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# DESCRIPTION DE L'APPAREIL DE WEBER DU TÉLÉOSTÉEN CRÉTACÉ MARIN *CLUPAVUS MAROCCANUS* ET SES IMPLICATIONS PHYLOGÉNÉTIQUES

par

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## RÉSUMÉ

L'auteur décrit l'appareil de Weber du téléostéen crétacé marin *Clupavus maroccanus* et commente les relations phylogénétiques de *Clupavus* au sein des Ostariophysi et avec trois autres Otophysi marins archaïques, *Lusitanichthys, Chanoides* et *Salminops.*

*Mots clefs* : *Clupavus maroccanus*, appareil de Weber, Otophysi archaïques, phylogénie.

# Description of the Weberian apparatus of the marine Cretaceous teleost *Clupavus maroccanus* and its bearing on the phylogeny

## SUMMARY

The author describes the Weberian apparatus of the marine Cretaceous teleost *Clupavus maroccanus* and debates about the phylogenetic relationships of *Clupavus* within the Ostariophysi and with three other archaic marine Otophysi, *Lusitanichthys, Chanoides* and *Salminops.*

*Key words* : *Clupavus maroccanus*, Weberian apparatus, archaic Otophysi, phylogeny.

## INTRODUCTION

*Clupavus* Arambourg, 1950 est assurément l'un des téléostéens crétacés les plus controversés quant à sa position systématique.

A l'origine, Arambourg (1950, 1954) et Lehman (1966) incluaient dans ce genre toutes les petites espèces téléostéennes primitives du Crétacé connues à l'époque et considéraient *Clupavus* comme une forme de transition entre les Leptolepidae et les

Clupéiformes de la sous-famille des Dussumieriinae. BERTIN et ARAMBOURG (1958) érigèrent même pour lui la famille des Clupavidae qu'ils situaient au sein du sous-ordre des Clupeoidei.

Toutefois, ces attributions ne reposaient pas sur des bases anatomiques solides. PATTERSON (1970) et TAVERNE (1973 a, b, 1975 a, b, 1976, 1977, 1982) montrèrent l'extrême hétérogénéité du genre *Cluvapus*. Aujourd'hui, l'espèce-type *Clupavus maroccanus* Arambourg, 1968 du Cénomanien marin du Djebel Tselfat (Maroc) est généralement regardée comme la seule espèce valide du genre.

*Clupavus maroccanus* est un petit téléostéen, assez mal préservé, connu par trente-cinq exemplaires complets ou fragmentaires conservés dans les collections de l'Institut de Paléontologie du Muséum National d'Histoire Naturelle à Paris.

TAVERNE (1973 a, 1977) en a décrit le squelette et l'a reconstitué selon un modèle clupéoïde. Il a inclus les Clupavidae dans le sous-ordre des Clupeoidei mais sans les apparenter plus particulièrement aux Dussumieriinae. Les conclusions de TAVERNE (1977) reposaient essentiellement sur l'anatomie du complexe urophore et sur l'identification d'un *recessus lateralis*.

Par la suite, GAYET (1981) a critiqué l'interprétation de TAVERNE (1977) et a rapporté l'existence d'un appareil de Weber chez *Clupavus maroccanus*, ce qui en faisait automatiquement un représentant du vaste groupe des Otophysi *sensu* ROSEN et GREENWOOD, 1970.

J'ai voulu tester cette hypothèse de parenté proposée par GAYET (1981) et j'ai donc repris l'étude du matériel concerné. Force m'a été de constater qu'un appareil de Weber existait bien chez *Clupavus maroccanus*, quoique quelque peu différent dans son anatomie du schéma proposé par GAYET (1981, fig. 15, p. 185), et que ce poisson appartenait donc effectivement au super-ordre des Otophysi et non pas aux Clupeoidei comme je l'avais pensé jusqu'alors.

Le présent travail sera donc essentiellement consacré à l'étude de cet appareil de Weber de *Clupavus maroccanus* et à ses implications sur la phylogénie des Otophysi. Je ne rappellerai que brièvement l'ostéologie générale de *Clupavus maroccanus*, insistant plutôt sur quelques détails qui ne figurent pas dans ma description précédente (TAVERNE, 1977) ou en rectifiant certaines erreurs. Je comparerai aussi *Clupavus maroccanus* avec quelques Otophysi fossiles archaïques récemment découverts.

## MATÉRIEL ET MÉTHODE

J'ai revu l'intégralité du matériel de *Clupavus maroccanus* récolté au Djebel Tselfat (Maroc) et conservé dans les collections du Muséum National d'Histoire Naturelle à Paris (cf. les listes publiées dans ARAMBOURG, 1954, p. 26 et TAVERNE, 1977, p. 699). Il me faut encore préciser qu'entre mes premiers examens de ce matériel qui se sont échelonnés de 1969 à 1974 et ma récente révision de 1987, j'ai pu constaté que les étiquettes numérotées de plusieurs spécimens avaient été interchangées.

Mon étude a été menée au moyen d'un stéréomicroscope WILD M5. Certains détails anatomiques ont été observés sous immersion dans l'eau. Les dessins ont été réalisés au moyen d'une chambre claire (camera lucida).

## ÉTUDE OSTÉOLOGIQUE DE CLUPAVUS MAROCCANUS

### Le crâne

La voûte crânienne (Fig. 1) est formée par de grands frontaux et de vastes pariétaux. Ces derniers sont séparés l'un de l'autre par une longue fontanelle fronto-occipitale, ainsi qu'on peut le voir sur le spécimen T140G et D. Le supraoccipital est rejeté en arrière de cette fontanelle et est encadré par les épiotiques. Les ptérotiques longent les pariétaux. L'exemplaire T.140G montre le canal supraorbitaire qui traverse le frontal et se prolonge sur le pariétal en une commissure pariétale. L'autre face du spécimen (T.140D) exhibe une brève commissure épiphysaire en avant de la fontanelle fronto-occipitale et qui relie entre eux les canaux supraorbitaires gauche et droit. Le pariétal supporte également le sommet de la commissure extrascapulaire. La base de cette commissure est portée par le supratemporal. Le canal postorbitaire traverse le ptérotique et se poursuit sur le supratemporal.

C'est l'exemplaire T.88G qui montre le plus clairement le mésethmoïde (Fig. 1). Il s'agit d'un petit os bifurqué vers l'arrière et qui porte, de chaque côté, un très fort processus latéral sur lequel s'articulent à la fois le maxillaire et le palatin. Les ethmoïdes latéraux sont bien développés. Il n'y a pas de rhinosphénoïde en arrière des ethmoïdes latéraux, ni de kinethmoïde en avant du mésethmoïde, ni non plus d'ethmo-palatin entre le palatin et le maxillaire ou de préethmoïde au-dessus du vomer.

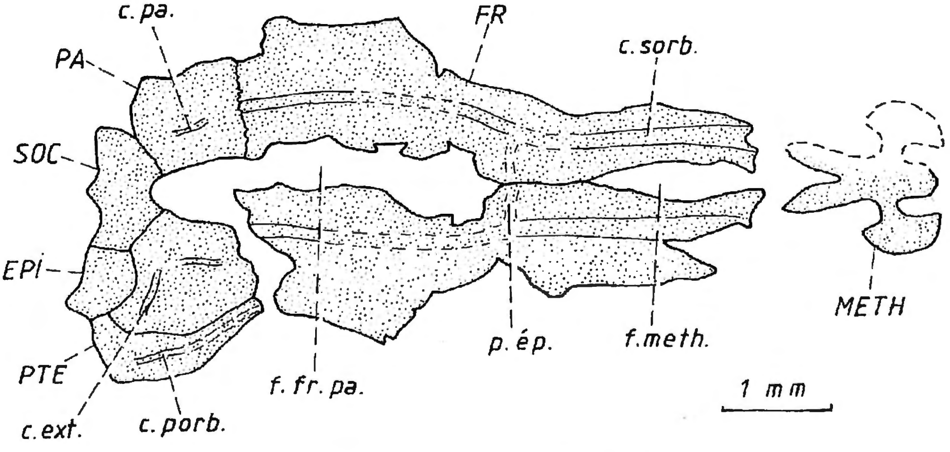

Fig. 1 — La voûte crânienne de *Clupavus maroccanus* d'après le spécimen T.140G et le mésethmoïde d'après le spécimen T.88G. Le pont épiphysaire est ajouté d'après le spécimen T.140D.

Les mâchoires sont édentées. Le prémaxillaire est allongé et porte un petit processus ascendant symphysaire. Le maxillaire est étroit dans sa partie antérieure et large dans sa moitié postérieure. Il y a deux grands supramaxillaires. La mandibule est de forme leptolépide, c'est-à-dire courte, haute et garnie d'un processus coronoïde en position avancée. Le rétroarticulaire est exclu de la fossette articulaire pour le carré.

Le vomer et le parasphénoïde sont édentés. Le spécimen T.243D montre un petit processus basiptérygoïde sur le parasphénoïde. L'orbitosphénoïde et les pleurosphénoïdes sont petits et largement séparés du parasphénoïde par la fenêtre optique. Taverne (1977) signale un basisphénoïde. Mais j'ai pu observer que le fragment osseux interprété comme un bélophragme sur l'exemplaire T.243D n'est qu'un morceau du prootique. Sur aucun autre individu, je n'ai pu identifier une pièce qui serait un indiscutable basisphénoïde. Il paraît donc que cet os faisait défaut chez *Clupavus maroccanus*.

Le cercle des os circumorbitaires semble complet. Le supraorbitaire s'allonge contre la portion antérieure du bord frontal et touche à l'antorbitaire qui est réduit, alors que le premier infraorbitaire (lacrymal) est assez vaste. Taverne (1977) ne décrit pas les autres os de la série qu'il n'a pu retrouver. En fait, l'exemplaire T.145 montre qu'il y a au total cinq infraorbitaires et que les deux infraorbitaires postérieurs sont vastes, couvrent partiellement l'hyomandibulaire et possèdent un bord antérieur situé nettement en avant de l'hyomandibulaire (Fig. 2). Le dermosphénotique n'est pas connu mais était certainement présent. Il y a un anneau osseux sclérotique fait de deux plaques.

J'ai retrouvé sur plusieurs spécimens (T.243G, T.245G, T.246 et T.257G) la structure que j'avais cru être un *recessus lateralis* (Taverne, 1977, p. 700). On peut y voir sur le ptérotique, au niveau du canal postorbitaire, deux orifices assez proches l'un de l'autre. Le second devait servir au raccord avec le canal mandibulo-préoperculaire et j'avais interprété le premier comme le point de passage du canal orbitaire. Cependant, la position et la forme des infraorbitaires postérieurs de *Clupavus maroccanus* ne permettent pas de voir dans cette structure un véritable *recessus lateralis*. En effet, les Clupéiformes qui possèdent tous un tel *recessus* offrent aussi des modifications concomitantes des ultimes infraorbitaires et du dermosphénotique. Tout d'abord, le composant membranodermique de ces os est réduit. Ensuite, on note un recul de ces os par rapport à l'hyomandibulaire, de façon à venir s'aligner directement sous le ptérotique, au niveau du *recessus* (cf. par exemple Ridewood, 1904, p. 451). Ce n'est manifestement pas le cas en ce qui concerne *Clupavus maroccanus*. Je pense donc maintenant que le canal orbitaire, chez ce poisson, rejoignait le canal supraorbitaire sur le frontal, au niveau du sphénotique, mais que ce canal orbitaire, parvenu sur le dermosphénotique, envoyait un diverticule postérieur qui, lui, s'en allait contacter le canal postorbitaire beaucoup plus en arrière, sur le ptérotique, à hauteur du premier orifice mentionné ci-avant. Une telle situation n'est pas exceptionnelle chez les Otophysi (cf. par exemple Roberts, 1969, fig. 3, p. 446).

Le suspensorium est partiellement visible sur plusieurs individus et notamment le T.256G où l'on peut observer que l'entoptérygoïde et l'ectoptérygoïde sont

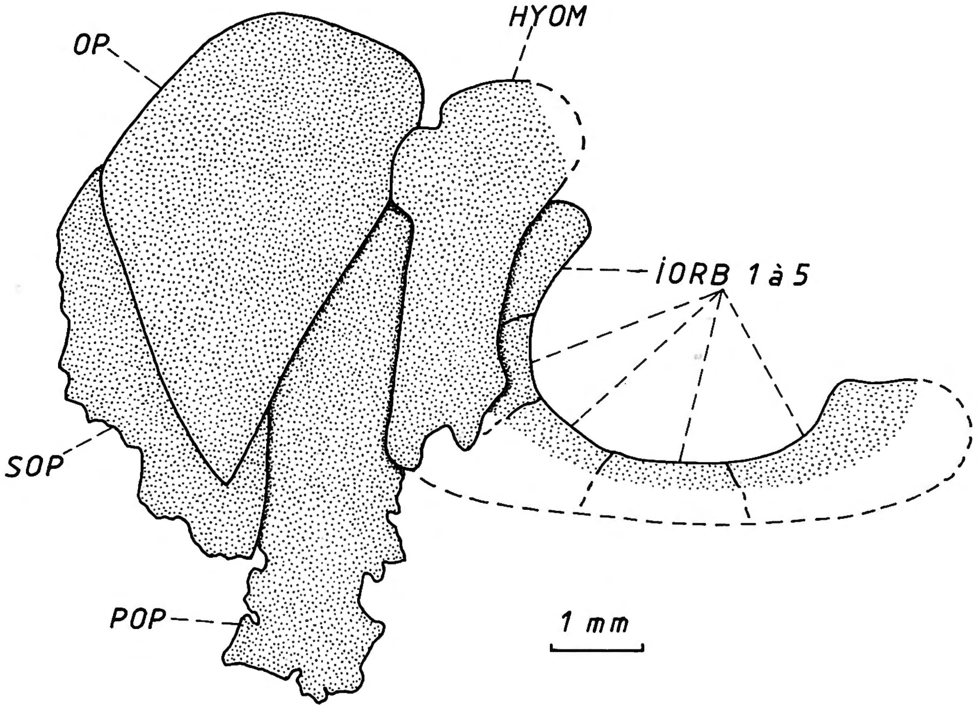

Fig. 2 — Partie de la joue et des os orbitaires gauches de *Clupavus maroccanus* en vue interne d'après le spécimen T.145.

allongés, étroits et édentés, que le métaptérygoïde est bas et de forme à peu près rectangulaire et qu'il n'y a pas de fenêtre entre ce métaptérygoïde et le carré. Le spécimen T.142D montre un petit palatin en forme de bâtonnet qui s'articule directement sur le maxillaire à l'avant et dont l'extrémité postérieure est coincée entre les pointes antérieures des entoptérygoïde et ectoptérygoïde. Il n'y a pas de fossette articulaire de l'entoptérygoïde pour le palatin. Il n'y a pas non plus de dermopalatin.

La série des os operculaires est bien développée. L'operculaire est arrondi dorsalement, pointu ventralement et surplombe un sous-operculaire vaste et allongé. Le préoperculaire montre de longues branches dorsale et ventrale. Il couvre presque complètement un grand interoperculaire. Les rayons branchiostèges sont peu nombreux mais aucun spécimen ne permet d'en faire un compte vraiment précis. Il n'y a pas de plaque gulaire.

## L'appareil de Weber

Gayet (1981, fig. 15, p. 185) a donné un schéma de son interprétation de l'appareil de Weber tel qu'elle l'a observé chez l'exemplaire T.88D. En fait, chez ce spécimen, l'appareil de Weber n'apparaît que comme une empreinte fort vague où seul l'os suspensorium est clairement visible. Les structures wéberiennes sont visibles également chez le spécimen T.243G mais, là aussi, sous forme d'empreintes assez vagues. Par contre, l'exemplaire T.142D a conservé des traces osseuses de l'appareil de Weber et non plus de simples empreintes, ce qui en permet une compréhension meilleure quoiqu'encore imparfaite vu le mauvais état de conservation (Figs 3 et 4).

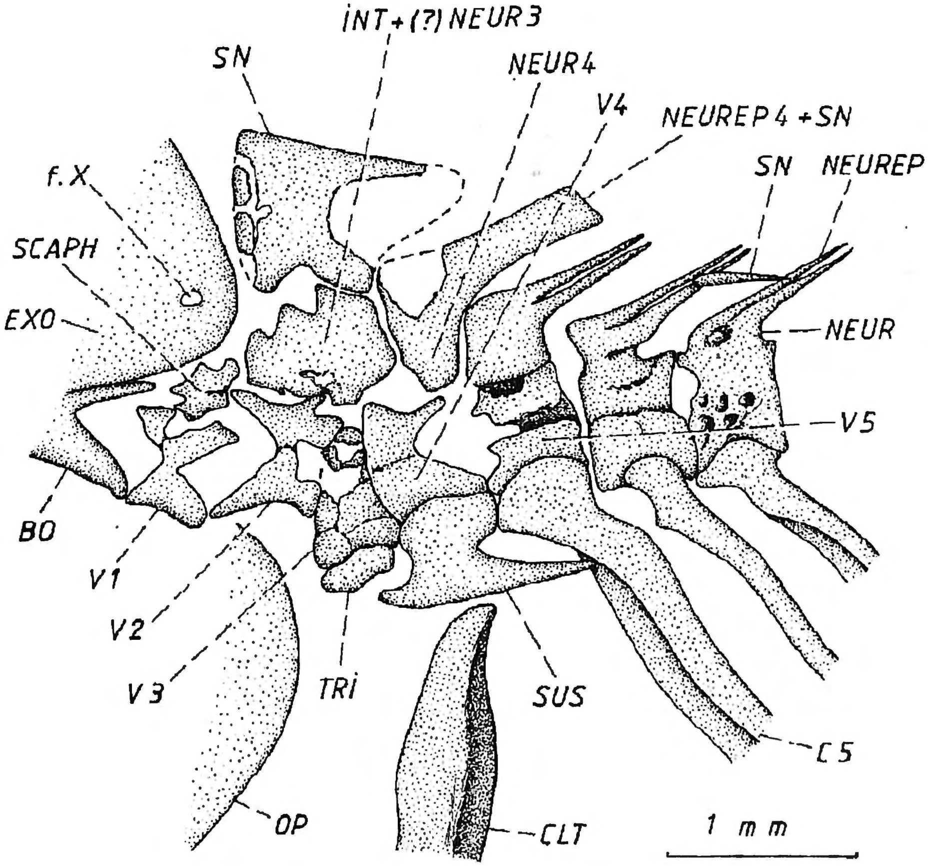

Fig. 3 — L'appareil de Weber de *Clupavus maroccanus* d'après le spécimen T.142D.

Les premiers vertèbres ne sont pas fusionnées et ne paraissent pas non plus notablement plus courtes que les vertèbres suivantes. La quatrième vertèbre est la première à porter un arc neural prolongé par une neurépine. Cette neurépine est forte et longue. Sur l'individu T.88D, elle se termine en pointe et est surplombée par un petit supraneural. Chez les spécimens T.142D et T.243G, on ne distingue plus ce petit supraneural mais la neurépine en question montre une extrémité postérieure très nettement élargie. Cela indique que, dans ce cas, le supraneural s'est soudé à la neurépine. Les neurépines de la cinquième vertèbre et des suivantes sont nettement plus grêles, moins longues et bifides. Au-dessus de la première vertèbre, on distingue un petit scaphium. Je n'ai pas pu identifier le claustrum, cette pièce n'étant clairement conservée sur aucun spécimen. Une vaste pièce neurale chevauche les deuxième et troisième vertèbres. Cette pièce peut être interprétée de plusieurs manières. Il pourrait s'agir d'un intercalarium. On sait que cet os est plutôt petit chez les Otophysi actuels (FINK et FINK, 1981, fig. 14, p. 325, fig. 15, p. 326, fig. 16, p. 327, p. 328 et fig. 18, p. 329) mais qu'il peut être, au contraire, de forte taille chez certains Otophysi fossiles archaïques (GAYET, 1981, fig. 11, p. 180, 1985, fig. 8, p. 99, fig. 22, p. 111, fig. 23, p. 112 ; PATTERSON, 1984, fig. 13, p. 444, fig. 14, p. 445). Il se pourrait également qu'on soit en présence de l'arc neural de la troisième vertèbre et que l'intercalarium de petite taille se soit perdu à la fossilisation. Il est possible enfin qu'il s'agisse de l'intercalarium et de l'arc neural de la troisième vertèbre soudés l'un à l'autre, quoiqu'une telle fusion ne soit pas connue chez d'autres Otophysi. Un unique et énorme supraneural surplombe cette pièce neurale et remplit l'espace qui va du bord occipital du crâne jusqu'à la neurépine de la quatrième vertèbre. Les éventuelles parapophyses de la deuxième vertèbre et des vertèbres suivantes ne sont guère visibles sur aucun spécimen. Seul l'exemplaire T.243G montre clairement l'empreinte du tripus. C'est un os allongé qui forme une sorte de crochet dirigé vers l'arrière et qui est appendu à la troisième vertèbre. L'os suspensorium est accroché à la quatrième vertèbre. Il est formé de deux branches, l'une antérieure qui est partiellement conservée sur l'exemplaire T.142D mais qui se voit intégralement sur le spécimen T.88D, l'autre postérieure qui forme un long crochet tourné vers l'arrière. C'est la cinquième vertèbre qui porte la première paire de côtes, lesquelles sont légèrement plus larges que les côtes ultérieures.

Il s'agit donc d'un appareil de Weber légèrement différent de ceux des Otophysi actuels, notamment par le développement important de l'éventuel intercalarium. Par contre, l'unique supraneural hypertrophié qui s'étend du crâne jusqu'au niveau de la quatrième vertèbre rappelle le cas des Characiformes (FINK et FINK, 1981, fig. 15, p. 326, fig. 16, p. 327).

Comme les appareils de Weber des diverses formes fossiles analysés par GAYET et CHARDON (1987), celui de *Clupavus maroccanus* pourrait être parfaitement fonctionnel si l'on postulait l'existence d'un manubrium malheureusement non conservé chez nos exemplaires fossiles. L'os suspensorium et le tripus étaient vraisemblablement appliqués contre la tunique de la portion antérieure de la vessie natatoire. Les variations de pression se transmettaient probablement du tripus au manubrium via un ligament, puis du manubrium au scaphium via un autre ligament, avant d'être alors répercutées dans le sinus impair périlymphatique et de là à l'oreille interne.

### Les ceintures

La ceinture scapulaire est complète et comporte, dans chacune de ses moitiés, un posttemporal, un hypercleithrum, un cleithrum, une scapula, un coracoïde, un mésocoracoïde et trois postcleithra dont le plus ventral s'allonge en une sorte d'épine qui passe sous la nageoire pectorale. A la ceinture pelvienne, l'os pelvien ne présente pas de bifurcation antérieure.

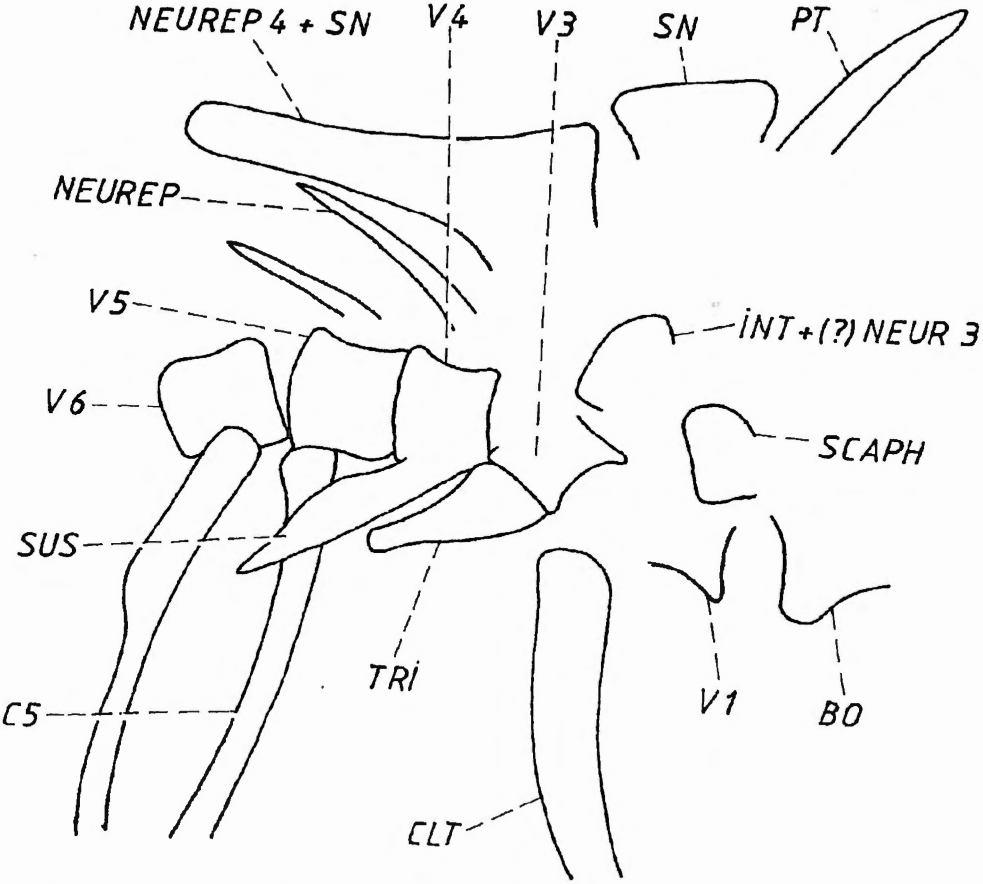

Fig. 4 — L'empreinte de l'appareil de Weber de *Clupavus maroccanus* d'après le spécimen T.243G.

## Le squelette caudal

Le complexe urophore de *Clupavus maroccanus* a été figuré par TAVERNE (1977, fig. 9, p. 711) et par GAYET (1981, fig. 16, p. 186 et fig. 17, p. 187). Rappelons que selon les exemplaires, les vertèbres préurale I et urale I peuvent être séparées ou plus ou moins fusionnées. Mais, même dans ce dernier cas, les deux centres qui composent la vertèbre complexe demeurent parfaitement discernables et la vertèbre complexe est très allongée. Le centre ural II est petit mais indépendant. La vertèbre préurale II porte une neurépine complète et la vertèbre préurale I une neurépine raccourcie. Il n'y a que deux épuraux. On compte six hypuraux. Le premier hypural est large et s'articule souvent sur la vertèbre urale I mais il peut aussi perdre sa tête articulaire comme chez certains Clupéiformes et certains Otophysi. Le deuxième hypural reste étroit et sa tête articulaire est soudée à la vertèbre urale I. On relève trois paires d'uroneuraux dont la première, qui est aussi la plus longue, se soude à la vertèbre préurale I. La nageoire caudale compte 19 rayons principaux dont 17 branchus. Les rayons le plus ventral du lobe supérieur et le plus dorsal du lobe inférieur montrent des extrémités antérieures élargies en palette.

