WADDINGTON, C.H. (1969) — *Towards a Theoretical Biology, Sketches.* University Press, Edinburgh.

WADDINGTON, C.H. (1970) — *Towards a Theoretical Biology, Drafts.* University Press, Edinburgh.

WADDINGTON, C.H. (1972) — *Towards a Theoretical Biology, Essays.* University Press, Edinburgh.

WATSON, J.D. and F.H.C. CRICK (1953) — A structure for deoxyribosenucleic acid. *Nature*, **171** : 737-738.

WEINBAUM, S., P. GANATOS, R. PFEFFER, G.B. WEN, M. LEE and S. CHIEN (1988) — On the time-dependent diffusion of macromolecules through transient open junctions and their subendothelial spread. 1. Short-time model for cleft exit region. *J. Theor. Biol.*, **135** : 1-30.

WEN, G.B., S. WEINBAUM, P. GANATOS, R. PFEFFER and S. CHIEN (1988) — On the time-dependent diffusion of macromolecules through transient open junctions and their subendothelial spread. 2.Long-time model for interaction between leakage sites. *J. Theor. Biol.*, **135** : 219-253.

WINFREE, A.T. (1974) — Rotating chemical reactions. *Sci. Am.*, **230** : 82-95.

WOLPERT, L. (1969) — Positional information and the spatial pattern of cellular differentiation. *J. Theor. Biol.*, **25** : 1-47.

WOLPERT, L. (1992) — The shape of things to come. *New Scientist*, **134** : 38-42.

ZIOMEK, C.A. and M.H. JOHNSON (1980) — Cell surface interaction induces polarization of mouse 8-cell blastomeres at compaction. *Cell*, **21** : 935-942.

APPENDIX : Definition of biological function in topological terms

It is important to clarify some of the misunderstanding that may arise from the interpretation of « function » as (biological) « effect ». In our opinion, this viewpoint is expressed in the assertion that « form precedes function » (De Loof, 1993). From the writings of THOM (1969, 1974), it is clear that « stable limit forms » are not primarily to be interpreted as the result of some biological process after differentiation and/or maturation of a biological object, being a macromolecular complex, a cell or an organ. A better understanding of the function notion is gained from the concept of « reification », used by JI (1988) to indicate the effectuating of the genetic information at the cellular level, and that is also called the intracellular dissipative structure (for a discussion of JI's argument see also ALLAERTS, 1992).

In general, biological functions can be related to the concepts of aptation and fitness (PRANGER, 1990), which approach allows for the incorporation of evolutionary-biological principles and causal reference into the biological function notion (NISSEN, 1970, 1971 ; PRANGER, 1990). In topological terms, and referring to THOM's (1974) definition of an asymptotic chreode, the biological function notion is related to an inverse mapping relation $\mathbf{G}^{-1}$, imaging aptations ($\mathbf{A}_i$) onto the developmental process represented in the subspace $\mathbf{W}$ of space-time $\mathbb{E}^4$:

$$\mathbf{G}^{-1} : \{\mathbf{A}_i\} \rightarrow \mathbf{W} \quad : \mathbf{W} \subset \mathbb{E}^4 \tag{1}$$

As biological phenomena can be parametrized in a local domain $\mathbf{B}^3 \times \mathbf{T}$ of space-time $\mathbb{E}^4$, the developmental representations ($\mathbf{F}$) of biological phenomena are in turn characterized by the mapping relation :

$$\mathbf{F} : \mathbf{B}^3 \times \mathbf{T} \rightarrow \mathbf{V} : \mathbf{V} \subset \mathbb{E}^3 \tag{2}$$

where $\mathbf{V}$ is the notation for the « unfolding space », spanned by a number of external variables (THOM, 1969 ; p. 318).

Two important implications result from the combination of the expressions (1) and (2), namely, that the biological functions thus defined have implicit reference to goals, as was mentioned by NISSEN (1971 ; p. 256). On the other hand, it ensues that biological functions are neither identical nor topologically equivalent (homeomorphic) to the developmental representations of the biological phenomena in space-time, obtained by so-called retraction from space-time onto some domain of the unfolding space, a well-known type of mapping relation in topology (ARMSTRONG, 1979). In turn, this implies that in terms of topology no chronological order can be established between biological form and function.

ADDITIONAL REFERENCES

ALLAERTS, W. (1992) — Inquiry into the spatio-temporal contingency of cellular communication systems. *Communication and Cognition*, **25** : 277-294.

ARMSTRONG, M.A. (1979) — *Basic Topology*. Springer Verlag, Berlin.

DE LOOF, A. (1993) — Differentiation : « Keep the genome constant but change over and over again its ionic and/or macromolecular environments ? » A conceptual synthesis. *Belg. J. Zool.*, **123** : 77-91.

NISSEN, L. (1970) — Canfield's functional translation schemata. *Brit. J. Phil. Sci.*, **21** : 193-201.

NISSEN, L. (1971) — Neutral functional statement schemata. *Philosophy of Science*, **38** : 251-257.

PRANGER, R. (1990) — Towards a pluralistic concept of function. Function statements in biology. *Acta Biotheoretica*, **38** : 63-71.

THOM, R. (1969) — Topological models in biology. *Topology*, *8* : 313-335.

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