## DISCUSSIONS

### Position de *Clupavus* au sein des Ostariophysi

La classification la plus élaborée des Ostariophysi jamais proposée est indubitablement celle que Fink et Fink (1981) ont établi sur base de la méthodologie cladiste mais appliquée aux seules formes actuelles de ce groupe. C'est donc par rapport à elle que nous devons tenter de situer *Clupavus* mais sans oublier toutefois que Gayet (1985, 1986b et 1993) s'est livrée à une critique très fouillée des données sur lesquelles repose l'étude de Fink et Fink (1981) et qu'elle a clairement montré que beaucoup des caractères considérés dans ce travail étaient sujets à caution quant à leur interprétation. La polémique entre ces différents auteurs s'est même envénimée jusqu'à l'échange de propos peu aimables (Fink *et al.*, 1984 ; Gayet, 1986a). Des réserves sont donc de mise.

Fink et Fink (1981) définissent les Ostariophysi par quinze caractères. Huit de ceux-ci (8, 54, 56, 57, 117, 118, 127) concernent des structures molles qui ne sont pas discernables chez *Clupavus*. Par contre, notre poisson est conforme aux caractères 7 (perte du basisphénoïde), 20 (perte du dermopalatin), 58 (perte du supraneural antérieur à la première vertèbre), 63 (élargissement des pièces neurales antérieures qui se connectent entre elles et avec les exoccipitaux pour former une sorte de toit au-dessus du tube neural), 64 (perte de l'arc neural autogène antérieur à la première vertèbre) et 111 (soudure des hémépines antérieures à la vertèbre préurale II aux centres vertébraux correspondants) mais diffère pour ce qui est du caractère 41 (perte des supramaxillaires). Ces six apomorphies partagées par *Clupavus* et les Ostariophysi modernes paraissent suffire à justifier l'inclusion du premier au sein des seconds (Fig. 5) même si, prise séparément, aucune de ces apomorphies n'est exclusive des Ostariophysi (Patterson, 1984, p. 449) et malgré que Gayet (1985, 1986b et 1993) ait montré que les caractères 7 et 58 souffraient quelques rares exceptions, que le caractère 63 était généralement absent chez les Gonorhynchiformes et que le caractère 111 avait dû s'acquérir en parallèle chez les Gonorhynchiformes et les Otophysi puisqu'il était souvent absent chez les formes fossiles des deux groupes. Quant au caractère 41, l'existence de supramaxillaires bien développés chez *Clupavus* et certains autres Otophysi fossiles (Gayet, 1981, 1985, 1986b ; Patterson, 1984) suffit à en démontrer la fausseté. Il est manifeste que la perte des supramaxilaires est apparue de façon indépendante chez les Gonorhynchiformes et les Otophysi et ne peut donc servir à caractériser l'ensemble des Ostariophysi.

Sans entrer dans une analyse détaillée des caractères, il est clair que *Clupavus* n'offre pas les apomorphies par lesquelles Fink et Fink (1981) et Gayet (1993) définissent les Gonorhynchiformes. *Clupavus* ne peut pas appartenir à cet ordre d'Ostariophysi, d'autant plus que son appareil de Weber le rattache manifestement aux Otophysi.

Selon FINK et FINK (1981), quatorze synapomorphies définissent les Otophysi. Les 123 et 126 traitent de structures qui ne se fossilisent pas. Par ailleurs, l'état de conservation de *Clupavus* ne permet de trancher pour ce qui est du caractère 81 (fusion des parapophyses des deux premières vertèbres aux centres vertébraux correspondants). Mais, de toutes façons, GAYET (1986b, p. 60) a exposé les raisons pour lesquelles ce caractère doit être rejeté des synapomorphies valables pour les Otophysi. Des onze caractères qui demeurent, *Clupavus* en possède sept : les 59 (perte du supraneural antérieur à l'arc neural de la deuxième vertèbre), 60 (le ou les deux supraneuraux antérieurs présentent une expansion ventrale qui s'articule sur les arcs neuraux des troisième et quatrième vertèbres), 66 (le premier arc neural modifié en scaphium et claustrum), 69 (le deuxième arc neural modifié en intercalarium), 85 (les parapophyses et les côtes de la troisième vertèbre modifiées en tripus), 88 (les parapophyses et les côtes de la quatrième vertèbre modifiées en os suspensorium) et 114 (le deuxième hypural soudé au centre vertébral correspondant). Il y a lieu, cependant, de se référer aux commentaires de GAYET (1986b, p. 57) concernant le caractère 59 et à son rejet du caractère 114 comme synapomorphie valable des Otophysi (*ibid.*, p. 62). *Clupavus* ne montre pas les caractères 30 (le métaptérygoïde en forme d'axe et déterminant une fenêtre avec le carré), 78 (les quatre premières vertèbres raccourcies par rapport aux suivantes), 102 (l'os pelvien bifurqué antérieurement) et 110 (les vertèbres préurale I, urale I, urale II ainsi que la première paire d'uroneuraux soudées en une vertèbre terminale prolongée par un pleurostyle). Mais, là aussi, GAYET (1986b, p. 53) a montré l'ambiguïté du caractère 30 et rejeté les caractères 78 (*ibid.*, p. 60), 102 (*ibid.*, p. 61) et 110 (*ibid.*, p. 61) de la liste des synapomorphies valables pour l'ensemble des Otophysi. Les synapomorphies liées à la présence d'un appareil de Weber (60, 66, 69, 85 et 88) que présente *Clupavus* suffisent, à elles seules, à reconnaître à ce poisson la qualité d'Otophysi.

FINK et FINK (1981) divisent les Otophysi en deux lignées : les Cypriniformes et les Characiphysi qui groupent, à leur tour, les Characiformes, les Siluroidei et les Gymnotoidei.

Ces auteurs caractérisent les Cypriniformes par dix-sept synapomorphies dont ils reconnaissent, cependant, que plusieurs ont été acquises en parallèle dans d'autres groupes d'Otophysi. Deux caractères (40 et 125) touchent à l'anatomie des tissus mous et ne sont guère utilisables vis à vis d'un fossile. Cinq autres caractères (47, 48, 50, 52 et 53) sont des spécialisations du squelette branchial et un sixième (37) concerne la position des processus ascendants des prémaxillaires par rapport à la ligne symphysaire et au mésethmoïde. Nous ne disposons pas d'informations concernant ces six caractères chez *Clupavus*. Les caractères 21, 22 et 25 sont des apomorphies de la région palato-ptérygoïdienne qui n'existent pas chez *Clupavus*. Des six caractères restants de la liste de FINK et FINK (1981), *Clupavus* en montre deux : les 42 (l'absence de dents aux machoîres) et 115 (la réduction à deux du nombre des épuraux). Toutefois, le caractère 42 est simplement une symplésiomorphie de l'ensemble des Ostariophysi (GAYET, 1986b, pp. 55-56 ; PATTERSON, 1984, p. 435) et le caractère 115 est apparu plusieurs fois dans les différentes lignées d'Ostariophysi (GAYET, 1986b, p. 62). Ces deux traits anatomiques ne peuvent donc pas avoir valeur de synapomorphies des Cypriniformes. Quant aux quatre derniers caractères, à savoir les 1 (présence d'un kinethmoïde), 4 (présence d'un préethmoïde), 84 (allongement très marqué des apophyses latérales de la deuxième vertèbre) et 96 (la réduction à un du nombre des postcleithra), ils ne sont pas présents chez *Clupavus*. La courte analyse qui précède montre que les synapomorphies les plus typiques des Cypriniformes et notamment celles des régions bucco-ethmoïdienne et palato-ptérygoïdienne font défaut à *Clupavus* et que ce poisson ne peut donc pas être un représentant de cet ordre.

Les Characiphysi sont définis par quinze synapomorphies dans FINK et FINK (1981). Le caractère 97 se rapporte au ligament de Baudelot, une structure non-fossilisable dont nous ne savons rien chez *Clupavus*. Les caractères 2, 3 et 39 concernent des spécialisations de la région bucco-ethmoïdienne que *Clupavus* ne possède pas. Les caractères 61, 62, 68, 72, 73, 75, 77, 79, 82 et 86 sont des apomorphies de l'appareil de Weber. L'état de *Clupavus* pour les caractères 73, 82 et 86 est inconnu. *Clupavus* ne présente pas les caractères 61, 68, 72, 75 et 79. Il offre, par contre, les caractères 62 (un seul grand supraneural modifié qui vient se placer contre l'arrière du neurocrâne) et 77 (l'arc neural de la cinquième vertèbre fusionné avec cette dernière). Mais GAYET (1986b, p. 60) a souligné l'ambiguïté de ce caractère 77 qui s'est réalisé aussi chez des groupes non-characiphysi et que certains Characiphysi fossiles ne possèdent pas. *Clupavus* offre la première moitié du caractère 112 (la soudure du parhypural au centre vertébral correspondant). Cependant, la fusion du parhypural à la vertèbre préurale I s'est réalisée tant de fois chez les téléostéens qu'on ne peut guère envisager ce trait comme une synapomorphie valable des Characiphysi. Un seul caractère spécialisé, le 62, rapproche donc *Clupavus* des Characiphysi. Tous les autres caractères, au contraire, l'en éloignent.

Remarquons encore que quelques exemplaires de *Clupavus* mais pas tous, offrent le caractère 113 (le premier hypural perd sa tête articulaire et se décroche de la vertèbre urale I) que FINK et FINK (1981, p. 341) considèrent comme une synapomorphie des Characiformes au sein des Characiphysi. Toutefois, ce caractère est assez faible puisqu'il ne se réalise pas chez tous les spécimens de *Clupavus* et qu'il apparaît aussi chez des Gonorhynchiformes et de nombreux Clupéiformes (PATTERSON, 1984, p. 448 ; GAYET, 1986b, p. 62).

Si l'on cherche à placer *Clupavus* dans le cladogramme de FINK et FINK (1981), la solution la plus parcimonieuse est de l'introduire dans les Characiphysi puisqu'il partage avec ces derniers la synapomorphie 62 (Fig. 5). *Clupavus* devient alors la lignée-sœur plésiomorphe de tous les autres Characiphysi puisqu'il ne présente pas les autres synapomorphies de ce vaste groupe. Par rapport aux données de FINK et FINK (1981), une telle position de notre téléostéen fossile impliquerait évidemment que les apomorphies 30, 78, 102 et 110 qui caractérisent l'ensemble des Otophysi et l'apomorphie 41 qui vaut pour la totalité des Ostariophysi, aient été réalisées à plusieurs reprises et de façon indépendante chez les Gonorhynchiformes, les Cypriniformes et les Characiphysi. Cela irait à l'encontre de la parcimonie. Mais en fait, le problème ne se pose pas vu que les travaux de GAYET (1981, 1985, 1986b, 1993) et de PATTERSON (1984) ont abouti, ainsi qu'on l'a déjà dit, au rejet de ces différents caractères. On peut également laisser *Clupavus* en tant que lignée-sœur plésiomorphe de tous les autres Otophysi si l'on estime que le caractère 62 a été acquis indépendamment chez *Clupavus* et chez les Characiphysi. Mais ce serait là une solution moins parcimonieuse que la première.

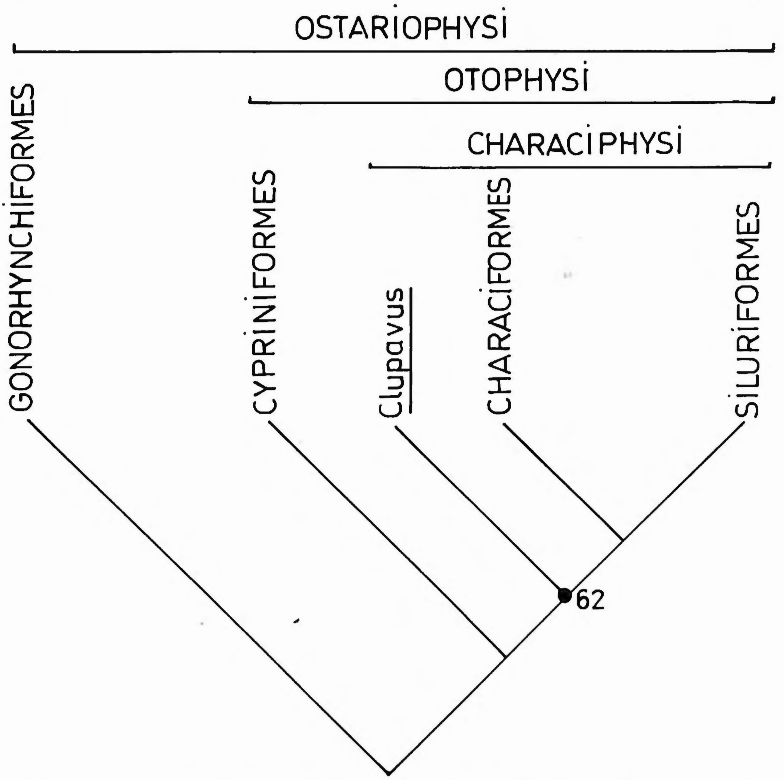

Fig. 5 — *Clupavus* introduit dans le cladogramme de Fink et Fink (1981) selon les commentaires du présent article. Le numéro 62 fait référence à l'apomorphie 62 (un seul grand supraneural entre le neurocrâne et la quatrième vertèbre) de Fink et Fink (1981).

## Comparaison entre Clupavus et Lusitanichthys

*Lusitanichthys characiformis* Gayet, 1981 est un petit téléostéen du Cénomanien moyen marin du Portugal. Il possède un appareil de Weber et, à ce titre, doit être rangé dans les Otophysi. Son étude anatomique a été menée par Gayet (1981, 1985). A premier abord, *Clupavus maroccanus* et *Lusitanichthys characiformis* se ressemblent beaucoup, à tel point que Gayet (1981) a intégré le second à la famille des Clupavidae.

Un examen comparatif des crânes montre cependant des différences considérables au-delà des ressemblances superficielles. En fait, l'ostéologie céphalique de *Lusitanichthys* se révèle nettement plus évoluée que celle de *Clupavus*. *Lusitanichthys* exhibe déjà un ethmo-palatin inséré entre le palatin et le maxillaire, un mésethmoïde aux processus latéraux raccourcis, un rhinosphénoïde en arrière de l'ethmoïde latéral, une hypertrophie considérable de l'autopalatin, un net raccourcissement de l'ectoptérygoïde, un entoptérygoïde qui vient surplomber vers l'arrière le métaptérygoïde et une fosse temporale qui, outre son ouverture postérieure traditionnelle, s'ouvre aussi dorsalement par une fenêtre entre le supraoccipital, l'épiotique et le pariétal. Ce sont là autant de structures apomorphes encore inconnues chez *Clupavus.*

Les appareils de Weber des deux poissons sont notablement différents. Celui de *Lusitanichthys* demeure en bonne partie plus archaïque puisqu'on y trouve encore un arc neural individualisé au niveau de la troisième vertèbre et qu'il n'y a pas fusion des deuxième et troisième supraneuraux. *Lusitanichthys* offre cependant un trait spécialisé qui n'existe pas chez *Clupavus*, le considérable raccourcissement de la troisième vertèbre.

Les squelettes caudaux des deux formes sont quasi identiques, si ce n'est qu'il y a toujours trois épuraux et cinq hypuraux chez *Lusitanichthys*, pour deux épuraux et six hypuraux chez *Clupavus*. Les mêmes variations par fusion d'éléments peuvent s'observer chez l'un comme chez l'autre.

### Comparaison entre *Clupavus* et *Chanoides*

*Chanoides macropoma* (Agassiz, 1834) provient du célèbre gisement éocène marin du Monte Bolca, en Italie. Son ostéologie a été étudiée par PATTERSON (1984) qui y a révélé la présence d'un appareil de Weber. Les différences qui séparent *Chanoides* de *Clupavus* sont déjà beaucoup plus marquées. Au niveau du crâne, en effet, *Chanoides* montre un mésethmoïde aux processus latéraux réduits, un kinethmoïde entre le vomer et les maxillaires, un ethmo-palatin entre le palatin et le maxillaire, un prémaxillaire dépourvu de proccessus ascendant, un unique supramaxillaire, un extramaxillaire, un gros palatin, une fossette articulaire palatine à l'extrémité antérieure de l'entoptérygoïde, un ectoptérygoïde raccourci et une ouverture dorsale de l'épiotique vers la fosse temporale sous-jacente.

L'appareil de Weber de *Chanoides* se rapproche davantage de celui de *Lusitanichthys* que de celui de *Clupavus*, puisque lui aussi présente une troisième vertèbre extrêmement raccourcie, un arc neural bien individualisé sur cette troisième vertèbre et deux vastes supraneuraux au niveau des deuxième et troisième vertèbres. L'intercalarium y est déjà notablement plus petit et le tripus fort réduit, ce qui différencie *Chanoides* non seulement de *Clupavus* mais aussi de *Lusitanichthys.*

Le squelette caudal de *Chanoides* montre encore un centre ural II indépendant mais une fusion déjà parfaite entre les vertèbres préurale I et urale I. Les autres éléments du complexe urophore ne diffèrent guère de ce qui peut s'observer chez *Clupavus*, si ce n'est que *Chanoides* a encore conservé trois épuraux.

## Comparaison entre *Clupavus* et *Salminops*

*Salminops ibericus* Gayet, 1985 est un minuscule téléostéen du Cénomanien supérieur marin du Portugal, connu par son seul exemplaire holotype, fort mal conservé de surcroît. Gayet (1985) en a étudié le squelette et a pu mettre en évidence l'existence d'un appareil de Weber.

*Salminops* paraît déjà nettement plus évolué dans la voie des Characiphysi classiques et même des Characiformes que *Clupavus* puisque ses mâchoires sont dentées, que les supramaxillaires manquent, qu'il existe une suture symphysaire digitée entre les deux dentaires, que le mésethmoïde a perdu les processus latéraux et que l'on trouve une fenêtre entre le métaptérygoïde et le carré.

Au niveau de l'appareil de Weber, *Salminops*, comme *Clupavus*, ne montre qu'un seul grand supraneural au-dessus des trois premières vertèbres et un vaste intercalarium. Par contre, l'arc neural de la troisième vertèbre est bien individualisé chez *Salminops* et l'os suspensorium y est nettement plus ramassé que chez *Clupavus*.

Dans le complexe urophore, la fusion des centres préural I et ural I est beaucoup plus poussée chez *Salminops* que chez *Clupavus*. Comme *Clupavus*, *Salminops* possède encore un centre ural II autogène et trois uroneuraux. *Salminops* offre aussi trois épuraux, soit un de plus que *Clupavus*.

## L'origine des Ostariophysi

Après *Lusitanichthys*, *Salminops* et *Chanoides*, *Clupavus* représente donc un quatrième genre d'Ostariophysi archaïques marins. *Clupavus* renforce ainsi l'idée déjà plusieurs fois avancée par Gayet (1981, 1982, etc.) que les Ostariophysi sont d'origine marine et non pas dulçaquicole comme on le pense généralement. De plus, toutes ces formes primitives appartiennent au bassin de la Mésogée eurafricaine. Il est donc possible que ce soit là le berceau géographique du grand groupe des Ostariophysi.

## LISTE DES ABRÉVIATIONS DES FIGURES DU TEXTE

BO : basioccipital
C5 : côtes de la cinquième vertèbre
CLT : cleithrum
EPI : épiotique (épioccipital)
EXO : exoccipital
FR : frontal
HYOM : hyomandibulaire
INT : intercalarium
IORB 1 à 5 : infraorbitaux 1 à 5
METH : mésethmoïde
NEUR : arc neural (neurarcual)
NEUR 3, 4 : arcs neuraux des troisième et quatrième vertèbres
NEUREP : neurépine (neuracanthe)
NEUREP 4 : neurépine de la quatrième vertèbre
OP : operculaire
PA : pariétal
POP : préoperculaire
PT : posttemporal
PTE : ptérotique
SCAPH : scaphium

SN : supraneural
SOC : supraoccipital
SOP : sous-operculaire
SUS : os suspensorium
TRI : tripus
v1 à 6 : six premières vertèbres
c. ext. : commissure sensorielle extrascapulaire
c. pa. : commissure sensorielle pariétale
c. porb. : canal sensoriel postorbitaire
c. sorb. : canal sensoriel supraorbitaire
f. X : foramen du nerf vague (X)
f. fr. pa. : fontanelle fronto-occipitale (fronto-pariétale)
f. meth. : fontanelle mésethmoïdienne
p. ép. : pont sensoriel épiphysaire.

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# HUMIVOROUS NASUTE TERMITES (ISOPTERA : *NASUTITERMITINAE*) FROM THE PANAMA CANAL AREA

by

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## SUMMARY

The taxonomic status of five species of humivorous nasutes from the Panama Canal area is examined. The following species are recognized : *Subulitermes zeteki* (Snyder, 1924), *Subulitermes denisae*, new species, *Atlantitermes kirbyi* (Snyder, 1926), *Ereymatermes panamensis*, new species, and *Coatitermes clevelandi* (Snyder, 1926). Their descriptions are herein given or complemented with emphasis on worker anatomy, diagnostic characters are provided and generic assignments are discussed.

*Key words* : Termitidae, taxonomy, new species, Neotropical Region.

## INTRODUCTION

The Nasutitermitinae comprise a large array of fully nasute genera showing, to a variable extent, adaptations towards a humivorous diet. AHMAD (1950) hypothesized that the full nasute soldier (characterized by a pear-shaped head capsule with a long nasus and reduced mandibles) evolved twice : once from a primitive form related to *Procornitermes*, which gave rise to a lineage comprising, among others, the genus *Nasutitermes* ; and once from a primitive form related to *Paracornitermes*, which gave rise to another lineage comprising, among others, the genus *Subulitermes*. Although the phylogeny proposed by AHMAD (1950) has been recently widely criticized (see MILLER, 1986), it is clear that the two lineages of full nasutes he proposed correspond to ecologically distinct groups : the former (the *Nasutitermes* group) comprises sound wood or grass feeding genera, whereas the latter (the *Subulitermes* group) comprises genera showing variously developed adaptations to a diet of soft vegetable matter or humus, such as an increase in the concavity of the molar areas and a reduction of the molar ridges of the worker mandibles

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(Sands 1965, Deligne 1966). The two groups are therefore traditionally referred to as, respectively, xylophagous and humivorous nasutes.

Three species of humivorous nasutes were described from Panama by Snyder (1924, 1926) : *Nasutitermes (Subulitermes) zeteki, Nasutitermes (Subulitermes) kirbyi* and *Nasutitermes (Convexitermes) clevelandi.* Since then, no further species has been added to this list (Nickle and Collins, 1992), although the generic taxonomy went through several changes. The subgenera *Subulitermes* and *Convexitermes* were erected to generic status (Fuller, 1921 ; Snyder, 1949). Later, Fontes (1979, 1982) created several new genera and the new combinations *Araujotermes zeteki, Atlantitermes kirbyi* and *Coatitermes clevelandi.* He subsequently published comparative studies of the digestive tube (Fontes, 1987a) and mandibles (Fontes, 1987b) of all Neotropical humivorous nasute genera, represented by their type species. The denominations proposed by Fontes were recently adopted by Nickle and Collins (1992).

Collections made in 1990-1991 in Barro Colorado Nature Monument and Parque Nacional Soberanía yielded two additional species of humivorous nasutes. The need for a clear taxonomic context to describe the new taxa led me to re-examine the status of the three previously known species. In this paper, I describe the new species as *Subulitermes denisae* and *Ereymatermes panamensis* and discuss their generic assignment together with that of the other three species formerly described by Snyder (1924, 1926).

## MATERIAL AND METHODS

The new material examined in this study comes either from the island of Barro Colorado in the Panama Canal (9° 10′N, 79° 50′W) or from Parque Nacional Soberanía, on the north side of the Canal, west of the town of Gamboa. Specimens were collected and fixed in FAA (formol-alcohol-acetic acid) and preserved in 70 % ethanol. Camera lucida drawings of digestive tubes were made after removal of abdominal walls, fat tissues and malpighian tubules. Pictures of mandibles and enteric valves were taken after dissection, dehydration by ethanol and toluene and mounting on microscope slides in balsam. Pictures of soldier heads and molar areas of worker mandibles were taken with a ISI-DS 130 scanning electron microscope after ethanol dehydration, immersion for at least 12 h in hexamethyldisilazane, air drying at 60° C, and metallization with gold. Soldier heads were treated by 6 % KOH for 2-6 h at 60° C before dehydration, as this method was found to clean the head capsule both externally and internally, especially from remnants from the frontal gland, and preclude deformation during dessication and metallization.

The terminology used for describing the mandibles follows that of Sands (1972) : the left mandible index is $L_a/L_1$, where $L_a$ is the distance separating the apical tooth from the fused first and second marginals, and $L_1$ the distance separating the fused first and second marginals from the third marginal. The molar areas are called molar prominence (left mandible) and molar plate (right mandible). Each genus or species heading is followed by a short bibliography, limited to the original description and publications of new combinations.

Abbreviations :
BCI : Barro Colorado Island, Panama.
IRSN : Institut Royal des Sciences Naturelles, Brussels, Belgium.
NMNH : U.S. National Museum of Natural History, Washington D.C., U.S.A.
STRI : Smithsonian Tropical Research Institute, Panama.

## DESCRIPTIONS

### Genus *Subulitermes* Holmgren, 1910

*Eutermes* subgenus *Subulitermes* : HOLMGREN, 1910, pp. 208, 218.

Type species : *Eutermes microsoma* Silvestri, 1901.

Soldier monomorphic, fully nasute ; rostrum thin, mandibles without points ; head capsule little or not constricted behind antennae.

Worker (according to FONTES, 1987a, b) : around 3 vestigial molar ridges on molar prominence, 4-5 on molar plate ; left mandible index 1.02-1.12 ; gizzard with complete armature, but weakly sclerotized ; mesentero-proctodeal junction oblique, no distinct mixed segment ; malpighian tubules in two pairs, separated by a short space at their point of attachment to the mesentero-proctodeal junction ; paunch not constricted after junction of enteric valve ; armature of enteric valve composed of six subequal swellings with small spines ; colon long and narrow.

### *Subulitermes zeteki* (Snyder, 1924)
(Figs 1, 6, 11, 16, 20)

*Nasutitermes (Subulitermes) zeteki* : SNYDER, 1924, p. 32 (soldier).

*Subulitermes zeteki* (Snyder) : SNYDER, 1949, p. 342.

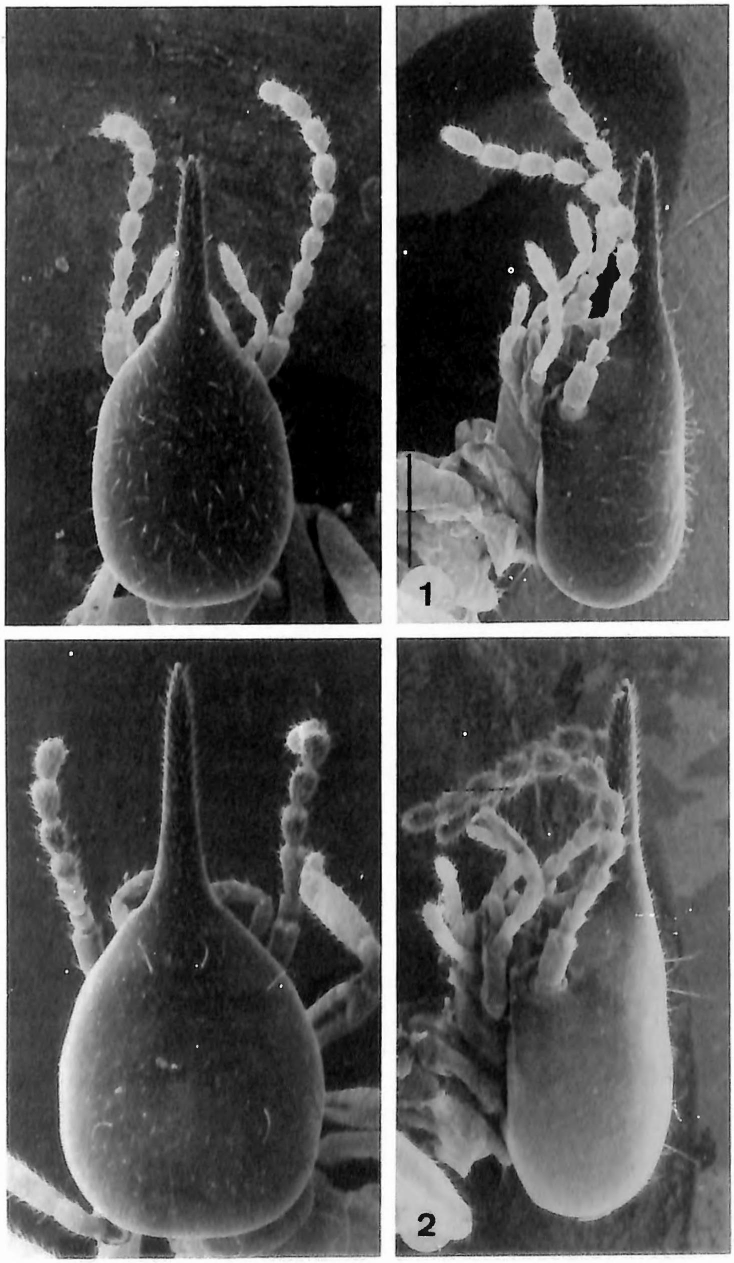
*Araujotermes zeteki* (Snyder) : FONTES, 1982, p. 100.

Material examined :

NMNH. # Z1731 : soldiers and workers from type series. Summit, Canal Zone, Panama, 29.vii.1922. Coll. J. Zetek and I. Molino, det. T.E. Snyder. One soldier, kept separately with two workers, possibly holotype, but not so designated on label. # Z2479 : 5 soldiers, 3 workers, 3 reproductive nymphs. BCI, 3.x.1924. Coll. J. Zetek, det. T.E. Snyder.

Coll. J.M. Pasteels. # 71 : BCI, 10.viii.1969. Large sample with soldiers, workers, larvae and reproductive nymphs, from old log.

Coll. Y. Roisin. # PANT7 : BCI, 8.xii.1990. Soldiers, workers and a few nymphs in small earth nest nearby stump occupied by *Embiratermes chagresi* (Snyder). # PANT12 : BCI, 10.xii.1990. Soldiers, workers and two nymphs from rotten stump. # PANT42 : BCI, 27.xii.1990. Soldiers, workers, larvae and reproductive nymphs, next to a nest of *Microcerotermes* sp. in dead palm tree on the ground. # PANT84 : BCI, 7.v.1991. Soldiers, workers, larvae and nymphs in decayed log. # PANT112 : BCI, 5.vi.1991. Soldiers and workers. # PANT118 : BCI, 12.vi.1991. Soldiers and workers under log in forest.



Figs 1-2. — Scanning electron micrographs of soldier heads, dorsal view (left) and profile (right). 1. *Subulitermes zeteki*. — 2. *S. denisae*, paratype. Scale bar = 0.25 mm.

# PANT125 : BCI, 15.vi.1991. Soldiers and workers. # PANT155 : BCI, 23.viii.1991. Soldiers, workers, larvae and 1 nymph under bark of log on forest floor.

Imago unknown. Fourth instar nymphs possess antennae with 12 articles, with article 3 presenting two constrictions, suggesting that the alate possesses 14-jointed antennae.

The soldier is the smallest Panamanian humivorous nasute (Table 1). Most specimens have unequivocally 11-jointed antennae, but in some colonies, article 3 tends to be constricted. Head capsule yellow, reddish on rostrum, elongated, almost straight in profile, bearing numerous hairs of various lengths (Fig. 1).

The worker has mandibles (Figs 6, 11) with five to seven ridges on molar prominence, at least 4 on molar plate ; left mandible index 0.90-0.95. Antennae 12-jointed. Digestive tract (Fig. 16) as described for *Subulitermes*. Enteric valve armature composed of six swellings bearing about 25 short spines (Fig. 20). Rudimentary lobes at junction between enteric valve and paunch. Head width unimodal, 0.48-0.57 mm (mean = 0.535 mm ; based on 2 × 100 individuals from colonies # PANT84 and 155).

### *Subulitermes denisae* sp. nov.
### (Figs 2, 7, 12, 17, 21)

Material examined :

Type colony : # PANT173 : Pipeline Road, near Limbo Camp, Parque Nacional Soberanía, Panama, 19.ix.1991. Large sample from rotten stump in forest, with soldiers, workers, larvae and reproductive nymphs. Holotype : soldier, in the collection of the IRSN.

Paratype colonies. # PANT19 : BCI, 13.xii.1990. Soldiers, workers and one reproductive nymph from stump of palm tree. # PANT176 : BCI, 27.ix.1991. Soldiers, workers and a few larvae from tree stump. Paratypes will be deposited in the IRSN, STRI and the University of Panama.

Name derivation : this species is dedicated to Denise Thorin, for her continuous support since we met in Panama.

Imago unknown. Nymphs of the fourth instar possess 13-jointed antennae, with article 3 presenting a constriction, suggesting that the alate possesses 14-jointed antennae.

Soldier larger than that of *S. zeteki* (Table 1). Antennae 12-segmented. Overall aspect not so elongated as *S. zeteki.* Head capsule yellow, reddish on rostrum, elongated, almost straight in profile, with 4 long setae at base of rostrum and 2 on vertex, and numerous very small hairs (Fig. 2).

Worker less elongated than in *S. zeteki.* Antennae 13-jointed. Mandibles (Figs 7, 12) very similar to those of *S. zeteki.* Molar prominence with 5-6 ridges, molar plate with at least 5 ridges. Left mandible index 0.75-0.97 (N = 10 workers from type colony). Digestive tube (Fig. 17) very similar to that of *S. microsoma* (see FONTES 1987a, figs 86-89). Enteric valve swellings (Fig. 21) garnished with 5-10 spines. Head width unimodal, 0.59-0.65 mm (mean = 0.62 mm ; based on 2 × 100 individuals from colonies # PANT173 and 176).

## Genus *Atlantitermes* Fontes, 1979

*Atlantitermes* : FONTES, 1979, pp. 220-222.

Type species : *Atlantitermes guarinim* Fontes, 1979.

The original description does not provide diagnostic criteria for this genus. The following peculiarities were mentioned in subsequent papers (FONTES, 1987a, b).

Soldier with slightly, yet distinctly constricted head. Worker mandibles with at least 5 ridges on molar prominence, 4-5 on molar plate. Left mandible index 0.68-0.77, lower than in *Subulitermes*. Digestive tube configuration resembling that of *Subulitermes*. Enteric valve armature composed of six cushions (three large ones alternating with smaller ones), all garnished with small spines on their surface and larger ones on their edge. Weak constriction at junction between enteric valve and paunch.

### *Atlantitermes kirbyi* (Snyder, 1926)
(Figs 3, 8, 13, 18, 22)

*Nasutitermes (Subulitermes) kirbyi* : SNYDER, 1926, pp. 14-15 (soldier).

*Subulitermes kirbyi* (Snyder) : SNYDER, 1949, p. 340.

*Atlantitermes kirbyi* (Snyder) : FONTES, 1982, p. 107.

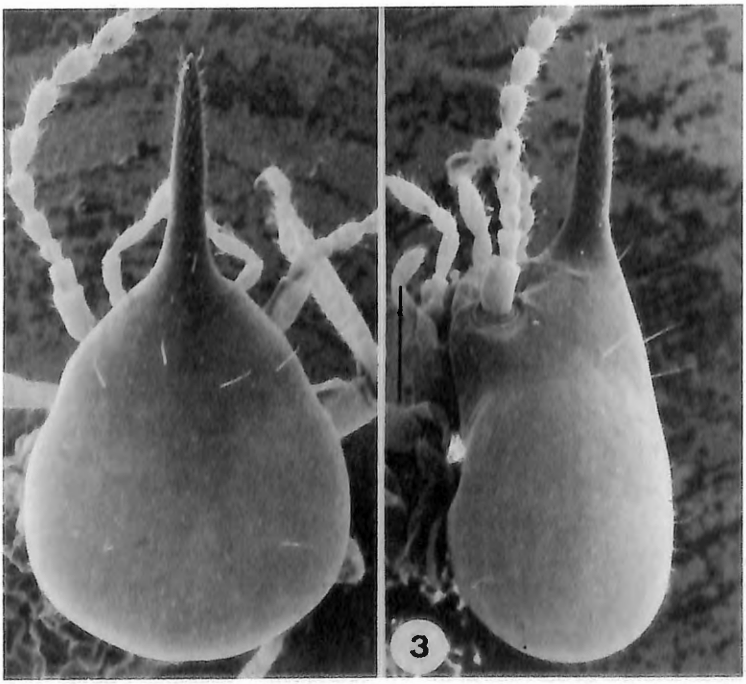


Fig. 3. — *Atlantitermes kirbyi*. Paratype soldier : head in dorsal view (left), in profile (right). Scale bar = 0.25 mm.

Material examined :

NMNH. Holotype soldier, BCI, Canal Zone, Panama, 3.ix.1925. Coll. H. Kirby. Paratype soldiers and workers, same data as holotype.

Soldier with 12-jointed antennae. Head capsule yellow, rostrum reddish. Head capsule (Fig. 3) slightly longer and distinctly wider than in *S. denisae* (Table 1), rostrum shorter and thicker, elevated. Four long setae near base of nose, two on vertex, and many minute hairs.

Worker with 13-jointed antennae. Mandibles as in Figs 8 and 13. Molar prominence and molar plate were worn on the two specimens examined, but the molar prominence showed at least 5 vestigial ridges. No ridge could be seen on the molar plate. Left mandible index difficult to calculate with precision due to mandible wear, but obviously high, near 1.4, on the two specimens examined. Digestive tube (Fig. 18) broader than in *A. guarinim*, paunch more voluminous. Enteric valve preceded by a slight, but distinct constriction. Armature (Fig. 22) as in generic description. Head width, 0.736-0.756 mm (based on 3 individuals from type colony).

## Genus *Ereymatermes* Constantino, 1991

*Ereymatermes* : CONSTANTINO, 1991, pp. 1-7, figs 1-18.

Type species : *Ereymatermes rotundiceps* Constantino, 1991.

This genus was created to accommodate a new species from Brazilian Amazonia.

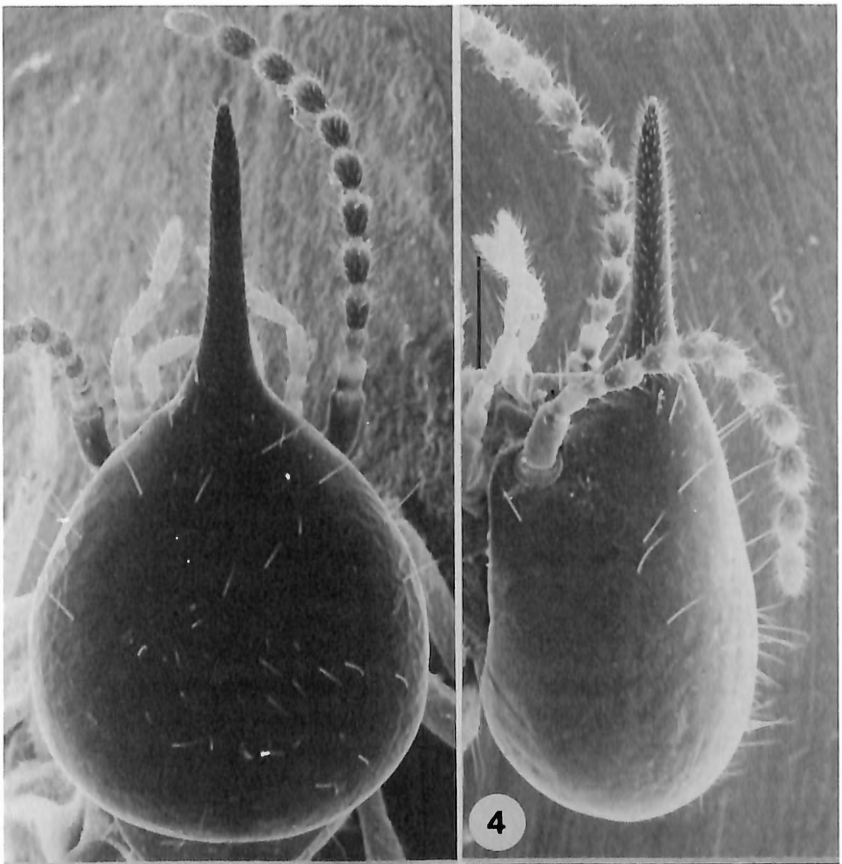
Soldier monomorphic, fully nasute ; rostrum thin, mandibles without points. Head capsule little or not constricted behind antennae ; antennae 12-segmented.

Worker remarkable for the configuration of its digestive tract. Enteric valve situated in a distinctive pocket and constituted by 6 equal flattened protrusions edged with numerous large spines, preceded by 6 dome-shaped swellings with 0-5 tiny spines. First section of the paunch U-shaped, delimited anteriorly by the enteric valve on the left and an almost symmetrical, yet unarmed, constriction to the right.

### *Ereymatermes panamensis* sp. nov.
(Figs 4, 9, 14, 19, 23)

Material examined :

Type colony : # PANT138 : BCI, 24.vi.1991. Soldiers, workers and larvae from underground chambers. Holotype : soldier, in the collection of the IRSN.



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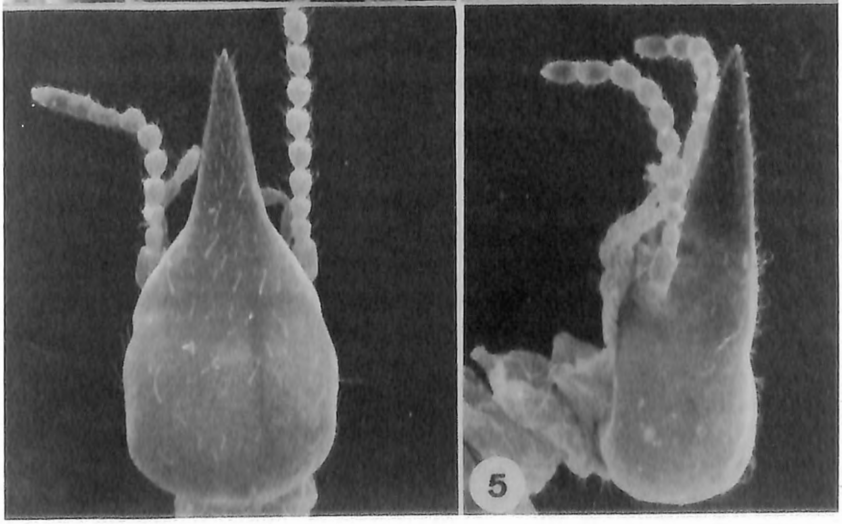

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Coll. Y. Roisin. # PANT13 : BCI, 10.xii.1990. Soldiers and workers from dead wood on forest floor. # PANT22a : BCI, 14.xii.1990. Soldiers and workers from stump of palm tree.

Imago unknown.

Soldier with 12-jointed antennae. Head capsule yellow, rostrum reddish. Head capsule not constricted behind antennae, pilose, regularly rounded posteriorly, nose thin, cylindrical, slightly upturned (Fig. 4). Very similar to the soldier of *E. rotundiceps*, except for being substantially smaller and having a relatively narrower head capsule. Distinguished from *S. denisae* by larger size (Table 1), wider, more rounded head capsule, covered with more numerous long setae, nasus very thin, slightly elevated. Distinguished from *A. kirbyi* by unconstricted and much more pilose head capsule, and more cylindrical, less elevated nose.

Worker with antennae of 13 segments. Mandibles as in Figs 9 and 14, with numerous but weak molar ridges ; left mandible index 1.5-1.7. General configuration of digestive tube (Fig. 19) and enteric valve (Fig. 23) indistinguishable from those of *E. rotundiceps* (compare with figs 13-17 in CONSTANTINO, 1991). Head width unimodal, 0.65-0.73 mm (mean = 0.695 mm ; based on 100 individuals from colony # PANT138). Distinguished from sympatric *Subulitermes* species by larger apical tooth and left mandible index, weaker molar ridges, and different digestive tract configuration and enteric valve armature. Difficult to distinguish from *A. kirbyi* : in this latter species, the paunch does not show a ventral constriction on the right side of the abdomen, and the enteric valve armature is different.

## Genus *Coatitermes* Fontes, 1982

*Coatitermes* : FONTES, 1982, pp. 104-105.

Type species : *Nasutitermes (Convexitermes) clevelandi* Snyder, 1926.

Soldier monomorphic, fully nasute, with very broad, conical rostrum.

Worker (after FONTES, 1987a, b) with at least 5 ridges on molar prominence, 4-5 on molar plate ; left mandible index 1.00-1.13. Configuration of worker digestive tract similar to that of *Subulitermes*. Enteric valve armature diagnostic, consisting of three major swellings alternating with minor ones, all bearing stout spines of various lengths (see FONTES, 1987a, fig. 60).

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Figs 4-5. — Scanning electron micrographs of soldier heads, dorsal view (left) and profile (right). — 4. *Ereymatermes panamensis*, paratype. — 5. *Coatitermes clevelandi*. Scale bar = 0.25 mm.

### *Coatitermes clevelandi* (Snyder, 1926)
(Figs 5, 10, 15, 24)

*Nasutitermes (Convexitermes) clevelandi* : SNYDER, 1926, pp. 15-16 (soldier, nymph).

*Convexitermes clevelandi* (Snyder) : SNYDER, 1949, p. 342.

*Coatitermes clevelandi* (Snyder) : FONTES, 1982, pp. 104-105, figs 9-16 (alate, soldier, worker).

Material examined :

Coll. Y. Roisin. # PANT3 : BCI, 5.xii.1990. Nest in rotten stump in forest. # PANT16 : BCI, 12.xii.1990. From terrestrial mound also occupied by *Anoplotermes parvus* Snyder. # PANT55 : Gigante Peninsula, 21.i.1991. Earth nest around tree stump, with queen, workers, soldiers, larvae and nymphs. # PANT60 : Gigante Peninsula, 29.i.1991. Nest in and under piece of dead wood on the ground, with queen. # PANT106 : Gigante Peninsula, 21.iii.1991. Nest at foot of *Astrocaryum* palm. Mixed with *Anoplotermes parvus*. # PANT128 : BCI, 15.vi.1991. Soldiers, workers, nymphs and alates from earthen sheeting running over crack in live tree, from ground to a height of at least 1.5 m. # PANT183 : Gigante Peninsula, 2.x.1991. Earthen construction about 1.5 cm thick on tree stump, with soldiers, workers, larvae and nymphs. Queen found in cell against the stump. This nest of *C. clevelandi* was contiguous to a nest of *Embiratermes chagresi* (Snyder) ; no aggression was observed between the two species as they came into contact when the nest was dissected.

The description of the imago by FONTES (1982) is adequate and needs few complements. The antenna is 14-segmented in the alate and tends to be so in the last two nymphal instars as well, although segments 3-5 are not completely separated.

Soldier almost as small as in *S. zeteki*. Unmistakable among Panamanian small nasutes for the broad conical shape of its rostrum (Fig. 5). Head capsule yellow, rostrum ferruginous, head capsule and rostrum covered with numerous short setae. Antennae 11-segmented.

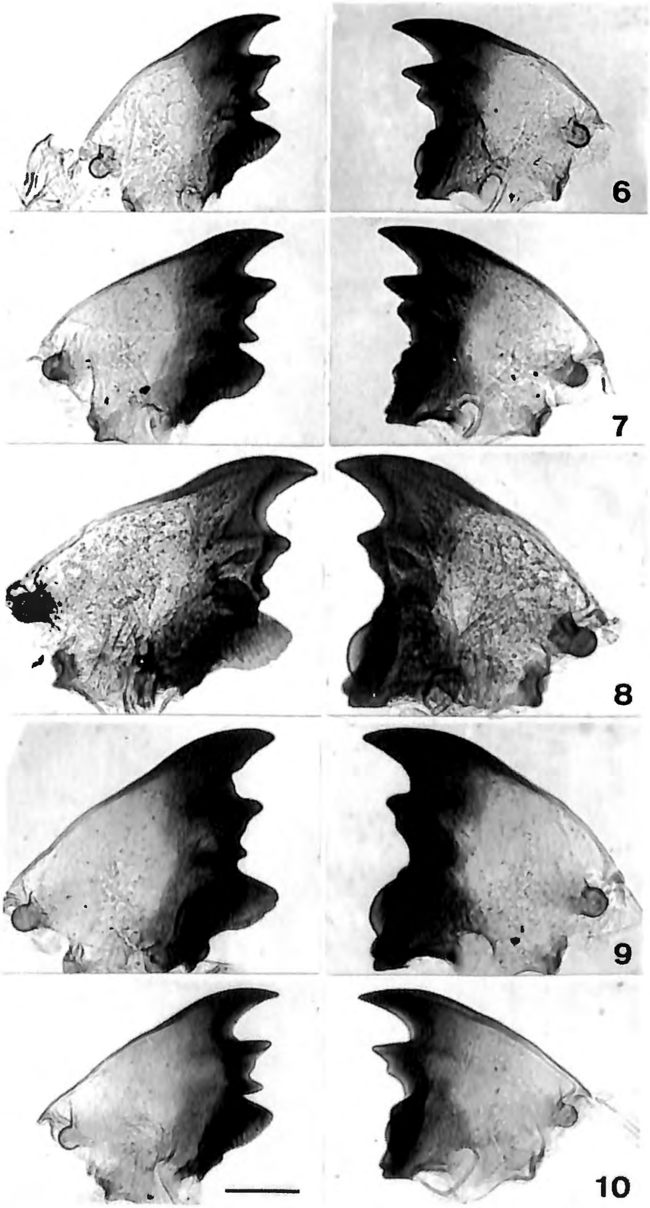
Worker with 12-segmented antennae, as in *S. zeteki*, but overall appearance much less elongated. Mandibles as in Figs 10 and 15. Both molar areas with 5 well-marked ridges and some faint ones. Left mandible index 1.07-1.37 (N = 10 individuals from colony # PANT183). The description of the digestive tract of workers by FONTES (1987a) fits the Panamanian specimens perfectly. Enteric valve armature diagnostic among Panamanian nasutes (Fig. 24). Head width unimodal, 0.57-0.64 mm (mean = 0.60 mm ; based on 3 × 100 individuals from colonies # PANT55, 60 and 183).

TABLE 1

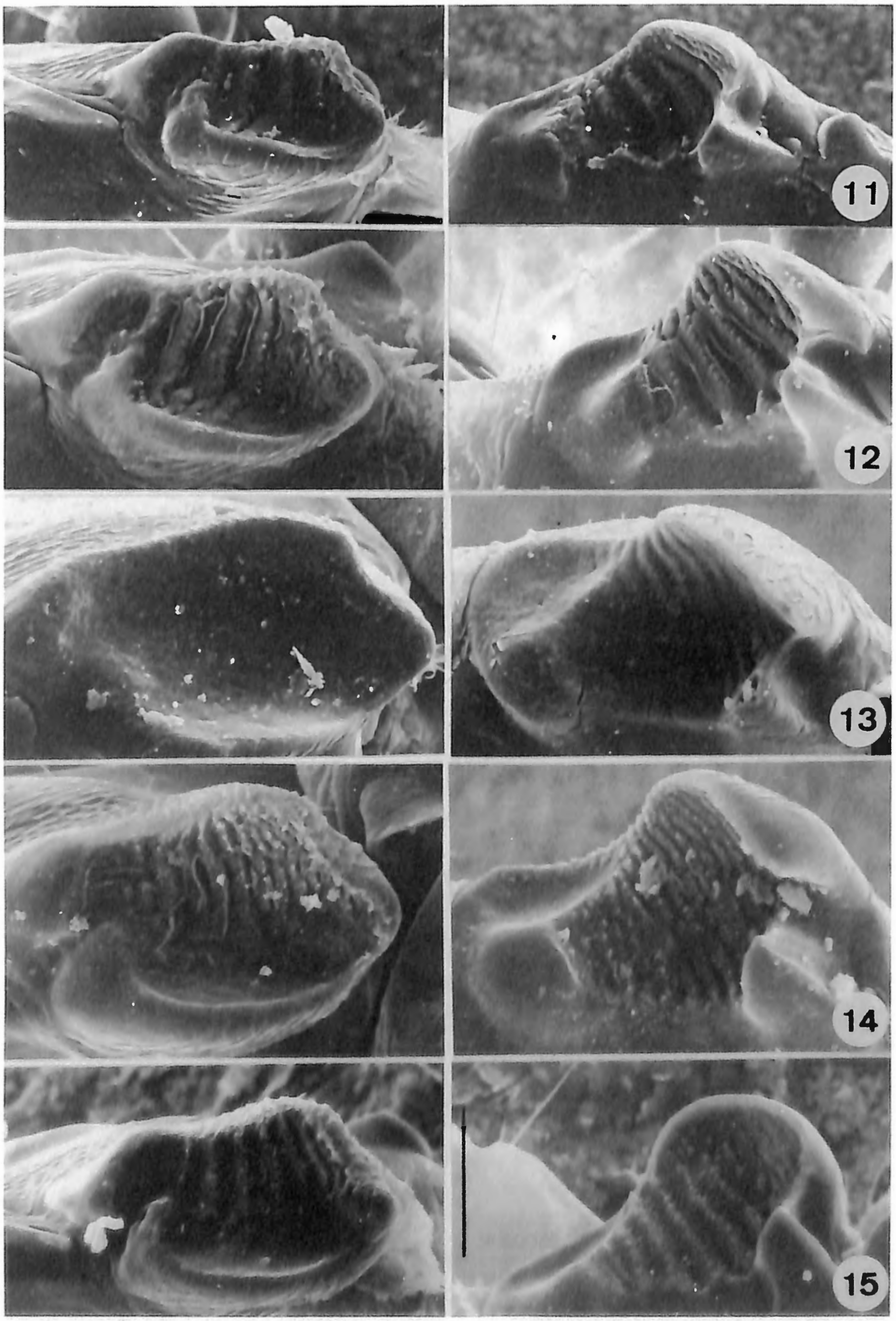
*Measurements of soldiers (in mm) of* Subulitermes zeteki, S. denisae, Atlantitermes kirbyi *and* Ereymatermes panamensis.

| | *Subulitermes zeteki* 12 soldiers from 4 colonies | | *Subulitermes denisae* 9 soldiers from 3 colonies | | *Atlantitermes kirbyi* 6 soldiers from type colony | | *Ereymatermes panamensis* 9 soldiers from 3 colonies | |
|---|---|---|---|---|---|---|---|---|
| | Range | Mean | Range | Mean | Range | Mean | Range | Mean |
| HL | 0.985-1.155 | 1.038 | 1.175-1.284 | 1.233 | 1.272-1.310 | 1.291 | 1.338-1.465 | 1.384 |
| RL | 0.376-0.510 | 0.416 | 0.504-0.562 | 0.530 | 0459-0.488 | 0.477 | 0.525-0.577 | 0.555 |
| HL-RL | 0.604-0.645 | 0.622 | 0.671-0.722 | 0.703 | 0.793-0.825 | 0.814 | 0.813-0.888 | 0.829 |
| HW | 0.455-0.517 | 0.485 | 0.544-0.610 | 0.588 | 0.686-0.692 | 0.688 | 0.680-0.812 | 0.731 |
| RW | 0.059-0.070 | 0.064 | 0.067-0.072 | 0.070 | 0.078-0.090 | 0.083 | 0.062-0.075 | 0.069 |
| HD | 0.303-0.381 | 0.345 | 0.395-0.439 | 0.417 | 0.455-0.486 | 0.468 | 0.475-0.541 | 0.493 |
| T3L | 0.473-0.562 | 0.512 | 0.626-0.683 | 0.660 | 0.689-0.757 | 0.726 | 0.683-0.744 | 0.711 |
| HL:HW | 2.074-2.234 | 2.140 | 2.023-2.210 | 2.096 | 1.848-1.910 | 1.876 | 1.804-1.979 | 1.895 |
| (HL-RL):HW | 1.182-1.364 | 1.285 | 1.152-1.252 | 1.194 | 1.153-1.203 | 1.183 | 1.094-1.196 | 1.135 |

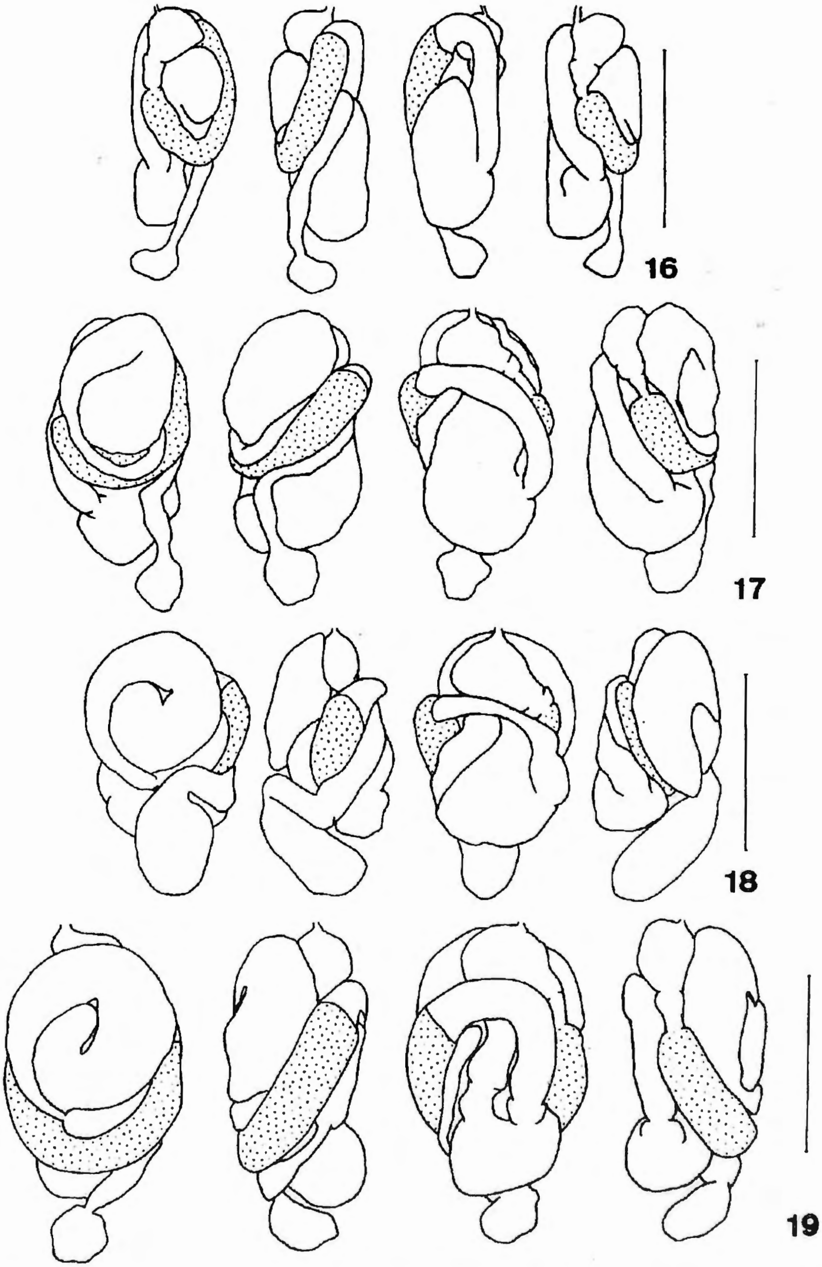
HL, head capsule length ; RL, rostrum length ; HW, head capsule width ; RW, rostrum width (at half length) ; HD, head capsule depth (excluding gula) ; T3L, length of hind tibia.



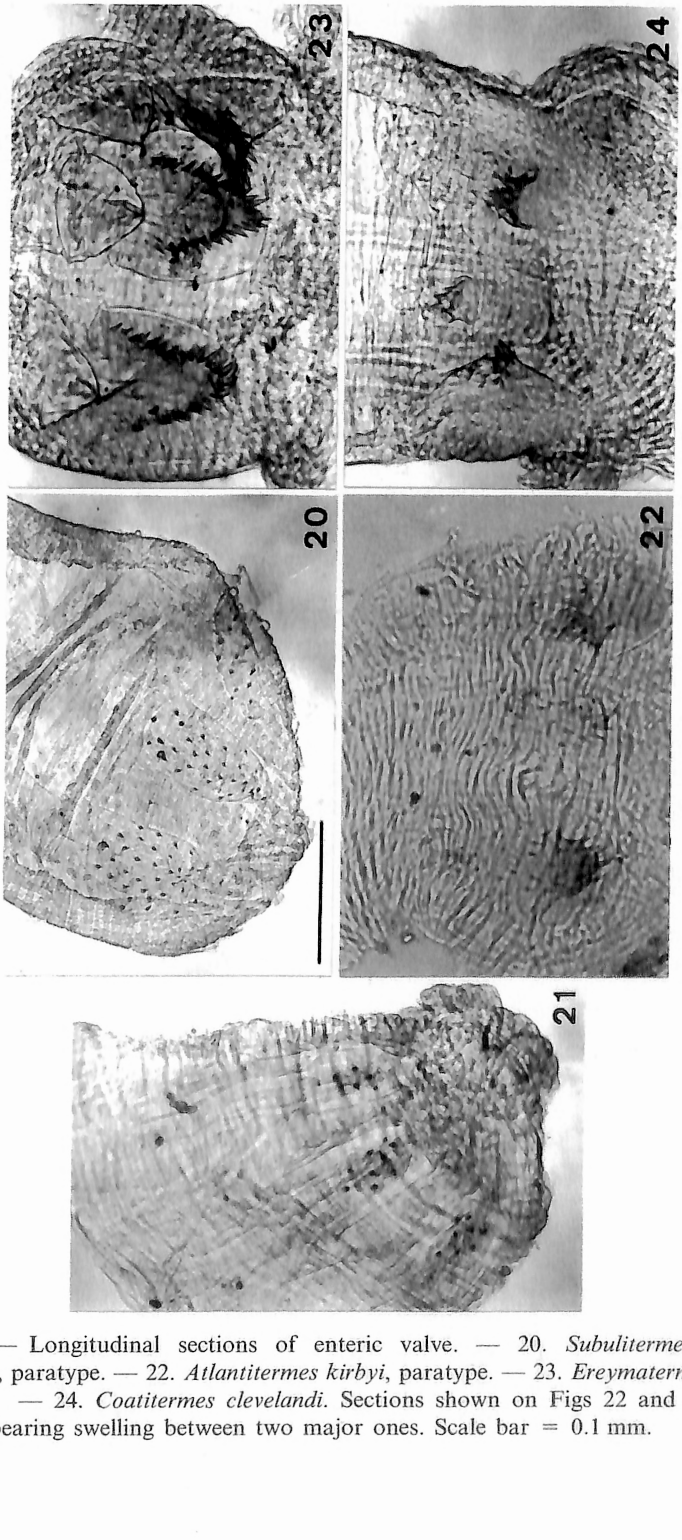
Figs 6-10. — Micrographs of worker mandibles, left and right. — 6. *Subulitermes zeteki.* — 7. *S. denisae*, paratype. — 8. *Atlantitermes kirbyi*, paratype. — 9. *Ereymatermes panamensis*, paratype. — 10. *Coatitermes clevelandi.* Scale bar = 0.1 mm. All left mandibles shown here are of the « narrow gap » type of FONTES (1987b), which is the more frequent; in some individuals (« broad gap »), there is a larger space between the third marginal tooth and the edge of the molar prominence. The meaning of these variations, without consequence for the identification of Panamanian nasutes, is under study.



Figs 11-15. — Scanning electron micrographs of molar areas of worker mandibles. Left, molar plate (right mandible); right, molar prominence (left mandible). — 11. *Subulitermes zeteki*. — 12. *S. denisae*, paratype. — 13. *Atlantitermes kirbyi*, paratype. — 14. *Ereymatermes panamensis*, paratype. — 15. *Coatitermes clevelandi*. Scale bar = 0.05 mm.



Figs 16-19. — Configuration of the worker digestive tube *in situ*. — 16. *Subulitermes zeteki*. — 17. *S. denisae*, paratype. — 18. *Atlantitermes kirbyi*, paratype. — 19. *Ereymatermes panamensis*, paratype. Viewed successively from above, right, below, left. Mesenteron stippled, malpighian tubules not represented. Scale bars = 1.0 mm. For adequate representations of the digestive tube of *Coatitermes clevelandi*, see Fontes (1987a : figs 74-77).



Figs 20-24. — Longitudinal sections of enteric valve. — 20. *Subulitermes zeteki*. — 21. *S. denisae*, paratype. — 22. *Atlantitermes kirbyi*, paratype. — 23. *Ereymatermes panamensis*, paratype. — 24. *Coatitermes clevelandi*. Sections shown on Figs 22 and 24 feature a minor spine-bearing swelling between two major ones. Scale bar = 0.1 mm.

## DISCUSSION

Fontes (1982, pp. 100-101) created the genus *Araujotermes* (type species : *Araujotermes caissara* Fontes, 1982) and proposed to transfer *Subulitermes zeteki* to it. *Araujotermes* is distinguished by the following criteria (Fontes, 1982, 1987a, b) : soldier with longer hairs than *Subulitermes* or *Atlantitermes*; head capsule not constricted (contrary to *Atlantitermes*), nose not elevated (contrary to *Subulitermes* and *Atlantitermes*) ; worker mandibles with at least 5 ridges on molar prominence and 4-5 on molar plate, left mandible index 0.80-0.83 ; apical tooth of mandibles less developed than in *Subulitermes*; enteric valve armature very similar to that of *Subulitermes*; two lobes at junction of enteric valve with paunch (none in *Subulitermes* and *Atlantitermes*).

The main argument to support the transfer of *S. zeteki* to *Araujotermes* is its worker mandible morphology, which appears closer to *A. caissara* than to *S. microsoma* by the number of molar ridges, although this number is often difficult to determine unambiguously (see figs 68-69 in Fontes, 1987b). However, the left mandible index of *S. zeteki* falls midway between the figures given by Fontes (1987b) for *Subulitermes* and *Araujotermes*. *S. microsoma* and *A. caissara* have very similar gut configurations and enteric valve armatures : a small difference is the presence of lobes at the junction between the enteric valve and the paunch in *A. caissara*. In this respect, *S. zeteki* is intermediate between these two species. By its number of enteric valve spines, *S. zeteki* resembles more *A. caissara*, but this number often varies between species wihin a single genus. The head profile of *S. zeteki* soldiers is almost straight, as in *A. caissara*. Finally, *S. zeteki* is unique for its 11-segmented antennae in the soldier, although in some colonies, the third antennal article shows signs of division. The worker of *S. denisae* comes close to *A. caissara* by its mandibular characters ; however, its digestive tube resembles more that of *S. microsoma* by the enteric valve armature, the shape of paunch and the complete absence of lobes at the junction between enteric valve and paunch. The soldier of *S. denisae* is much less hairy than that of *A. caissara*.

The soundness of the distinction between *Araujotermes* and *Subulitermes* is difficult to appreciate without comparative data on a large array of species. Unfortunately, Fontes' (1987a, b) anatomical work is limited to the type species of each genus. *S. zeteki* resembles more *A. caissara* than *S. microsoma*, but *S. denisae* is intermediate between these species in several respects. Gut configurations and left mandible indices do not allow a clear separation of the two genera. Minor variations in soldier head profile or pilosity can hardly be used as diagnostic characters at the genus level. The absence of unambiguous diagnostic criteria suggests that *Araujotermes* should be treated as a junior synonym of *Subulitermes*. I therefore propose to retain the combination *Subulitermes zeteki*.

The transfer of *Subulitermes kirbyi* to *Atlantitermes*, proposed by Fontes (1982), is supported by the constricted shape of the soldier's head capsule, very similar to that of *A. guarinim*. The enteric valve armature of the worker is well developed and greatly resembles FONTES' (1987a : Fig. 61) drawings of *A. guarinim*. However, the worker gut of *A. kirbyi* appears broader than that of *A. guarinim* (compare Fig. 18 herein with figs 90-97 in FONTES, 1987a), and its left mandible index is considerably higher (1.4 vs 0.77 ; compare Fig. 8 herein with figs 13-15 in FONTES, 1987b). In addition, the molar plate of the two examined paratypes of *A. kirbyi* was completely devoid of ridges (compare Fig. 13 herein with figs 64-65 in FONTES, 1987b), although one cannot exclude that this condition was due to mandible wear. Mandibular characters thus favor the removal of *A. kirbyi* from *Atlantitermes*, but soldier morphology and worker enteric valve armature go against it. Thus far, for the sake of nomenclatorial stability, it seems wise to retain the combination *A. kirbyi*, although this implies an extension of the definition of the genus *Atlantitermes*.

Nowadays, characters of the worker mandibles (left mandible index, molar ridges) and digestive tube (general configuration, armature of enteric valve, etc.) are often considered diagnostic at the genus level in termite taxonomy. However, none of the three abovementioned species fits precisely within any existing genus when all those criteria are considered. Such discrepancies outline the need for reliable phylogenetic studies, which would allow an assessment of all characters traditionally used in the generic taxonomy of humivorous nasutes. Characters of the worker mandible seem especially subject to caution. The whole complex of genera related to *Subulitermes* might have to be revised when data on a sufficient number of species are available.

The remaining species of Panamanian humivorous nasutes belong to better defined genera. *Ereymatermes panamensis* is very similar to *E. rotundiceps* ; in particular, both species have almost identical mandibles, gut configurations and enteric valves, which leaves no doubt that they are congeneric. As to *Coatitermes clevelandi*, the present observations of Panamanian samples of this species, collected at or near the type locality, corroborate those of FONTES (1982, 1987a, b) on Brazilian specimens. They support the validity of the genus *Coatitermes*, created to accommodate this species (FONTES, 1982).

## ACKNOWLEDGEMENTS

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# *HALICYCLOPS CANEKI* N. SP. (COPEPODA, CYCLOPOIDA) FROM CELESTÚN LAGOON (YUCATÁN, MEXICO)

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## SUMMARY

*Halicyclops caneki* n. sp. is described from Celestún Lagoon (northwest of the Yucatán Peninsula) and is compared with its congeners *H. herbsti* Rocha and Iliffe, and *H. bowmani* Rocha and Iliffe, known from the Bermuda cave system. *H. magniceps* previously reported from the peninsula is considered as a possible junior synonym of *H. caneki.* The new species was found among several other copepods living between the *aufwuchs* covering submerged mangrove pneumatophores.

*Key words* : Cyclopoida, *Halicyclops*, taxonomy, new species.

## INTRODUCTION

More than 20 different species of *Halicyclops* are currently recognized in the central west Atlantic coastal region, extending from Brazil in the south to Cape Hatteras in the north. The enormous lagoonal and estuarine Brazilian coast is known to accommodate at least ten different species (HERBST, 1955 ; ROCHA, 1983a ; 1983b ; 1984 ; REID, 1985 ; LOTUFO and ROCHA, 1993). Four species are known to inhabit coastal waters of the United States Gulf Coast (ROCHA and HAKENKAMP, 1993), 5 from several localities in Central America and the Caribbean (HERBST, 1987 ; and see REID, 1990), and 3 from anchialine caves in Bermuda (ROCHA and ILIFFE, 1993). An unnamed male specimen was reported by PLEŞA (1981) from Cuba.

The presence in this region of typical European Atlantic and Mediterranean species (e.g. *H. aequoreus* (Fischer, 1860), *H. neglectus* (Kiefer, 1935), *H. septentrionalis* (Kiefer, 1935), and *H. magniceps* (Lilljeborg, 1853)) is questionable (REID, 1990 ; ROCHA and HAKENKAMP, 1993 ; present study).

Celestún Lagoon (Laguna de Celestún), type-locality of the herein described *H. caneki* n. sp., is located at the northwestern edge of the Yucatán Peninsula and is a 20 km long narrow southwards directed estuary, bordered by a dense red mangrove forest. This highly productive estuary is currently under study by hydrologists and ecologists (Valdés *et al*, 1988). The northern part receives important quantities of freshwater through discharges from the underground water table of the yucatecan karst. The relationship between rainfall and underflow nutrient load carried into the estuary has recently been documented by Herrera-Silveira (1994).

## MATERIAL AND METHODS

The sample was taken with a hand net (mesh 80 µm), scraping the *aufwuchs* covering the submerged pneumatophores of mangrove trees (direction of Celestún Village, at the right side of the bridge spanning the estuary; estimated coörd. 20° 49′ 59″ N — 90° 21′ 50″ W; Leg. F. Fiers, 15 March 1993, MEX 93-95). The sample was fixed in 4 % buffered formaldehyde. The animals were transferred to 75 % denaturated ethyl alcohol for long-term storage. Observations and dissections were made in glycerine with coverglasses sealed for permanent slides. Observations and drawings were made at 1250X on a Leitz Dialux 20 light microscope, equipped with a drawing tube.

Eleven females, 2 males and 3 juveniles of *Halicyclops caneki* n. sp. were preserved in 75 % denaturated ethanol (COP 3826, designated paratypes), and dissected specimens (holotype female, paratype female and allotype male) were labeled COP 3823a-b, COP 3824a-b and COP 3826a-b, respectively.

Associated harpacticoid copepod fauna : Darcythompsoniidae : *Leptocaris* spec. 1., *Leptocaris* spec. 2, *Kristensenia pallida* Por ; Tisbidae : *Tisbe* spec. ; Diosaccidae : *Robertsonia* cfr *salsa* Gurney ; *Schizopera* cfr *knabeni* Lang ; Ameiridae : *Nitocra laingensis* Fiers, *Nitocra* spec. ; Canthocamptidae : *Mesochra wolski* Jakubisiak ; Argestidae : *Actinocletodes woutersi* Fiers ; Cletodidae : *Enhydrosoma lacunae* Jakubisiak ; Laophontidae : *Folioquinpes chathamensis* (Sars).

The type-specimens of *H. caneki* as well as the associated harpacticoid fauna were deposited in the collections of the Recent Invertebrate Section of the Royal Belgian Institute of Natural Sciences, Brussels.

## DESCRIPTION

### ***Halicyclops caneki* n. sp.**

*Synonymy*

? *Halicyclops magniceps* (Lilljeborg, 1853) : Wilson, 1936 : pp. 82.

### *Etymology*

The species is named after the legendary mythical Mayan hero Jacinto Canek (EMILIO ABREU GÓMEZ, 1983. Canek. Dante, Mérida, 108 pp.).

### *Description*

*Female* : Length ranging from 597 to 628 µm (holotype : 623 µm) with a typical *Halicyclops* appearance (Fig. 1a, c). Largest width near posterior margin of cephalothorax (± 240 µm ; in holotype 242 µm) and prosome/body length ratio of 1/1.65. Posterolateral edges of cephalothorax and pedigerous somites not produced. Genital double somite with nearly parallel lateral margins (in Fig. 2a : urosome somewhat flattened during mounting), without marked lateral extensions in anterior half; slightly longer than broad; length/width ratio : 1/0.85.

Posterior hyaline fringes of prosomal and fifth pedigerous somites not incised, of urosomal somites finely incised, except for posteroventral fringe of genital double somite being deeply incised (Fig. 2a), and dorsomedian part of pre-anal somite being slightly crescentic produced and showing somewhat larger crenulations than lateral and ventral region (Fig. 1d).

Anal somite with spinules along the posterolateral and posteroventral margins, above articulation with caudal rami. Anal operculum nearly straight and anal sinus wide, furnished with row of hairs on both sides (Fig. 1d).

Integument of all somites with dense pattern of minute pores. Cephalothorax with a lock-shaped dorsal pore depression in the anterior half, and an ovate one near the posterolateral edge. Pedigerous somites 2, 3, 4 and first abdominal somite with a lateral rounded to ovate pore depression (Fig. 1a, c ; Fig. 2a). Large active glandulae in front of genital field, below pore depressions of first abdominal somite, in the anterior half of abdominal somites 2-4 having pore orifices opening below hyaline fringe of preceding somite, and in the caudal rami showing pore orifice opening close to the posteroventral margin (Fig. 2a : glandulae dotted in illustration).

Caudal ramus (Fig. 1d) slightly longer than wide (L/W ratio : 1/1.13 in holotype, 1/1.12 to 1/1.15 in paratypes), with distinctly produced distal dorsal edge, bearing dorsal seta. Integument of ramus smooth, except for some minute spinules near the implantation of distal lateral and dorsal seta, and along ventral distal margin. Lengths of armament (µm) : lateral seta, 19 ; distal lateral seta, 34 (twice as long as ramus) ; outer median one 190 ; inner median one, 315 ; dorsal one, 67 (three times as long as caudal ramus). Inner distal seta absent. Lateral and dorsal setae plumose ; outer median setae spinulose in proximal half along outer side of the stem, but plumose in distal half ; inner median seta with smooth proximal half, spinulose in second third, and plumose in distal third, with fine setules along outer side of stem, more rigid setules along medial side.

Antennule (Fig. 2b) six-segmented with proportional lengths (L/W) of segments : 0.90-0.75-0.50-1.88-0.90-2.60. First segment with two parallel rows of spinules. Segments (Roman numerals) with number of setae (Arabic numerals), spines and esthetascs in parentheses : I(8) — II(12) — III(5+sp) — IV(5) — V(3+esth) — VI(10+esth). Esthetasc on segment V, implanted near articulation with segment IV, and reaching nearly halfway segment VI.

Antenna (Fig. 3a) typically three-segmented. Basipodite with short exopodal seta and two inner setae. First endopodal segment with a single set; second endopodal segment, 2.90 times as long as wide, having 8 lateral setae and seven apical setae. Caudal surface of basipodite with two short proximal rows of slender spinules and some minute spinules nearly halfway the inner margin. Frontal surface of basipodite without ornamentation. Caudal surface of second endopodal segment with two transversal rows of minute spinules one in the posterior third and one in the median third.

Mandible (Fig. 3c) with normal armament of three setae ; surface smooth except for a row of minute spinules in the outer half and for two spinules near the biting edge.

Labrum (Fig. 3e) rather wide, with a mediodistal row of blunt teeth and a laterodistal serrate hyaline fringe, on both sides.

Arthrite of maxillule (Fig. 3h) armed with four slightly curved medial claws ; dorsal margin with an outer spine and plumose seta, and a median group of three setae and a blunt spine. Coxa with two smooth setae and one armed one medially and one plumed seta on the outer margin ; palp, shorter than wide, set with three plumed setae.

Praecoxa of maxilla (Fig. 3i) with two long plumed endal setae ; coxa with a single serrate endal spine in the proximal half, and a long distal endite bearing a long and blunt proximal armament and a distal armed spine. Claw of basis and additional spine ornamented with spinules over the entire distance ; basis with an additional slender seta. One segmented palp bearing three robust spines (apical ones armed) and two slender and smooth setae.

Maxilliped (Fig. 3g) slender, two-segmented. Coxa and basis each bearing three spines ; the latter with two slender subdistal setae.

Legs 1 (Fig. 4a), P2, P3 (Fig. 4b) and P4 (Fig. 4c) with three-segmented rami. Leg 1 coxopodite furnished with rows of spinules near the outer distal edge on frontal and caudal surface and a spinule row near the proximal outer margin on the caudal surface ; basis ornamented with a comb of spinules along median distal margin and near the implantation of medial spine ; medial margin of basis with fragile hairs. Protopodites of legs 2-4 equally ornamented : with, on coxopodites, minute spinules along the distal half of outer margins and along the outer third of distal margin ; and with, on basipodites, a median spinule row and a hairy medial margin. Medial coxal seta of leg 1 reaching beyond second endopodal segment, of leg 2 and 3 not quite to distal end of first endopodal segment, and of leg 4 only just beyond basis. Outer seta of bases short, not reaching to distal ends of first exopodal segments. Medial spine on basis of leg 1 as long as first two endopodal segments, and serrate.

All outer spines of exopodites and all terminal endopodal spines serrate. Exopodite spine formula 3,4,4,3, and setal formula 5,5,5,5. Inner seta of first exopodal segment of leg 1 short, only reaching towards distal margin of segment 2. Outer distalmost seta of third exopodal segment of leg 1 ornamented with few setules. All other setae on exopodal and endopodal rami densely plumed, except for proximal inner serrate seta on third endopodal segments of leg 2 and 3, and both inner serrate setae on third endopodal segment of leg 4. Distalmost spine of leg 1 endopodite, slightly longer than segment (± 1/1.3), and outer spine much shorter than segment (± 1/0.66). Distalmost endopodal spines on leg 2 and 3, 1.5, and of leg 4, 1.45 times as long the segment. Outer spines on third endopodal segments of leg 2-4, respectively 0.65 (proximal ones) and 0.89 (sub-distal ones) times longer than segments. Length/width ratio of third endopodal segment of leg 4 : 1/1.55.

P2 and P3 identical in all aspects, former not illustrated.

Coupler of leg 1 (Fig. 2d), sub-quadrate with pair of crescentic extensions, each ornamented with long slender spinules, surface smooth. Couplers of leg 2 and 3 sub-quadrate, without spinules on paired rounded extensions, and smooth surface. Leg 4 coupler sub-rectangular with convex median margin, and minutely produced paired extensions ; entirely smooth.

Leg 5 (Fig. 2c) nearly 1.5 times longer than wide (holotype : 1/1.42, paratypes : 1/1.41-1/1.53) with a slightly concave medial margin. Typically armamented with a medial spine, a distal plumose seta, and two outer spines ; with medial spine 1.15 times longer than segment, distal seta 1.30 times longer than segment, and outer lateral spines as long as the segment. Leg 5 surface smooth, except for spinules along the medial and outer margins, and at implantation of armament.

Leg 6 (Fig. 1a, c) with two blunt elements (ventralmost twice as long as median one) and a plumed, 30 µm long, seta. Genital field (Fig. 2a and a') with a deep semi-circular genital pore leading to an ovate seminal receptacle ; lateral arms bent in medial third, and distinctly more strongly sclerotized in medial half than in outer half.

*Male.* — Length of allotype : 377 µm, of paratypes 369 and 375 µm, like female general aspect, except for sexual dimorphism in urosomites (Fig. 5c), and as follows : posteroventral margins of urosomites with regularly and finely incised hyaline fringe ; density of pores on each somite probably identical with female, but not observed (Fig. 5a, b).

Antennule typically geniculate ; 12-segmented with full complement of esthetascs on first segment ; general shape as 13-segmented antennule in *H. clarkei* see Herbst, 1982 (Fig. 25), except for two fused ultimate segment ; segments (Roman numerals) with armament of setae (Arabic numerals), spines and esthetascs in parentheses : I(8 + 2 esth) — II(4) — III(4) — IV(3) — V(3) — VI(1 + sp) — VII(5) — VIII(3) — IX(2) — X(2) — XI(2) — XII(10 + 2 esth).

Ultimate segment of antenna (Fig. 3b) somewhat shorter than in female (L/W ratio : 1/2.75) ; less ornamented on surface ; and 4 lateral setae out of 8 clustered together in proximal third.

Leg 5 more elongated than in female (L/W ratio : 1/1.80), with 2 outer spines, a distal plumose seta, a medial distal spine and a medial proximal plumose seta, having the following segment length/armament length ratio : 1/1.20 (proximal outer spine), 1/0.85 (distal outer spine), 1/0.66 (distal seta), and 1/0.64 (medial spine and seta). Ornamentation as in female leg 5.

Leg 6 (Fig. 5c) with large paired sub-quadrangular plates, each bearing an outer and median plumed seta, and a medial large spine.

## DISCUSSION AND COMPARISON

Of the 22 species known in the central west Atlantic region, *H. caneki* resembles most *H. herbsti* and *H. bowmani* recently described from the Bermuda limestone cave system (Rocha and Iliffe, 1993). *H. caneki* shares with *H. herbsti* the coarsely incised hyaline fringe along the posterior ventral margin of the genital double somite (but lacking the coarse fringe on the second abdominal somite); the only slightly produced pseudo-operculum on the preanal somite; the reduced armature of the caudal rami, lacking the medial terminal seta; and the full armament of the second endopodal segment of the antenna bearing 8 lateral setae instead of the usual 5. *H. caneki* however, is easily distinguishable from its congener by the distinctive pattern of pore depressions on the cephalothorax and thoracic somites which are entirely absent in *H. herbsti.* Other differences between both species are: the longer outer apical seta on the caudal rami (up to twice as long as the rami in *H. caneki*, only 1.2 times longer in *H. herbsti*); the relatively shorter terminal segment of the antenna (2.90 times as long as wide in *H. caneki*, 3.25 times in *H. herbsti*); and the longer outer terminal spine on the third endopodal segment of leg 4 (1.42 times the segment length in *H. caneki* and only 1.29 in *H. herbsti*). Although *H. herbsti* was only partially described based on a single female specimen, the differences listed here clearly distinguish it from the here described *H. caneki.*

The pattern of ovate lateral pore depressions on several somites and especially the lock-shaped median depression on the cephalothorax in *H. caneki* shows a striking resemblance to the pattern known in *H. bowmani.* However, *H. bowmani* differs in many aspects from the present species, viz. the coarsely serrate pseudo-operculum; the more slender female leg 5 exopodal segment bearing a very long terminal plumose seta; and the presence of a dimorphic serrate seta on the median leg 4 endopodite.

The single male specimen reported by Pleşa (1981) from Cuba is at once distinguished from *H. caneki* by the slender shape and short outer spines of the male leg 5 exopodite, and by the short caudal rami bearing a small but distinct medial terminal seta.

Few *Halicyclops* species seem to possess 8 setae along the lateral margin of the second endopodal segment of the antenna, although this feature has not always been described in detail. Besides the above mentioned *H. herbsti*, thus far this armature complement has been observed in *H. maculatus* Rocha and Hakenkamp, 1993 from Maryland (U.S.A.). *H. caneki* is at once distinguished from *H. maculatus* by its shorter caudal rami; the less pronounced pseudo-operculum; the smooth prosomal hyaline fringes; and not at least by the absence of sexual dimorphic setal ornamentation in legs 1-4.

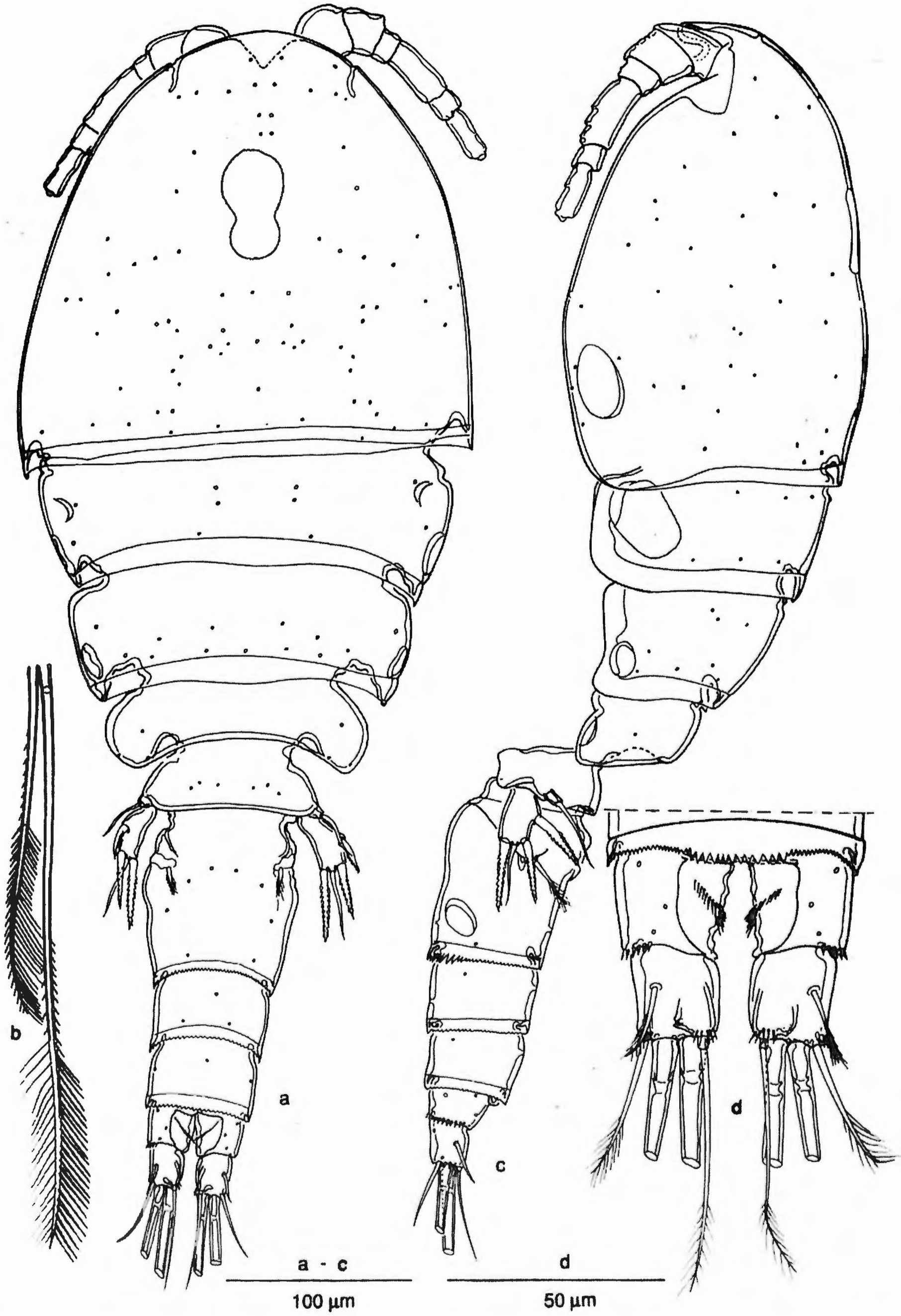

Fig. 1. — *Halicyclops caneki* n. sp., female — a, habitus, dorsal — b, principal terminal setae of left caudal ramus — c, habitus, lateral — d, anal somite and posterior region of pre-anal somite, dorsal (a-d of COP 3824).

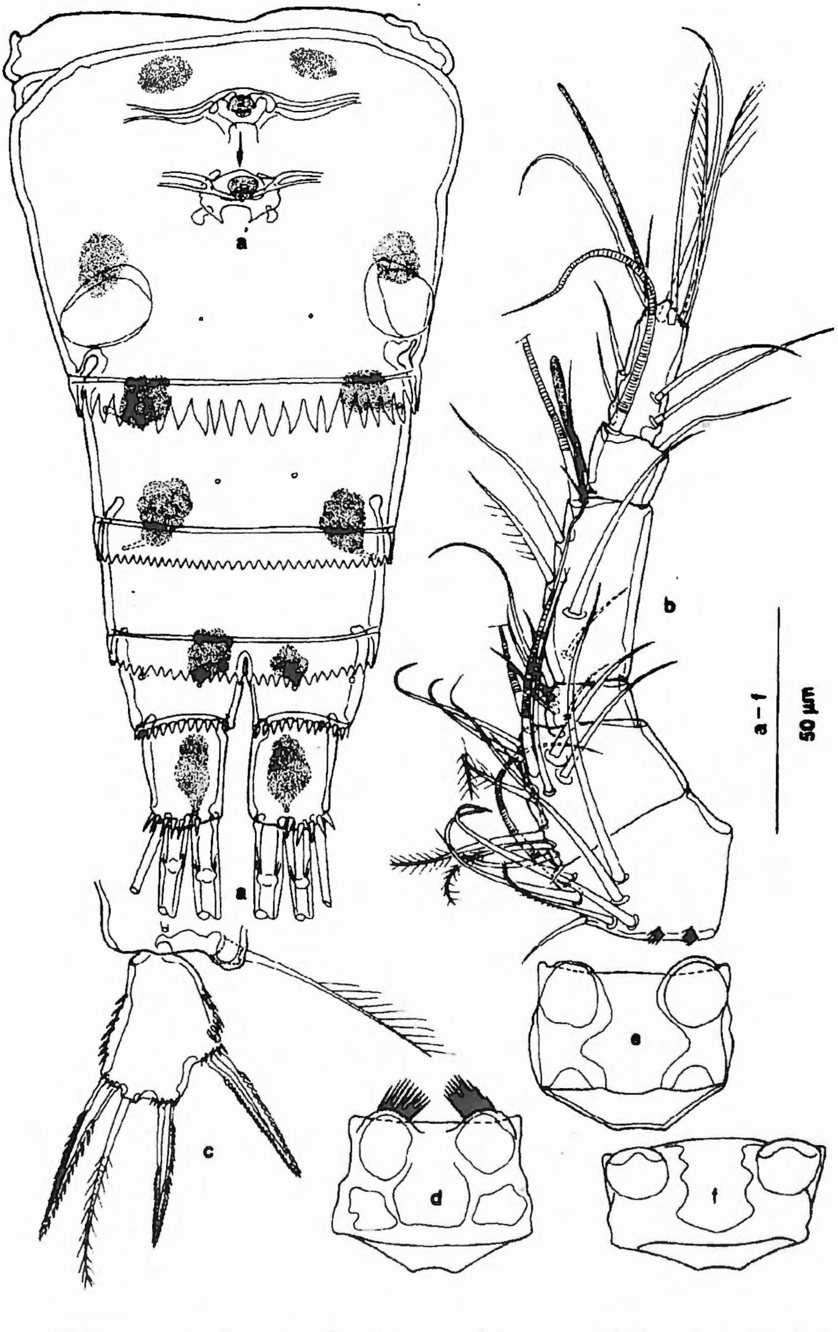

Fig. 2. — *Halicyclops caneki* n. sp., female — a, abdomen, ventral — b, antenna, ventral view — c, P5 — d, P1 coupler — e, P2 coupler — f, P4 coupler (a-c, f of COP 3824 ; d-e, in frontal view, of COP 3823).

Fig. 3. — *Halicyclops caneki* n. sp. — a, antenna, frontal — b, ultimate endopodal segment of male antenna, frontal — c, mandible — d, rostrum, ventral — e, labrum, ventral — f, labrum, dorsal — g, maxilliped — h, maxillule — i, maxilla (a, h of COP 3823 ; b, d, e of COP 3825 ; c, e, g, i of COP 3824).

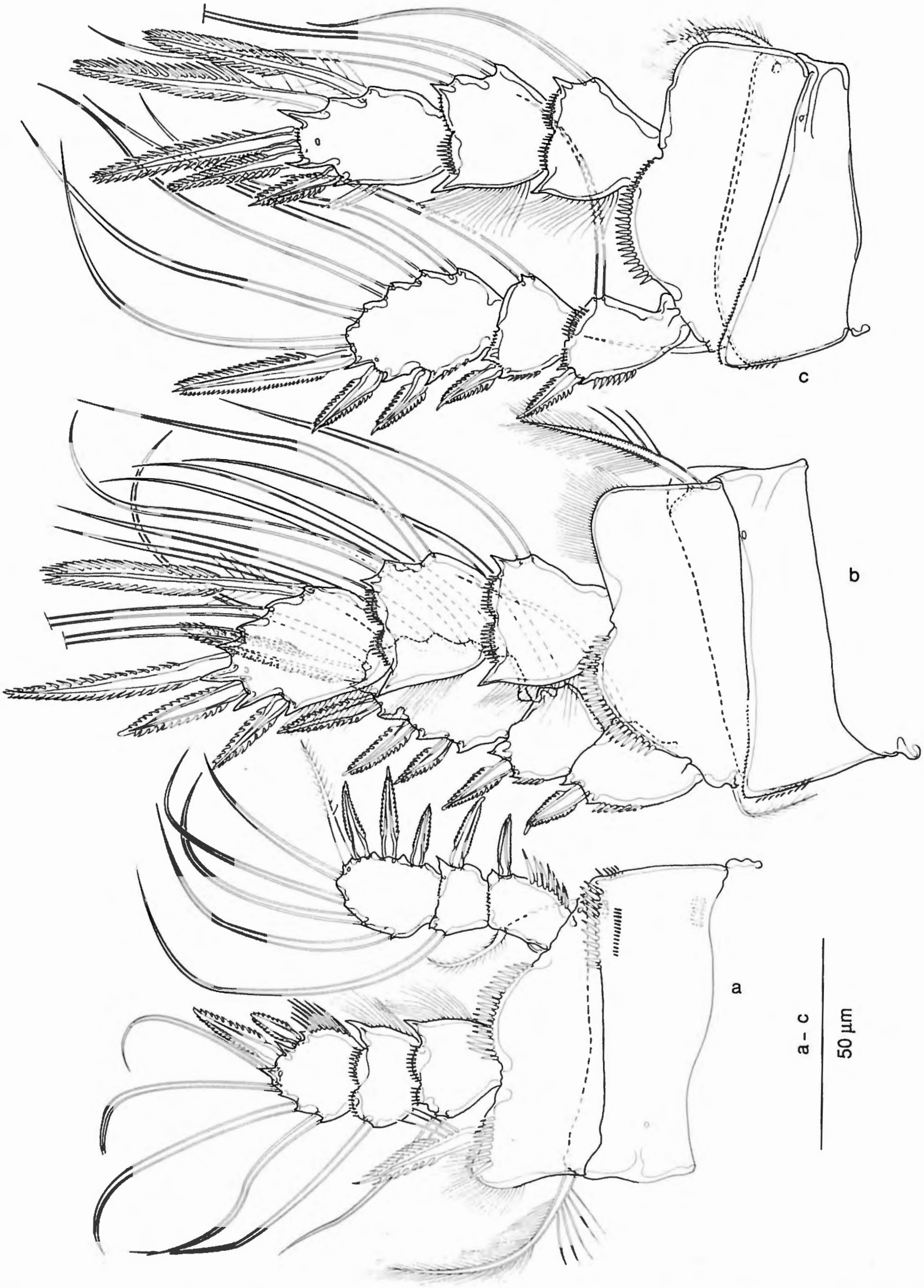

Fig. 4. — *Halicyclops caneki* n. sp., female — a, P1 — b, P3 — c, P4 (a of COP 3823, b,c of COP 3824, all illustrated in frontal view).

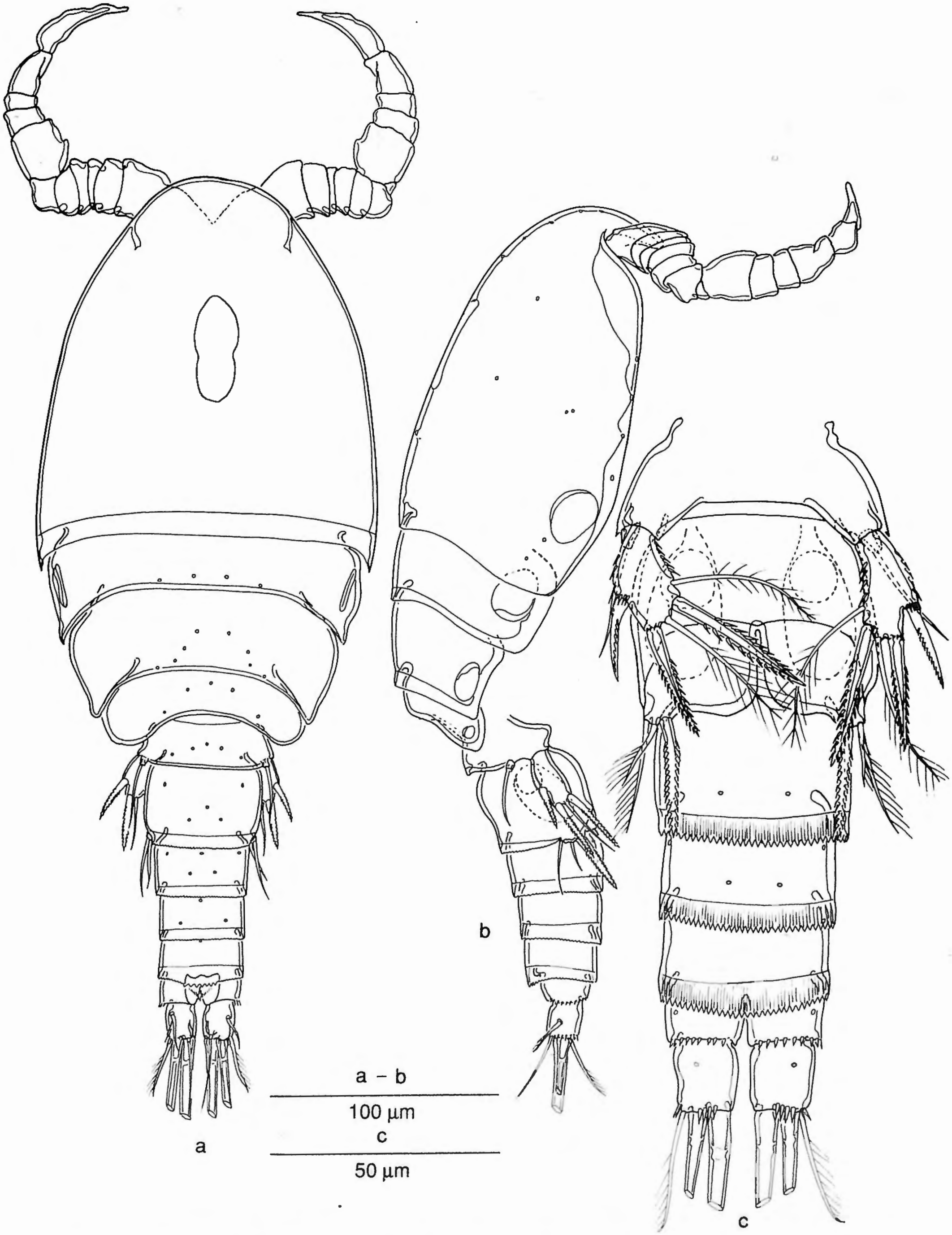

Fig. 5. — *Halicyclops caneki* n. sp., male — a, habitus, dorsal — b, habitus, lateral — c, abdomen and ultimate thoracic somites, ventral (a-c of COP 3825).

The only *Halicyclops* reported from Yucatán is *H. magniceps* (Lilljeborg, 1853) identified by WILSON (1936) on specimens found in samples from saline pools near Progreso (northern Yucatán). However, it is highly probable that Wilson misidentified his specimens (REID, 1990 ; ROCHA and HAKENKAMP, 1993) and it seems not inconceivable that the here described *Halicyclops caneki* is conspecific with Wilson's *H. magniceps* as Celestún and Progreso are two coastal localities in the same area with a comparable mangrove ecosystem.

The pools along the road Mérida-Progreso are still in excistence today, but changed drastically in the last decade because of badly engineered road constructions, affecting the natural water flow of the several basins. Sampling along the shores of these basins in the hope to find *Halicyclops* and to compare them with the Celestún Lagoon specimens, revealed no copepods at all (pers. observation).

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# ON THE HOMOLOGY OF THE INCISOR TEETH IN THE RABBIT (*ORYCTOLAGUS CUNICULUS*)

by

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## SUMMARY

The homology of the rabbit incisors has remained controversial despite abundant phylogenetic, developmental and morphological research. In this study, development and morphology of the incisors were investigated by means of serial histological sections and by stereomicroscopy in 10 fetal, 25 juvenile and 3 adult New Zealand White rabbits. A vestigial and a major incisor develop in both the upper and lower jaw, while a diphyodont minor incisor is located caudal to the major incisor in the upper jaw. Additionally, a unique case of incisor polydonty in an adult wild rabbit was investigated. The left incisive bone of this case bore a large supernumerary medial incisor which had all characteristics of a typical atavistic expression of the vestigial primordium of the first incisor. From this case the concept was deduced that the major incisor in the rabbit is monophyodont and corresponds to the second incisor, while the minor incisor in the upper jaw represents the diphyodont third incisor.

*Key words* : Rabbit, incisor teeth, polydonty, dentition, homology.

## INTRODUCTION

Lagomorphs have been distinguished as an order separate from the rodents because of their duplicidentate upper jaw dentition (Horowitz *et al.*, 1973, Thenius, 1989). In the rabbit, four upper and two lower incisors are formed bilaterally during fetal development. In adult dentition, a major and minor incisor are present in each upper jaw, and a major incisor in each mandible.

This situation is a vast reduction of the basic diphyodont dentition of adult eutherian mammals presenting bilaterally three upper and lower incisors (Becker, 1970; Miles and Grigson, 1990). The regression of one upper and two lower incisors in the rabbit has puzzled scientists for more than 150 years. Despite numerous phylogenetic, developmental and morphological studies, the homology of the remaining incisors is still controversial. Different hypotheses about the homology of these incisors have been reviewed by HIRSCHFELD *et al.* (1973), OOË (1980) and THENIUS (1989).

In the present study, the literature data were checked against morphological and developmental observations in perinatal rabbits and confronted with a unique finding of incisor polydonty in an adult wild rabbit (*Oryctolagus cuniculus* L., 1758).

## MATERIAL AND METHODS

Along with the macerated skull of an adult wild rabbit with incisor polydonty and hypertrophy, 38 rabbits of the New Zealand White breed of *Oryctolagus cuniculus* L., 1758 were studied. The latter animals ranged in age from 21 and 28 days *in utero* (6 and 4 specimens, respectively), 1 through 35 days postnatally (20 specimens), 2 months (5 specimens) and older than 6 months (3 specimens). Size and position of all incisors were determined for each animal. Gestation period in the rabbit is 31 days.

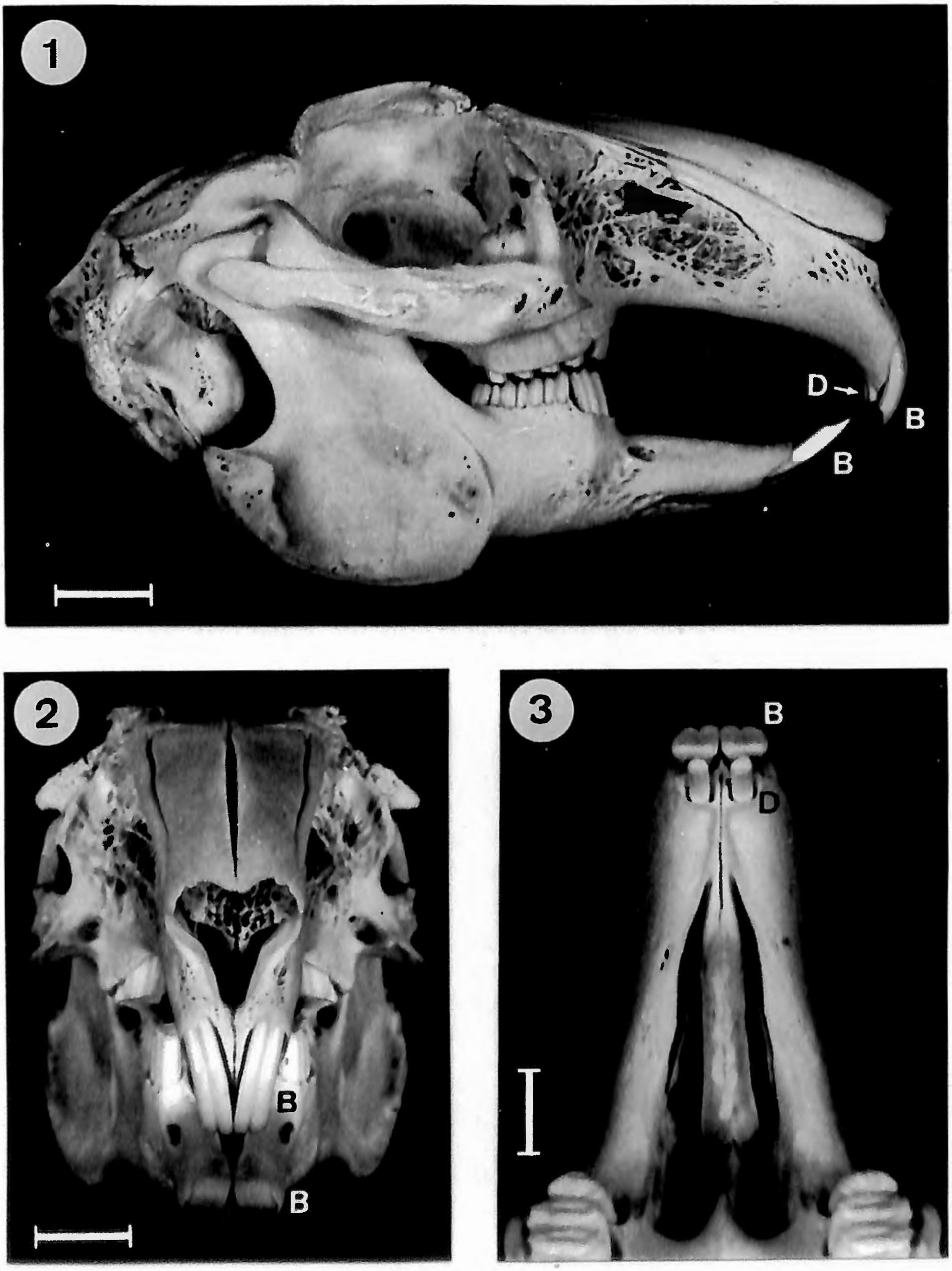
Dental development was investigated histologically in 7 fetal heads embedded in hydroxyethylmethacrylate (Technovit 7100, Kulzer) or paraffin, by means of 10 µm thick transverse and horizontal serial sections coloured with a trichrome or haematoxylin-eosin staining. Early postnatal dentition was examined histologically in two heads of 8 day old rabbits, embedded in paraffin and cut sagittally in serial sections that were subsequently stained with haematoxylin-eosin. Serial histological sections were digitalized for three-dimensional reconstruction of dental arrangement by means of a HP-program as described by VANDEN BERGHE *et al.* (1986). The incisors of all other rabbits were studied stereomicroscopically, both *in situ* and after extraction, using a Zeiss OPMI-FC Epitechnoscope.

The polydontic skull was examined macroscopically and radiographically (exposure settings : 44 KV, 350 mA, 0.02 sec, Trimax T2-HD screen).

## RESULTS

### **Dentition in the adult rabbit** (Figs 1-3)

The *major incisors* (B) are long, curved and hypsodont, *i.e.*, continually growing and open-rooted. The clinical roots of the upper and lower major incisors have a wide open root canal, and are deeply implanted in the incisive bones and the



General legend : A = vestigial incisor, B = major incisor, C = deciduous minor incisor, D = permanent minor incisor.

Figs 1-3. — Dentition in the adult rabbit. — 1. Right lateral view (bar = 1 cm). - 2. Rostral view (bar = 1 cm). - 3. Ventral view of the upper incisors (bar = 5 mm).

mandibulae, respectively. The clinical crowns of the upper major incisors converge ventromedially and are strongly curved. They bear a deep longitudinal groove along the convex vestibular surface, and a shallow oblong groove on the concave lingual surface. The clinical crowns of the lower major incisors are less strongly curved and converge dorsomedially. They present a longitudinal lingual groove but no vestibular groove.

The *minor incisors* (D) lie along the caudomedial surface of the upper major incisors. They are much shorter and thinner than the latter, slightly curved and open-rooted.

## Development of the incisor teeth

(Figs 4-14)

A *vestigial incisor* (A) was present in both the upper and lower jaws at day 21 of fetal life. This rudimentary tooth was closely adjacent to the rostral oral mucosa and was located rostromedial to the major incisor (B) (Figs 6, 7, 9 and 10). It was connected with the enamel organ of the latter tooth through an epithelial cord (Figs 6 and 9). At day 28 of fetal life, the vestigial incisor was either erupting or effectively erupted (Figs 11 and 12), and it was no longer seen in neonatal rabbits.

The *major incisor* (B) was present in the upper and lower jaws of all fetal and postnatal rabbits investigated. This long bicuspidal tooth was still covered by the oral mucosa at day 28 of fetal life, but was erupted at birth in both the upper and lower jaws.

The *deciduous minor incisor* (C) was observed in the upper jaw at day 21 of fetal life, lying ventromedial to the caudal segment of the major incisor (Fig. 7). During further development, the dental root of this incisor became distinctly bifurcated. At birth (day 1), this incisor could be palpated through the oral mucosa, but its eruption only occurred at day 4 postnatally. This tooth was shed early in the second month of life ; in one case it was already lost unilaterally at the end of the first month (Figs 13-14).

The *permanent minor incisor* (D) of the upper jaw was not yet visible at 21 days of fetal life. The germ stage of this tooth was apparent at fetal day 28 (Figs 4 and 5). It lay ventral to and closely associated with the enamel organ of the deciduous minor incisor. Eighteen days after birth, the permanent minor incisor could be palpated caudal to the major incisor through the bulging oral mucosa. Eruption of the permanent minor incisor was observed 23 days after birth, *i.e.*, before shedding of the deciduous minor incisor. Consequently, at the end of the first month of life, three incisor teeth were aligned rostro-caudally in each upper jaw, *i.e.*, the major incisor (B), the deciduous minor incisor (C) and the permanent minor incisor (D) (Figs 13-14).

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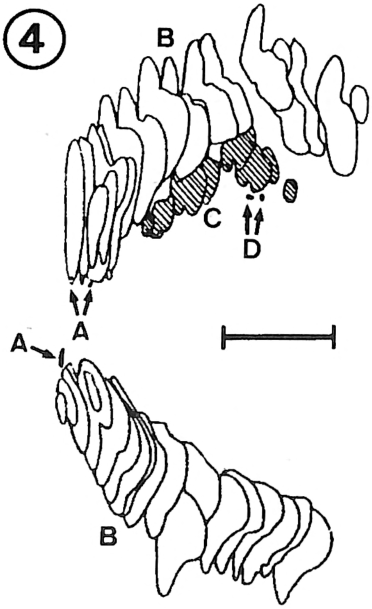

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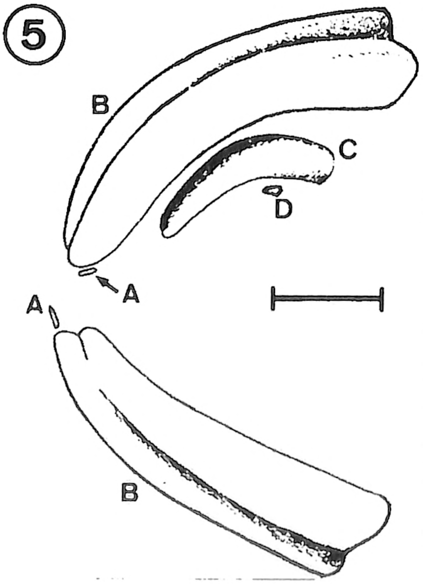
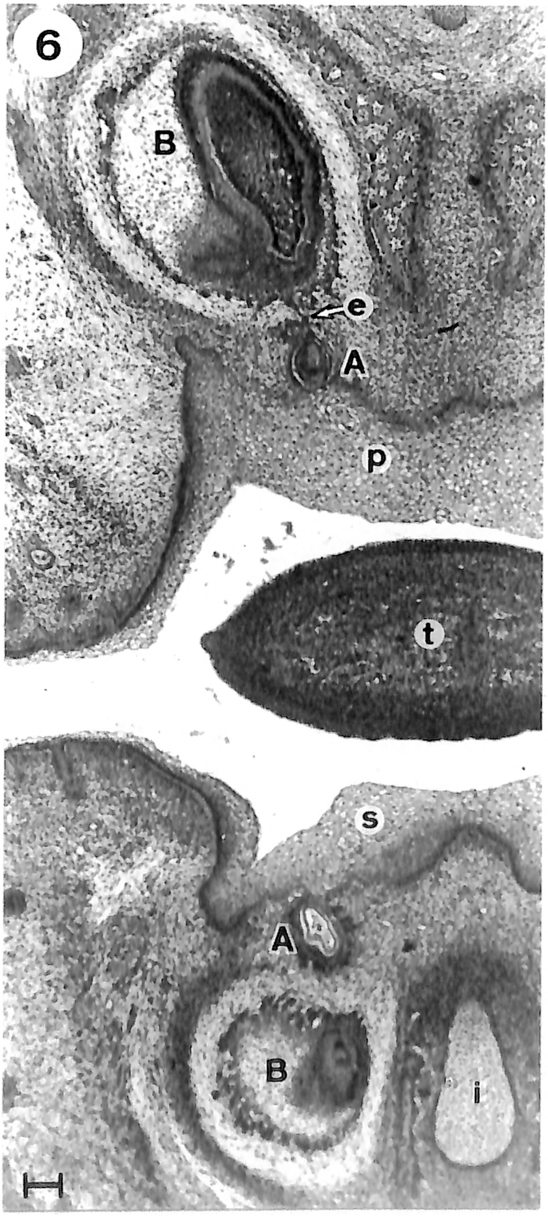
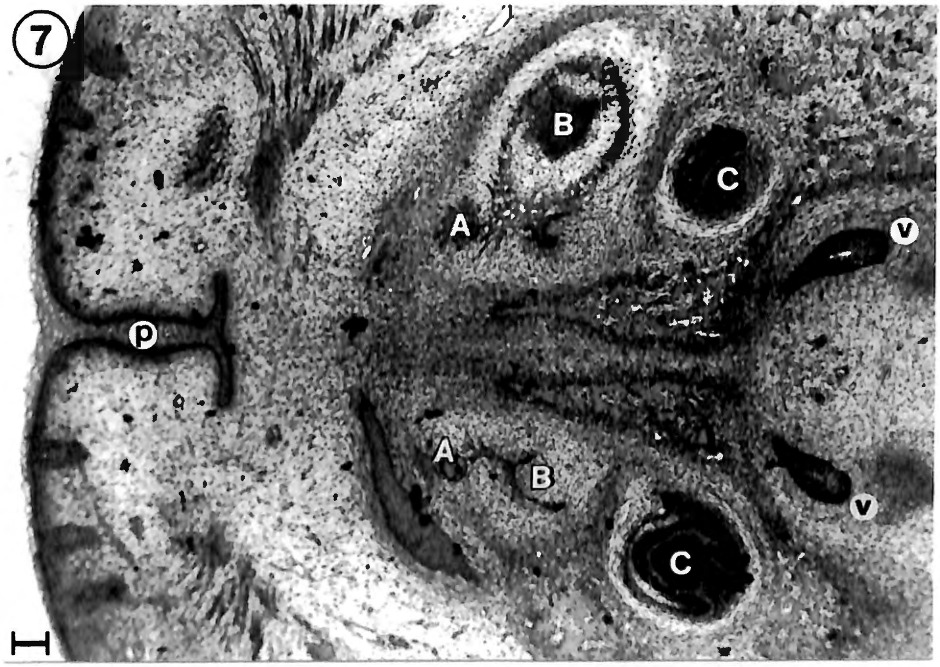




Figs 4-5. — Rostrolateral view of the left incisors in a fetal rabbit of 28 days post conception (bar = 1 mm) — 4. Compiled transverse serial sections. - 5. Dental outline reconstruction.

Fig. 6. — Transverse section of the left vestigial (A) and major (B) incisors in a fetal rabbit of 21 days post conception. e = epithelial connection between the enamel organs of the vestigial and major incisors, i = intermandibular cartilage, p = palatal mucosa, s = sublingual mucosa, t = tongue (bar = 100 μm).



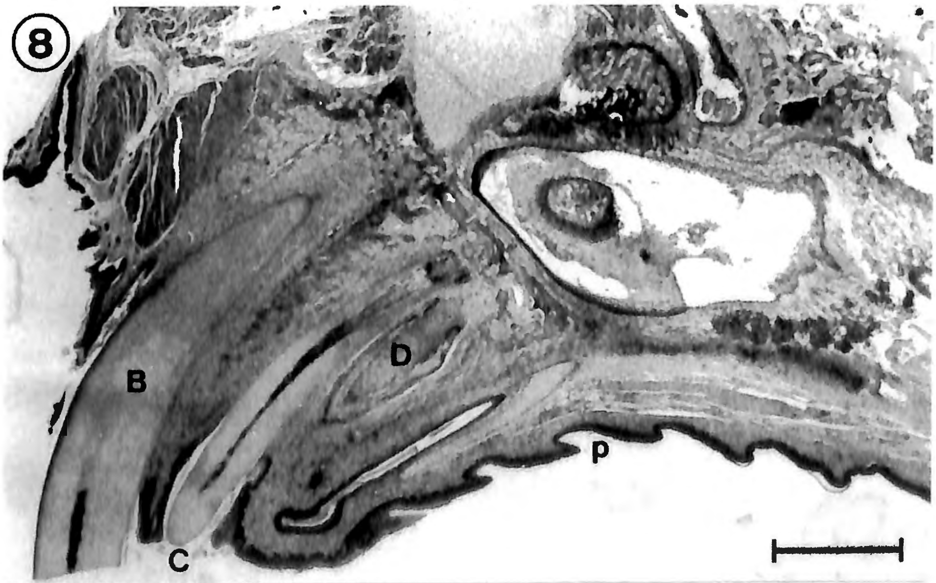
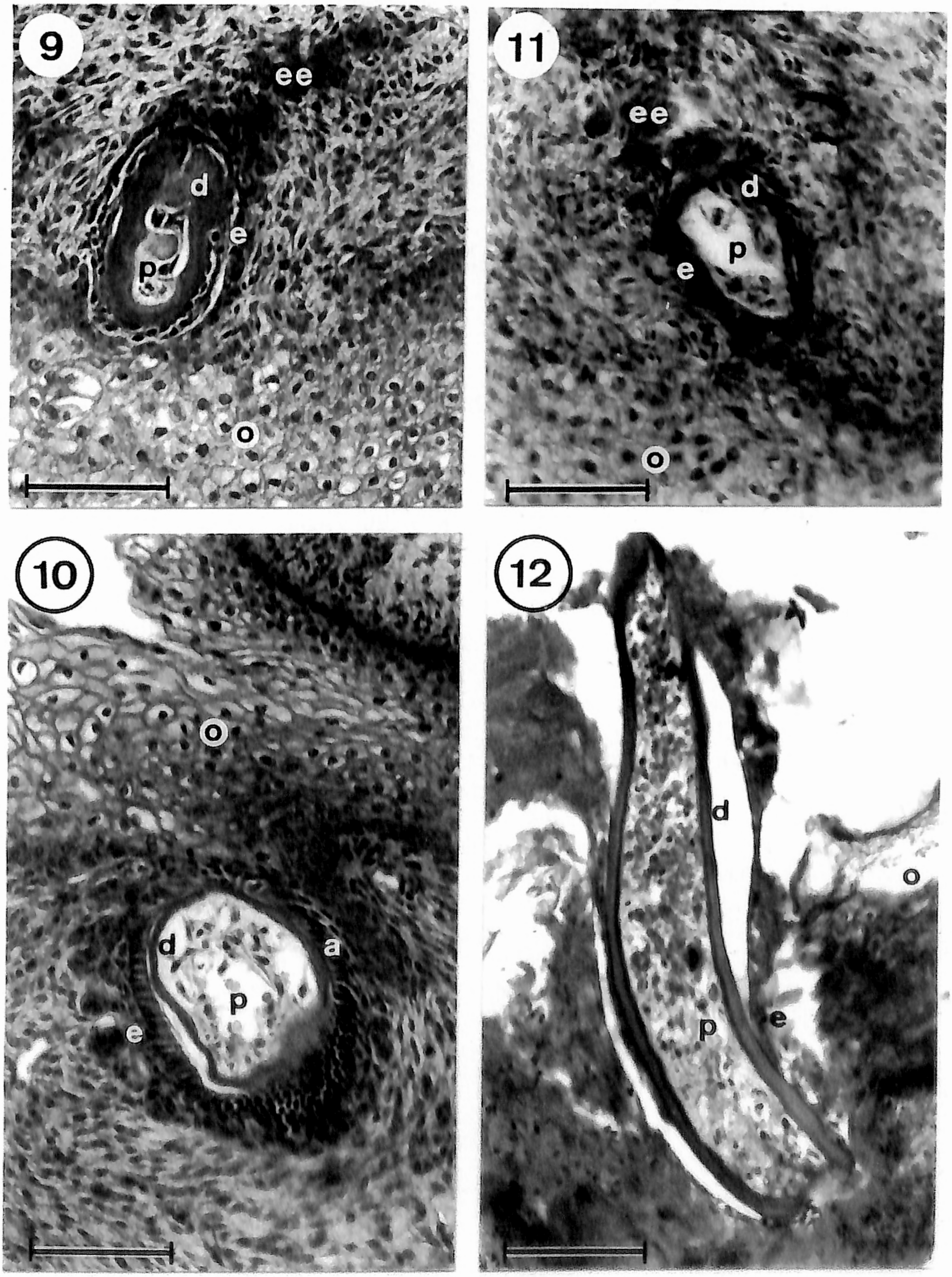
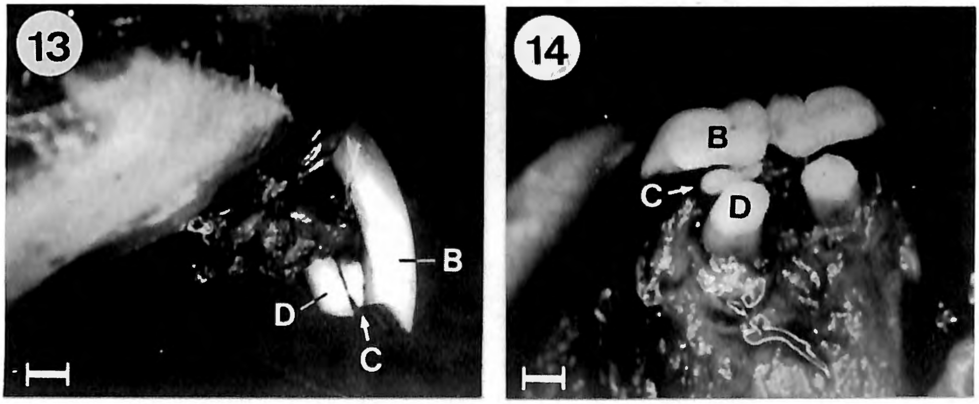


Fig. 7. — Horizontal section of the vestigial (A), major (B) and deciduous minor (C) upper incisors in a fetal rabbit of 21 days post conception. p = philtrum, v = vomeronasal organ (bar = 100 µm).

Fig. 8. — Sagittal section of the major (B), deciduous minor (C) and permanent minor (D) upper incisors in a 8 days old rabbit. The permanent minor incisor (D) has developed into the bell stage. p = palatal mucosa (bar = 1 mm).



Figs 9-12. — Legend on p. 322.



Figs 13-14. — Upper incisors in a 1 month old rabbit with deciduous minor incisor (C) still present between the major incisor (B) and the permanent minor incisor (D) on the right side (bars = 1 mm). — 13. Right lateral view. - 14. Ventral view.

### Incisival polydonty in a wild rabbit
(Figs 15-17)

The mandibular incisors, as well as the upper and lower premolars and molars of this adult skull were normal in size and shape. In the upper jaw, however, the incisors presented manifest positional deviation, hypertrophy and polydonty.

In the left upper jaw, three incisors were present. Size, shape and intraosseous position of the major incisor (B) were normal, but the orientation of the crown segment of this tooth was sagittal instead of rostromedial. This deviation was caused by the presence of an additional large medial incisor (A′). The general shape of the latter tooth was very similar to that of a regular major incisor, although its root was shorter and its crown broader. The root of this additional incisor was embedded in the incisive bone and the crown curved rostromedially, forming occlusal contact with the incisor of the right mandible. A normal minor incisor (D) lay caudal to the large incisors. It emerged from the incisive bone at the level of the medial lobe of the major incisor (B) and its crown was directed rostroventrally along the caudal surface of the additional major incisor (A′). Medial to the major and additional major incisors lay a mass of active osteosclerotic tissue (Fig. 16). The latter enclosed a central excavation that was ventrally opened. Contents of the excavation were not present in this macerated specimen.

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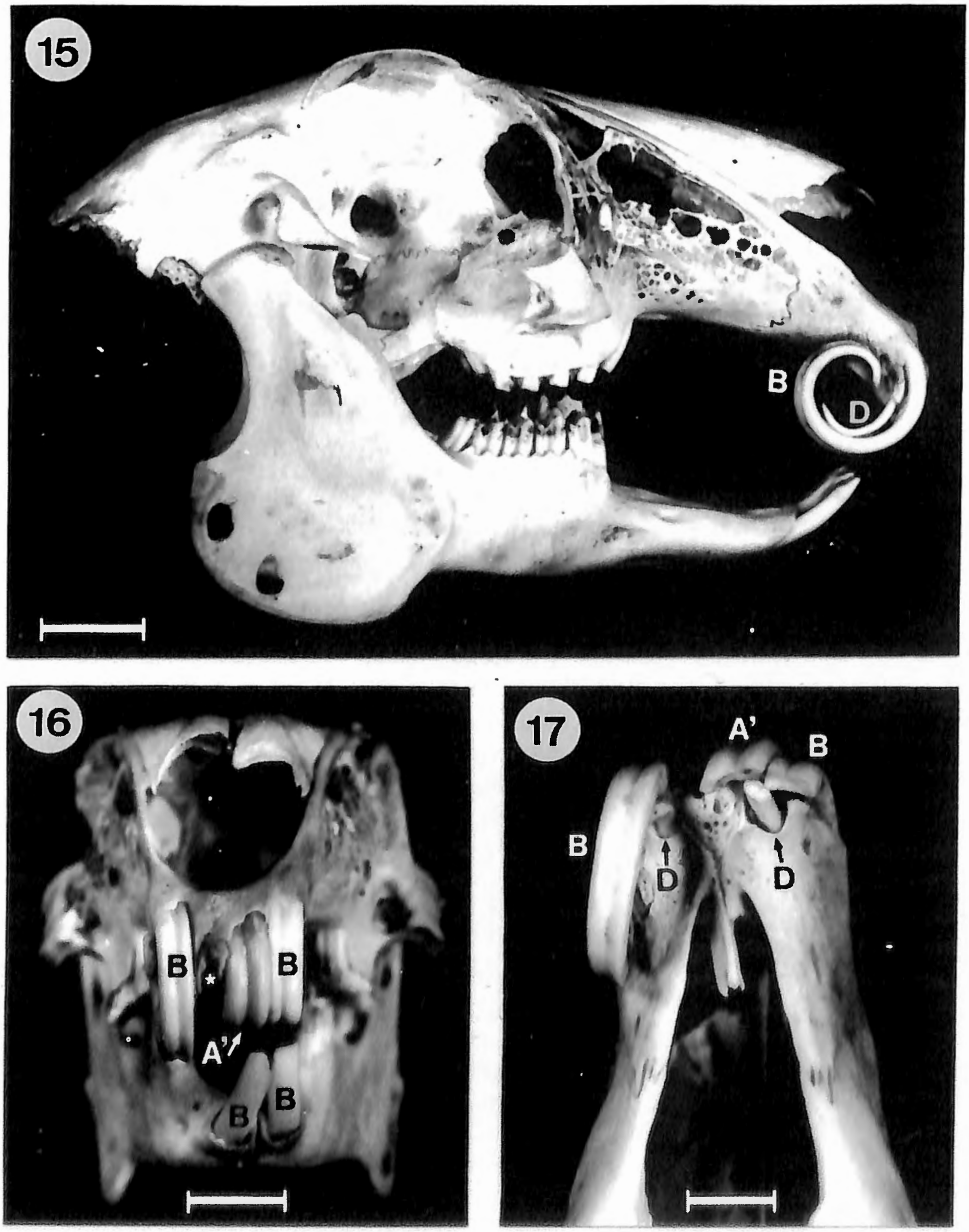
Figs 9-12. — Histology of the vestigial incisors (bars = 100 µm). a = ameloblasts, d = dentin, e = enamel organ, ee = epithelial extension between enamel organs of the vestigial and major incisors, o = oral mucosa, p = dental pulp. — 9. Upper vestigial incisor in a fetus of 21 days post conception. - 10. Lower vestigial incisor in a fetus of 21 days post conception. - 11. Upper vestigial incisor in a fetus of 28 days post conception. - 12. Lower vestigial incisor in a fetus of 28 days post conception.



Figs 15-17. — Skull of an adult wild rabbit with polydonty and hypertrophy of the incisors. — 15. Right lateral view showing coiled upper incisors (B and D) (bar = 1 cm). - 16. Rostral view demonstrating the position of the major incisors (B), the large additional incisor (A') and a medial osteosclerotic tissue mass (asterisk) in the upper left incisive bone (bar = 1 cm). - 17. Ventral view of the upper incisors (bar = 5 mm).

The right upper jaw contained two hypertrophied incisor teeth. The major incisor (B) was sagittally oriented and formed no contact with the lower incisors. Its crown was coiled for 360°, the apical part of the crown being more strongly curved than the basal segment. The minor incisor (D) was also elongated, forming a semicircle along the inner curvature of the major incisor.

Both the left and right mandibles bore a large incisor (B), the size and shape of which were normal (Fig. 16). The lower left incisor formed occlusal contact with the major incisor of the left upper jaw (B). The crown of the lower right incisor was deviated dorsally to the left and thus made contact with the additional incisor of the left upper jaw (A′). This arrangement had caused normal attrition and length of the left upper incisors and both lower incisors.

## DISCUSSION

The exact homology of the rabbit incisors has remained uncertain, because only four upper and two lower incisor primordia are found in the rabbit during development.

All evidence available indicates that the minor incisor is diphyodont, as two teeth are successively formed from the enamel organ within the same dental alveole (POUCHET and CHABRY, 1884 ; FREUND, 1892 ; HIRSCHFELD *et al.*, 1973 ; SYCH and READE, 1987). The tooth that develops first has all features of being deciduous as it is smaller, lies more rostral and erupts earlier than the subsequent tooth by which it is replaced (KRAUSE, 1884 ; HIRSCHFELD *et al.*, 1973 ; HOROWITZ *et al.*, 1973). The latter incisor persists throughout life and is therefore truly permanent.

In contrast, the nature of the vestigial and major incisors is still uncertain. The major incisor is generally considered as permanent because it persists throughout life, but it is still controversial whether or not this tooth has a deciduous predecessor. Most authors consider the vestigial incisor as the deciduous predecessor of the major incisor, because the germs of both teeth are closely adjacent and present epithelial contiguity, while the vestigial anlage is smaller, develops earlier and erupts faster than the large incisor (HUXLEY, 1880 ; POUCHET and CHABRY, 1884 ; FREUND, 1892 ; PETERS and STRASSBURG, 1968 ; HIRSCHFELD *et al.*, 1973 ; SYCH and READE, 1987). According to ADLOFF (1910), however, the positional contiguity of the vestigial and the major incisors merely results from the large outgrowth of the latter, and both dental germs develop separately as the first and second incisors, respectively. A similar opinion is held by NISHIYAMA (1932) who considered the epithelial connection between the germs of both teeth as a secondary link. More recently, even the permanent nature of the major incisor has been challenged by OOË (1980) who considered this tooth as deciduous because it develops distal (*i.e.*, lateral) instead of lingual (*i.e.*, caudal) to the vestigial incisor.

The controversial nature of the vestigial incisor, combined with the reduced number of incisors, has entailed differing numerical classifications of the rabbit incisors (Table 1).

TABLE 1

*Homology of the vestigial (A), major (B), deciduous minor (C) and permanent minor (D) incisors of the rabbit as proposed by various authors. (I : incisor ; d : deciduous ; p : permanent ; * : see discussion)*

| *A* | *B* | *C* | *D* | *Authors* |
|---|---|---|---|---|
| Id1 | Ip1 | Id2 | Ip2 | Woodward (1892) |
| - (*) | Id1 | Id3 | Ip3 | Weber (1928) |
| I 1 | I 2 | — | I 3 | Adloff (1910), Nishiyama (1932) |
| Id1 | Id2 | Id3 | Ip3 | Ooë (1980) |
| I 1 | I 2 | Id3 | Ip3 | *This article* |

For the reasons described above, Adloff (1910), Nishiyama (1932) and Ooë (1980) conclude that regression has reduced the first incisor to a vestigial remnant, and that the major and minor incisors therefore correspond to the second and third incisors, respectively. More evidence for this probability is offered by the case of polydonty described here. This case presents indeed all characteristics of a typical atavistic polydonty, *i.e.*, development of a supernumerary dental primordium that is normally found lingering in the reduced dentition of a particular species (Becker, 1970). Several decades ago, Nishiyama (1932) pointed out the possibility that the phylogenetically reduced dental primordium in the rabbit might occasionally come to expression, but to our knowledge such a case has never been reported hitherto. The additional large incisor present in this aberrant dentition could be interpreted as the outgrowth of either a deciduous predecessor of the major incisor or a monophyodont first incisor. The former possibility seems unlikely, however, because the supernumerary incisor was similar in size and morphology to the major incisor. Therefore the supernumerary and the major incisors most likely correspond to the first and the second monophyodont incisors, respectively, and consequently the minor incisor is equivalent to the third incisor. It is evident that the interpretation of such aberrant morphological findings remains always speculative, even when it seemingly offers the missing link that has long been sought. One cannot completely overlook the possibility that the supernumerary incisor could also be the expression of atypical polydonty, *i.e.*, a casual variation that has no phylogenetic basis but results from malformations such as dichotomy of teeth primordia or transposition of the dental lamina (Becker, 1970 ; Miles and Grigson, 1990).

A completely different interpretation of the numerical reduction of the rabbit incisors is provided by Weber (1928), who designates the deciduous incisors as Id1 and Id3, adding that the latter is replaced by the permanent minor incisor I3. This description states that the second incisor is lost, but no arguments or facts are given to document that presumption. This record is ambiguous as it does not state clearly whether the first deciduous incisor corresponds either to the vestigial or the major incisor. This ambiguity was not uncommon in older records in which the vestigial incisors were overlooked and the major teeth were considered to be deciduous because they happen to be formed very early (see WOODWARD, 1892). This interpretation has therefore been used in compiling Table 1.

More investigators share the opinion that the phylogenetic reduction of the rabbit incisors has affected the third incisor, whereby the functional major and minor incisors are considered as the first and second incisors, respectively (FREUND, 1892 ; WOODWARD, 1892). For a long time this viewpoint was based upon the erroneous belief that, of the three incisors present in the upper jaw of young rabbits, the third or outer one was lost (WOODWARD, 1892). More recently, THENIUS (1989) has also referred to some statements claiming that a third incisor might be formed but is lost soon after birth. FRIANT (1957 and 1961) has described a similar case of exceptional dentition in the upper jaw of a 20 days old rabbit, having a third incisor that lay behind the major and deciduous minor incisors. The caudal tooth allegedly erupted around the twentieth day of life and was shed soon afterwards without replacement. The description further claimed that the permanent minor incisors erupt after their deciduous predecessors are lost. However, this description and the iconographic evidence of this case contain controversial data, and most probably they actually refer to the normal situation of three aligned teeth (major, deciduous minor and permanent minor incisor) that are present in rabbits at that age. Therefore we feel that no conclusive evidence is given for claiming that regression of the incisors in rabbits has focused on the third incisor.

In view of the literature reports and our histological findings, the unique case of polydonty that is described in this study endorses the concept that in the rabbit (1) the vestigial incisor is monophyodont and corresponds to the first incisor, (2) the major incisor is also monophyodont and corresponds to the second incisor, and (3) the deciduous and permanent minor incisors in the upper jaw represent both stages of the diphyodont third incisor.

## ACKNOWLEDGEMENTS

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# EARLY DEVELOPMENT OF CEPHALIC BONY ELEMENTS IN *CHRYSICHTHYS AURATUS* (GEOFFROY SAINT-HILAIRE, 1808) (PISCES, SILURIFORMES, CLAROTEIDAE)

by

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## SUMMARY

The inception and development of the bony cephalic skeleton of *Chrysichthys auratus* is described from hatching to 28 days. The larval development is divided, into morphological levels rather than following days after hatching or fry length. Fry were cleared by trypsin and stained with alizarine. The bony cephalic development passes through periods of fast and slow growth. These rates are not the same in different parts of the skull. The operculum, dentary and two branchiostegal rays are present after two days. The first bone appearing in the braincase is the parasphenoid; many of other bones develop subsequently and at the same time : the interoperculum, maxilla, lacrimal and upper pharyngeal jaw. The splanchnocranium continues to develop at a relatively fast rate while the neurocranium grows slowly. The braincase begins to close when the bucco-pharyngeal apparatus is almost complete.

*Key words* : Early development, fish skull, cephalic bones, Pisces, Siluriformes, Claroteidae, *Chrysichthys*.

## INTRODUCTION

Researchers have long shown interest in the postembryonic development of the cephalic skeleton of teleostean fish (PARKER, 1873; STÖR, 1882; TISCHOMIROFF, 1885; WINSLOW, 1897), but all investigators have not pursued the same objectives and few studies make it possible to establish the precise chronology of the events which mark the development of a teleostean skull. Knowledge of this chronology, associated with the appearance and transformation of movements during growth, is crucial to understand the changes which occur during the development of functions, such as ventilation and feeding, which are vital to fry at all stages of their existence (OSSE, 1990; SURLEMONT and VANDEWALLE, 1991). To obtain such knowledge, we have undertaken a morpho-functional study of the postembryonic development of the cephalic region of *Chrysichthys auratus*, an African catfish of the Claroteidae family. The aim is to contribute to general knowledge on the biology of *Chrysichthys*, which in certain countries might potentially be raised as a food source (HEM, 1986; HEM *et al.*, 1994).

The present paper concerns a morphological study of the development of the bony skeleton of *Chrysichthys auratus* from hatching (24 hours after fertilization) to the age of 28 days. The study thus encompasses the eleutheroembryo and larval stages as defined by KRUPKA (1988). The nomenclature used to describe the developing skeletal structures is based principally on the work of DE BEER (1937) and DAGET (1964).

## MATERIAL AND METHODS

*C. auratus* fry were obtained by semi-natural fertilization carried out at the Faculty of Agronomical Sciences at Cotonou (Benin). The fry were raised at a temperature of 27° C. Batches of 30 fry were sampled on days 1 (hatching), 2, 3, 4, 6, 8, 10, 12, 15, 18, 21, 24, and 28 post-fertilization. The fry were fixed in a $CaCO_3$-buffered 10 % formalin solution. The fry were trypsin-cleared, alizarin-red-stained, and finally stored in glycerin (TAYLOR and VAN DIJK, 1985).

Initially, the fry developed rather synchronously, but as their age increased, they exhibited variations in their developmental state. This is why we chose to describe levels of development. Figures 1 to ten represent the levels in the development of the bony skeleton, distinguishable in the 13 batches of fry.

Although the presentation of our results begins with the youngest fry, we were actually able to establish homologies and recognize structures only by comparing them with adult Bagridae (see for example JAYARAM, 1970; SKELTON, 1981; GHIOT et. al., 1984) then with those of the oldest fry and progressing by successive comparisons from the oldest fry to the youngest.

## RESULTS

### *Level 1 : 1-day-old fry (fry 1 day after fertilization or at hatching)*

At hatching, no bony skull element is discernible.

### *Level 2 : 2-day-old fry* (Fig. 1)

The first dermal ossifications have appeared : the thin, flat opercles, the small but already thick dentaries, and two pairs of branchiostegal rays.

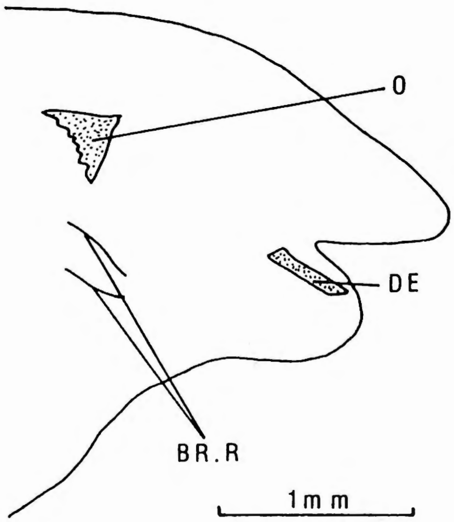

Fig. 1. — *Chrysichthys auratus.* — Lateral view of the cephalic bony elements at the second level (24 hours after hatching). Abbreviations : BR.R, branchiostegal rays ; DE, dentary ; O, opercle.

*Level 3 : 3-day-old fry* (Fig. 2)

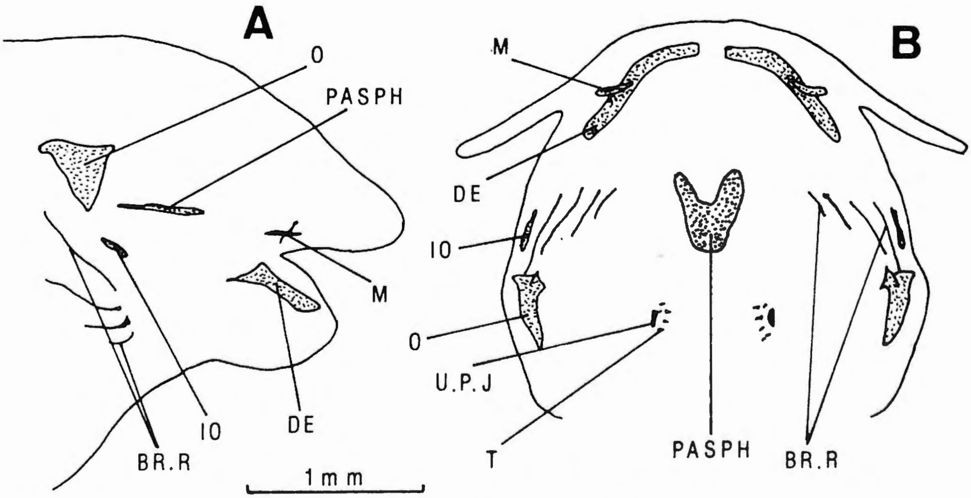

Fig. 2. — *Chrysichthys auratus.* — Lateral (A) and dorsal (B) views of the cephalic bony elements at the third level. Abbreviations : BR.R, branchiostegal rays ; DE, dentary ; IO, interopercle ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; T, teeth ; U.P.J, upper pharyngeal jaw.

The number of dermal ossifications has considerably increased. The interopercles, the maxillae, the parasphenoid, two additional pairs of branchiostegal rays, and the upper pharyngeal jaw, already bearing teeth, are present. The parasphenoid appears well developed from the start, with two diverging anterior processes. The two outer pairs of branchiostegal rays are longer and are certainly those which appeared at level 2. The upper pharyngeal jaws appear to be formed as a single piece and it is impossible to determine which pharyngobranchial constitutes them. The opercles have become shell-shaped and the dentaries have lengthened.

*Level 4 : 4- and 6-day-old fry* (Fig. 3)

The first endochondral ossification has appeared : the basioccipital. Its anterior limit is unclear. The premaxillae are present and already bear teeth, and there are six pairs of branchiostegal rays. The outermost pairs have thickened and lengthened. Anteriorly and dorsally, the opercles bear a protuberance which is the beginning of the articular cavity for the hyomandibula-opercular joint. The other bones already present have developed further and the dentaries bear teeth.

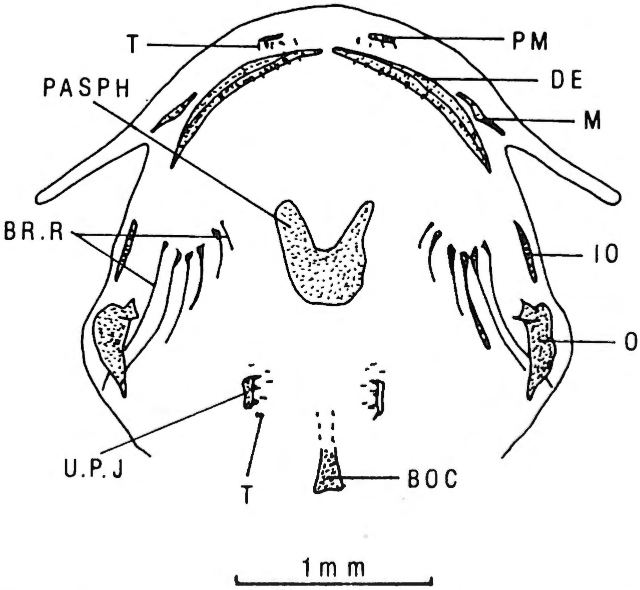

Fig. 3. — *Chrysichthys auratus.* — Dorsal view of the cephalic bony elements at the fourth level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; DE, dentary ; IO, interopercle ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; PM, premaxilla ; T, teeth ; U.P.J, upper pharyngeal jaw.

*Level 5 : 6- and 8-day-old fry* (Fig. 4)

At this stage, there are 7 pairs of branchiostegal rays, one pair of ceratohyals, and pharyngeal teeth corresponding with the lower pharyngeal jaws. These teeth, located below the upper pharyngeal jaws, are aligned in two curved rows. The other skeletal parts are somewhat enlarged.

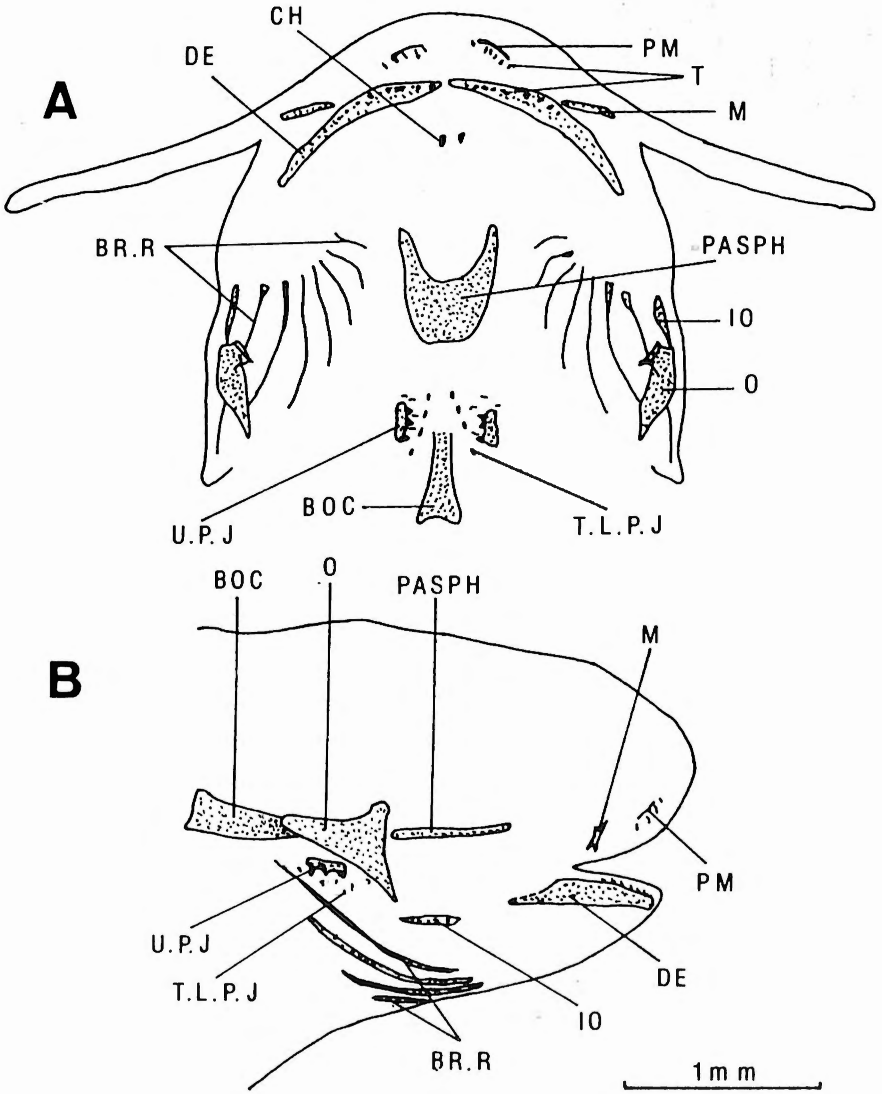

Fig. 4. — *Chrysichthys auratus.* — Dorsal (A) and lateral (B) views of the cephalic bony elements at the fifth level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; CH, ceratohyal ; DE, dentary ; IO, interopercle ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; PM, premaxilla ; T, teeth ; T.L.P.J, teeth of the lower pharyngeal jaw ; U.P.J, upper pharyngeal jaw.

*Level 6 : 8-, 10-, and 12-day-old fry* (Fig. 5)

Additions to the neurocranium are two curved, somewhat upper exoccipital appendages, one on each side of the basioccipital. The bony lower pharyngeal jaws have appeared. Towards the front have appeared a Y-shaped urohyal and a pair of apparently double visceral ossifications which we have called ceratohyals (but these may be hypohyals). There are now nine pairs of branchiostegal rays. The parasphenoid is considerably enlarged and its anterior processes have practically disappeared. The lacrimal began to ossify.

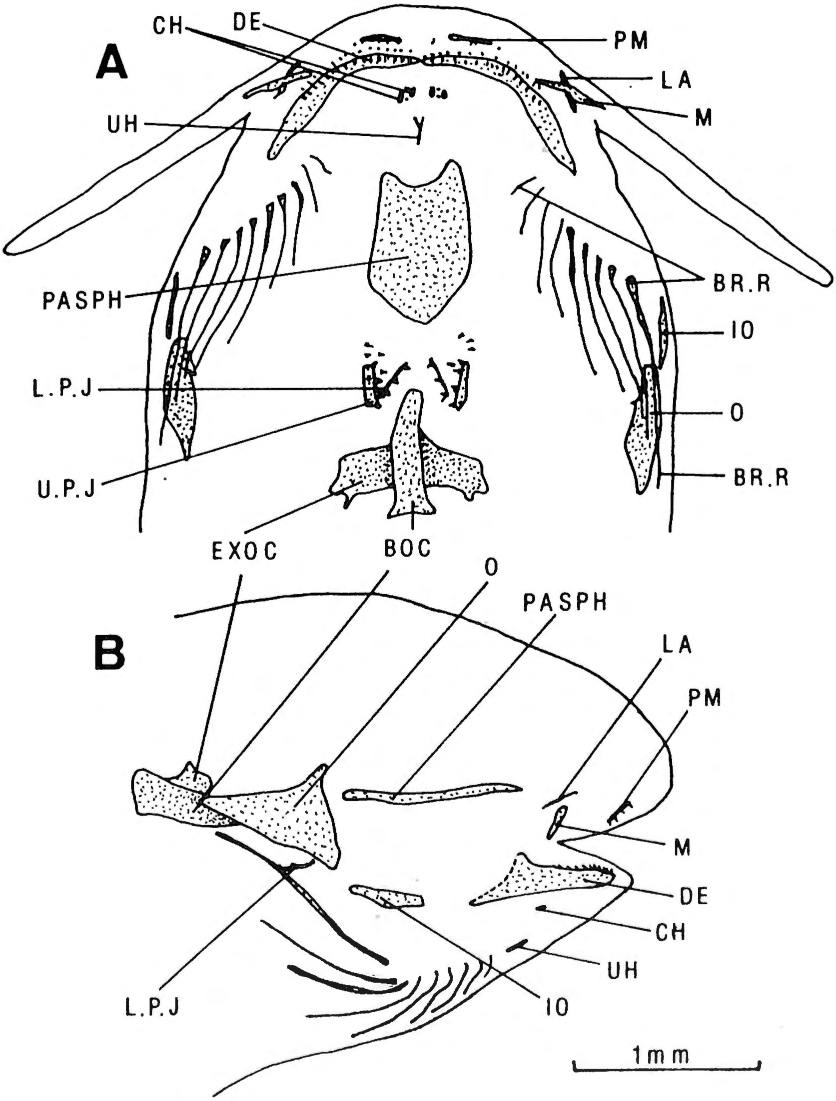

Fig. 5. — *Chrysichthys auratus.* — Ventral (A) and lateral (B) views of the cephalic bony elements at the sixth level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; CH, ceratohyal ; DE, dentary ; EXOC, exoccipital ; IO, interopercle ; LA, lacrimal ; L.P.J, lower pharyngeal jaw ; M, maxilla ; O, opercle ; PASPH, parasphenoid ; PM, premaxilla ; UH, urohyal ; U.P.J, upper pharyngeal jaw.

*Level 7 : 10-, 12-, and 15-day-old fry* (Fig. 6)

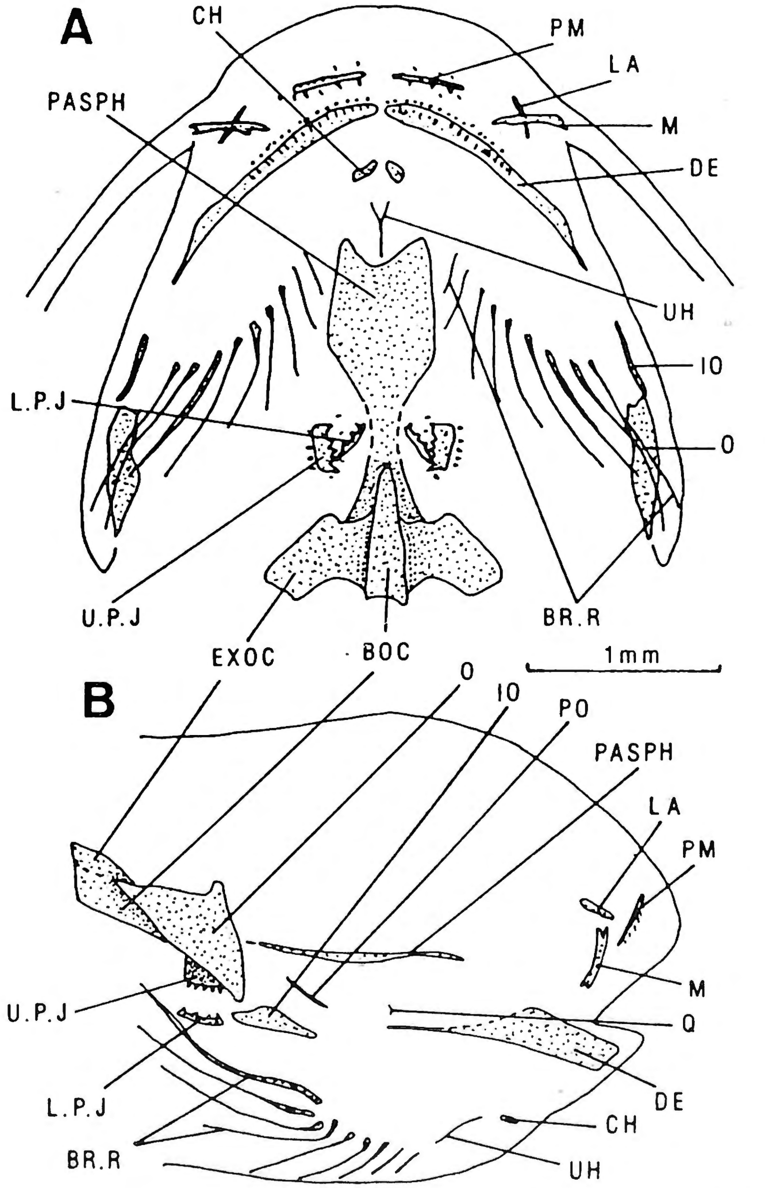

Fig. 6. — *Chrysichthys auratus.* — Ventral (A) and lateral (B) views of the cephalic bony elements at the seventh level. Abbreviations : BOC, basioccipital ; BR.R, branchiostegal rays ; CH, ceratohyal ; DE, dentary ; Exoc, exoccipital ; IO, interopercle ; LA, lacrimal ; L.P.J, lower pharyngeal jaw ; M, maxilla ; O, opercle ; PM, premaxilla ; UH, urohyal ; U.P.J, upper pharyngeal jaw.

The most remarkable fact is the joining of the parasphenoid with the occipital region, quite conspicuous in the ventral view. The remainder of the skeletal system is growing. This is particularly obvious for the dentaries, the opercles, the exoccipitals, the ceratohyals, and the upper pharyngeal jaws.

*Level 8 : 15- and 18-day-old fry* (Fig. 7)

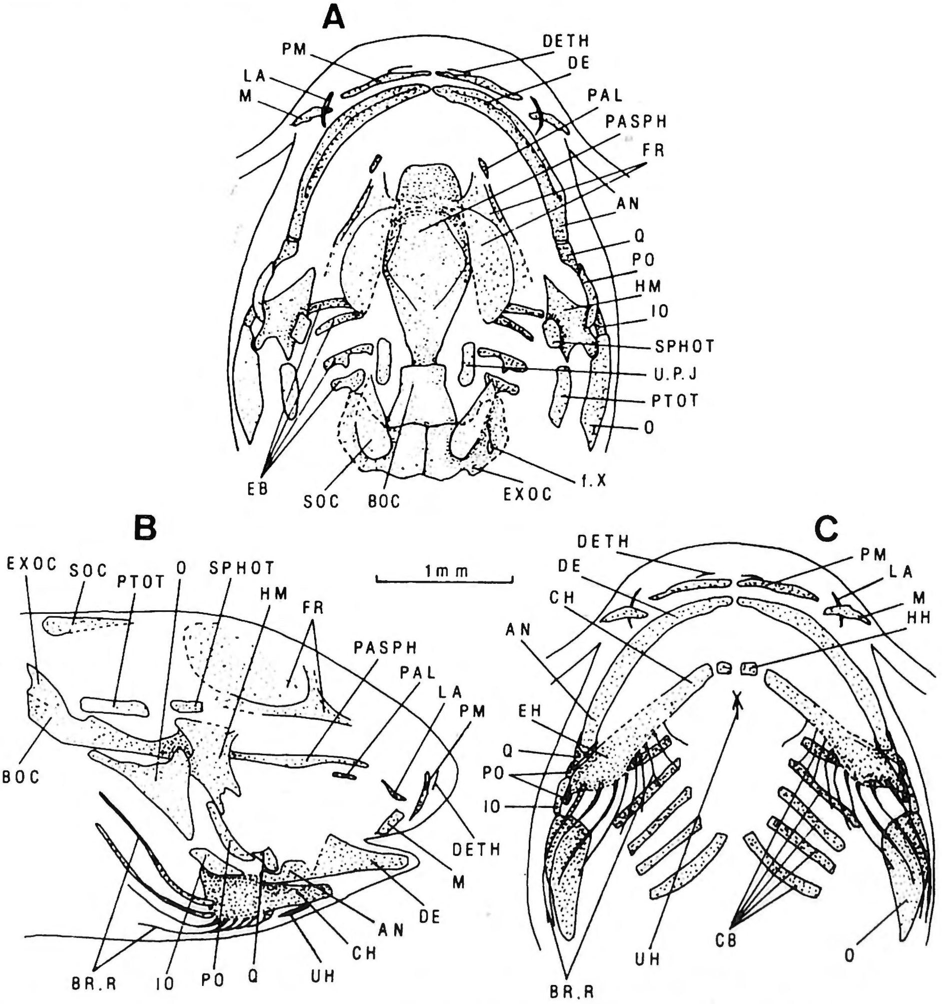

Fig. 7. — *Chrysichthys auratus.* — Presentation of the cepalic bony elements at the eigth level. (A) Dorsal view of the neurocranium, jaws, suspensorium, and dorsal part of the branchial basket; (B) lateral view of the skull; (C) ventral view of the jaws, suspensorium, hyoid bar and ventral part of the branchial basket. Dotted lines represent unclear limits. Abbreviations : AN, angular; BOC, basioccipital; BR.R, branchiostegal rays; CB, ceratobranchial; CH, ceratohyal; DE, dentary; DETH, dermethmoid; EB, epibranchial; EH, epihyal; EXOC, exoccipital; FR, frontal; f.X, foramen for the vagus nerve; HH, hypohyal; HM, hyomandibula; IO, interopercle; LA, lacrimal; M, maxilla; O, opercle; PAL, palatine; PASPH, parasphenoid; PM, premaxilla; PO, preopercle; PTOT, pterotic; Q, quadrate; SOC, supraoccipital; SPHOT, sphenotic; UH, urohyal; U.P.J, upper pharyngeal jaw.

This level is characterized by the simultaneous appearance of many ossifications. The neurocranium has progressed considerably. The frontals are already well developed, although their limits are not clear. It is possible to distinguish the sensory canals and the primordium of the epiphyseal junction. Each frontal is con-

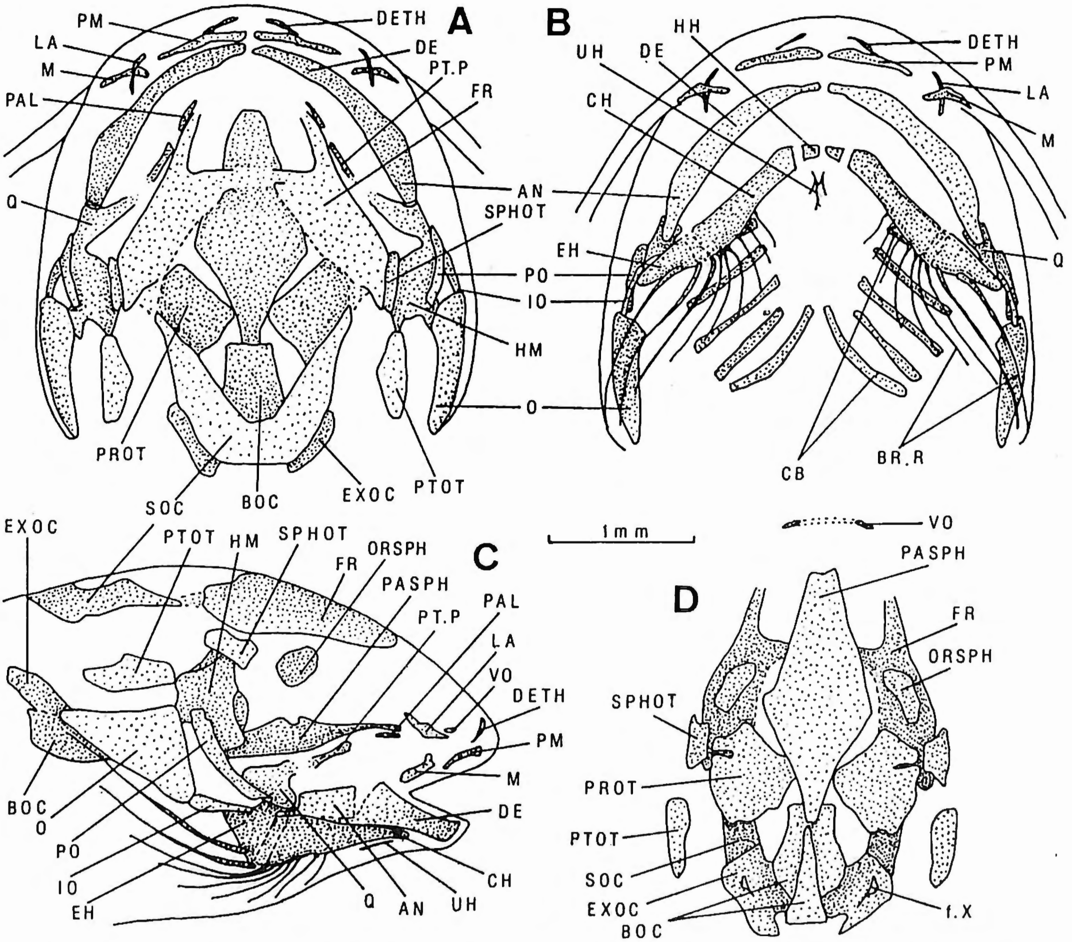

Fig. 8. — *Chrysichthys auratus.* — Presentation of the cephalic bony elements at the ninth level. (A) Dorsal view of the neurocranium, jaws and suspensorium ; (B) ventral view of the jaws, the suspensorium, hyoid bar and ventral part of the branchial basket ; (C) lateral view of the skull ; (D) ventral view of the neurocranium. Dotted lines represent unclear limits. Abbreviations : AN, angular ; BOC, basioccipital ; BR.R, branchiostegal rays ; CB, ceratobranchial ; CH, ceratohyal ; DE, dentary ; DETH, dermethmoid ; EH, epihyal ; EXOC, exoccipital ; FR, frontal ; f.X, foramen for the vagus nerve ; HH, hypohyal ; HM, hyomandibula ; IO, interopercle ; LA, lacrimal ; M, maxilla ; O, opercle ; ORSPH, orbitosphenoid ; PAL, palatine ; PASPH, parasphenoid ; PM, premaxilla ; PO, preopercle ; PROT, prootic ; PTOT, pterotic ; PT.P, pterygoid process ; Q, quadrate ; SOC, supraoccipital ; SPHOT, sphenotic ; UH, urohyal ; VO, vomer.

tinued by a « horn » which is probably the beginning of the taenia marginalis ossification. Towards the front, two small dermethmoids have appeared. Towards the back, the supraoccipital region displays two distinct ossifications and laterally the pterotics have appeared. The latter two parts, however, are independent. Ventrally, the joining of the parasphenoid and basioccipital is complete. The parasphenoid has enlarged considerably towards the front and has widened in its middle.

The lower jaw has appeared, composed of two elements : the dentary is continued by an articulo-angular, but in places, their limits are unclear. A small quadrate is also present, with the articulo-angular, it seems, already articulating with it. The preopercle is present and in contact with the hyomandibular, still incomplete in its upper portion. It already bears a posterior process pointing towards the opercle. Laterally with respect to the parasphenoid, a small palatine ossification has appeared. The hyoid arch is well developed and comprises hypohyals and two hyoid bars composed of an anterior ceratohyal region and a posterior epihyal region, separated by an indistinct ossified zone. The shape of the urohyal has become more complex. The branchial basket includes all the ceratobranchials and all the epibranchials but the pharyngobranchials are not recognizable in the upper pharyngeal jaws.

### *Level 9 : 18-, 21-, 24-, and 28-day-old fry* (Fig. 8)

The neurocranium has received the addition of the orbitosphenoids, at the level of the orbit, and of the prootics. Towards the front, the dermethmoids have further developed and the vomerine ossifications have appeared. The limits of the frontals are more obvious, the sphenotics have come closer to the frontals and extend beneath them. There appears to be a fronto-occipital junction and the posterior regions of the supraoccipital ossifications have fused. The exoccipitals are each pierced by the foramen of the vagus nerve.

The quadrate has lengthened. Between it and the palatine has appeared an ossification corresponding to the pterygoid process. The hyomandibular extends beneath the sphenotic and the interopercle touches the opercle. Ventrally, the ceratohyal is easier to distinguish from the epihyal.

### *Level 10 : 24- and 28-day-old fry* (Fig. 9)

The bones of the dome of the skull have all grown. The pterotic, the sphenotic, and the orbitosphenoid have all considerably developed vertically to constitute the lateral wall of the braincase. The latter is extended posteriorly by the exoccipital which stretches upward. Anteriorly, the vomerine ossifications have lengthened. At the level of the suspensorium, the novelty is the appearance of a small ossification situated latero-ventrally with respect to the palatine. This may be an ectopterygoid.

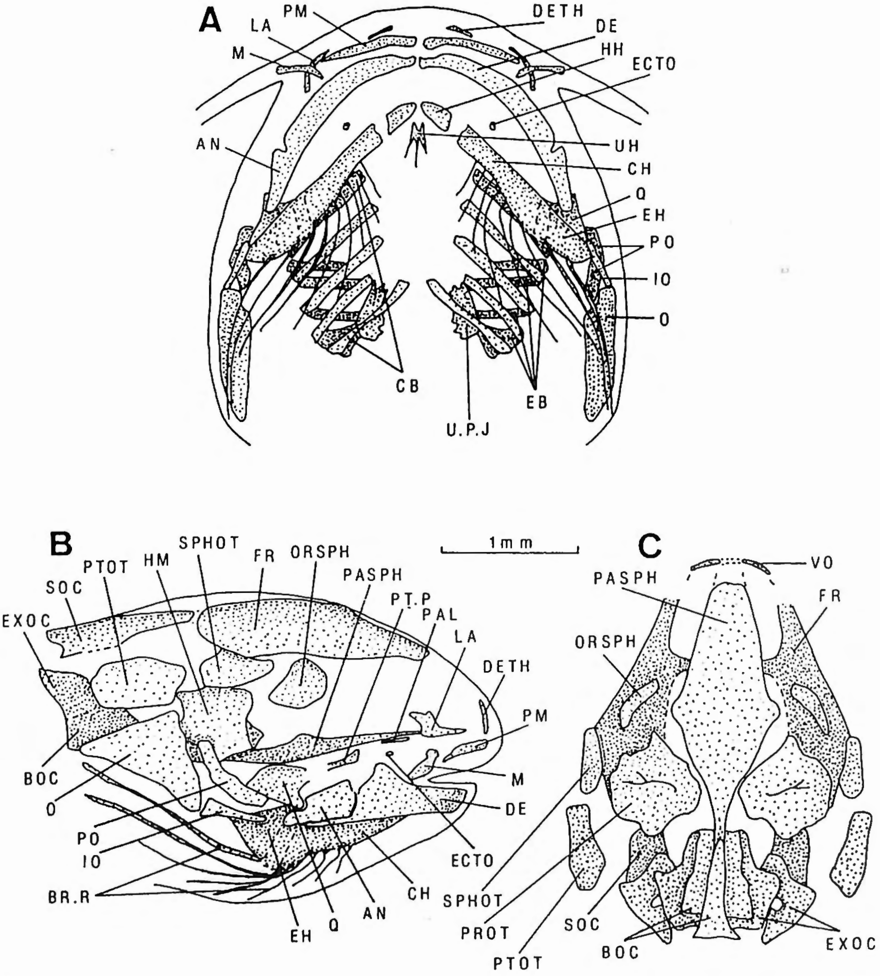

Fig. 9. — *Chrysichthys auratus.* — Presentation of the cephalic bony elements at the tenth level. (A) Ventral view of the splanchnocranium; (B) lateral view of the skull; (C) ventral view of the neurocranium. Dotted lines represent unclear limits. Abbreviations : AN, angular; BOC, basioccipital; BR.R, branchiostegal rays; CB, ceratobranchial; CH, ceratobranchial; DE, dentary; DETH, dermethmoid; EB, epibranchial; ECTO, ectopterygoid; EH, epihyal; EXOC, exoccipital; FR, frontal; HH, hypohyal; HM, hyomandibula; IO, interoperculaire; LA, lacrimal; M, maxilla; O, opercle; ORSPH, orbitosphenoid; PAL, palatine; PASPH, parasphenoid; PM, premaxilla; PO, preopercle; PROT, prootic; PTOT, pterotic; PT.P, pterygoid process; SOC, supraoccipital; SPHOT, sphenotic; UH, urohyal; U.P.J, upper pharyngeal jaw; VO, vomer.

The hypohyals and the urohyal have extended. Epibranchials 3 and 4 are in contact with the upper pharyngeal jaws, where it is still impossible to distinguish individual components.

*Level 11 : 24- and 28-day-old fry* (Fig. 10)

The supraoccipital ossification has practically come into contact with the frontals, which are linked by a complete epiphyseal bridge. The taenia marginalis ossification plunges toward the dermethmoid which has grown upward. Next to the latter, a nasal has appeared. The vomer is now a single piece, in contact with the parasphenoid. Laterally, two small ossifications have been added to the nasal region. These are probably two elements of the lateral ethmoid.

Posteriorly, the supraoccipital, the pterotic, and the sphenotic have almost completely united. The exoccipital and the supraoccipital are not yet truly joined. The sphenotic, the prootic, and the orbitosphenoid are still independent.

The mandible displays distinct dentaries and angulars. The quadrate has reached the pterygoid process. The hyomandibular articulates with the sphenotic and the pterotic. The hyohyals touch. The branchial basket has been enriched with two basibranchials, with dentate plates on the dorsal face of the 5th ceratobranchials and the ventral face of the upper pharyngeal jaws, and with the first gill rakers borne by the two first ceratobranchials. There are not yet any ossified hypobranchials.

## DISCUSSION

It is not easy to compare the cephalic bony development in different teleosts. Few descriptions begin at hatching, the observed stages are often far apart, the living or farming conditions of the fry are variable, and finally, stages are defined differently according to the author. Having made these reservations, one can say that the postembryonic development of the skull bones of teleosts seems not to be very constant (De Beer, 1937 ; Bamford, 1948 ; Jollie, 1984 ; Matsuura and Yoneda, 1987 ; Vandewalle *et al.*, 1992a), although the first bones to appear are always the dermal elements of the splanchnocranium.

There is no bony structure in *Barbus barbus* (L., 1758) or *Clarias gariepinus* (Burchell, 1822) at hatching (Surlemont *et al.*, 1991 ; Vandewalle *et al.*, 1992a). The same is true for *Chrysichthys auratus*. In the siluriform *Clarias gariepinus*, the first bone appears after 48 hours : the opercle (Surlemont *et al.*, 1989). In another catfish, *Galeichthys felis* (Valenciennes, 1840), there is, at 8 mm, nothing but a small dentosplenial (Bamford, 1948). Tilney and Hecht (1993) report that development is very slow in *Galeichthys feliceps* (Valenciennes, 1840) and that the first bones to develop are the cleithra, followed, at 43 days, by the opercles, the dentaries, the maxillaries, and the first four pairs of branchiostegal rays. In three species of the genus *Silurus*, the maxillaries and premaxillaries appear first (Kobayakawa, 1992). In the cyprinid *Leuciscus rutilus* (L., 1758), the first ossification is the fifth ceratobranchial which is in fact the pharyngeal jaw (Hubendick, 1942). In another cyprinid, *Barbus barbus*, on the contrary, the opercle, a thin maxilla, a dentary, a small angular, and a small retroarticular appear at 8 days along with a branchiostegal ray (Vandewalle *et al.*, 1992a). In *Lophius gastrophysus* (Ribeiro) 8 mm long, there are already a maxilla, a premaxilla, a dentary, an articular, and

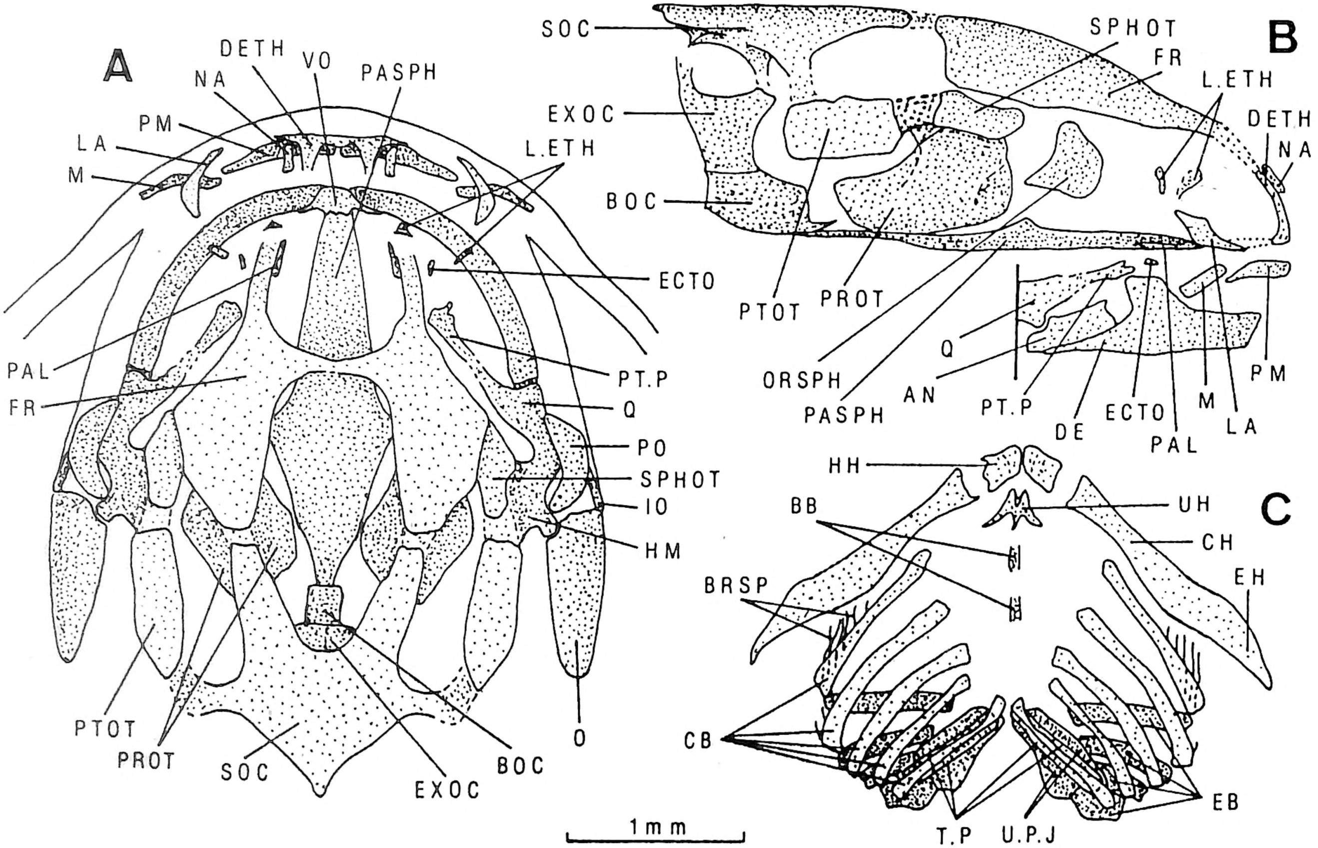

Fig. 10. — *Chrysichthys auratus.* — Presentation of the cephalic bony elements at the eleventh level. (A) Dorsal view of the neurocranium, jaws, suspensorium and operculum ; (B) lateral view of the neurocranium and anterior part of the splanchnocranium ; (C) ventral view of the hyoid bars and branchial basket. Dotted lines represent unclear limits. Abbreviations : An, angular ; BB, basibranchial ; BOC, basioccipital ; BRSP, Branchiospines or gill rakers ; CB, ceratobranchial ; CH, ceratohyal ; DE, dentary ; DETH, dermethmoid ; EB, epibranchial ; ECTO, ectoptérygoid ; EH, epihyal ; EXOC, exoccipital ; FR, frontal ; HH, hypohyal ; HM, hyomandibula ; IO, interopercle ; LA, lacrimal ; L.ETH, lateral ethmoid ; M, maxilla ; NA, nasal ; O, opercle ; ORSPH, orbitosphenoid ; PAL, palatine ; PASPH, parasphenoid ; PM, premaxilla ; PO, preopercle ; PROT, prootic ; PTOT, pterotic ; PT.P, pterygoid process ; Q, quadrate ; SOC, suparoccipital ; SPHOT, sphenotic ; T.P, tooth plate ; UH, urohyal ; U.P.J, upper pharyngeal jaw ; VO, vomer.

a preopercle (MATSUURA and YENODA, 1987). In *Nerophis aequoreus* (L., 1758), the first ossifications are the premaxilla, the maxilla, the dentary, and the angular (KADAM, 1961), while in *Salmo gairneri* (Richardson, 1836), there is first at least the opercle (VERRAES, 1977). *Chrysichthys auratus* is relatively precocious with, at two days of age, the presence of an opercle, a dentary, and two branchiostegal rays.

Throughout the eleutheroembryonic and larval periods, the splanchnocranium develops more rapidly than the neurocranium. This is a general phenomenon in teleosts (DE BEER, 1937). In *Barbus barbus*, all the ossifications of the suspensorium are present at 20 days, whilst the neurocranium still counts only four bones (VANDEWALLE *et al.*, 1992a). The buccal and pharyngeal jaws grow particularly fast. This situation is encountered also in *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991) and in many Perciforms (OTTEN, 1982 ; ISMAIL *et al.*, 1982 ; MORRIS and GAUDIN, 1982 ; POTTHOFF *et al.*, 1987 ; POTTHOFF and TELLOCK, 1993 ; WATSON and WALKER, 1992). The same is true in *Chrysichthys auratus.* In the latter species, it is noteworthy that from the time of its appearance, the maxilla is oriented towards the maxillary barbel ; from level 4 onwards, it occupies the place it has in the adult, where it supports the maxillary barbel and partially ensures its mobility (GHIOT *et al.,* 1984).

The first endochondral ossifications of the splanchnocranium of *Chrysichthys auratus* appear rather late, at level 8, but numerous ones appear all at once (hyomandibular, quadrate, palatine). In *Barbus barbus*, the quadrate appears first and progressively the rest of the endochondral suspensorium (VANDEWALLE *et al.,* 1992a). In *Chrysichthys auratus*, the shape of the quadrato-mandibular articulation seems to indicate that it is functional from the time it appears. This is not true in *Barbus barbus* (VANDEWALLE *et al.*, 1992a), where this articulation does not seem functional until the hyomandibular is present and well developed. As just mentioned, this situation arises more abruptly in *Chrysichthys auratus.* In both species, by the time the quadrato-mandibular articulation seems functional, so do the hyomandibulo-opercular and cranio-hyomandibular articulations, or nearly so. Thus, three of the four principal articulations of the suspensorium are constituted. They very likely enable the dilation of the buccal and opercular cavities which is necessary for breathing and feeding (OSSE, 1969 ; VANDEWALLE, 1979, 1980 ; LAUDER, 1983, 1985). Only the palatine region remains very incomplete. These observations agree with those of JOLLIE (1975) on *Esox lucius* (L., 1758).

The formation of the anterior region of the suspensorium varies from species to species. In all known cases, it is late. In *Barbus barbus*, the entopterygoid appears first, then the ectopterygoid and the palatine, and finally the metapterigoid. In this species, at 24 days, these different bony elements are separate from each other and the palato-ethmoideal articulation is not yet functional. In *Clarias gariepinus* (VANDEWALLE *et al.,* 1993), an entopterygoideal ossification is reported to form in front of the cartilaginous processus pterygoideus. Perhaps this ossification merely corresponds with the processus pterygoideus of *Chrysichthys auratus.* In the latter species, the palatine appears first, followed by the processus pterygoideus and finally by a small ossification which we have called ectopterygoid because of its ventro-lateral position with respect to the palatine. These three parts are not joined.

The delayed construction of the anterior portion of the suspensorium is probably related to the absence of a functional necessity during the larval period, since specimens can carry out their essential functions, notably breathing and feeding, with a suspensorium whose posterior part alone is complete.

In *Chrysichthys auratus* as in many other species (JOLLIE, 1975 ; VERRAES, 1977 ; SURLEMONT and VANDEWALLE, 1991 ; VANDEWALLE *et al.*, 1992a), the opercle is present at an early stage of development. In the adult, this element is essential to gill ventilation because it contributes to creating the water current from front to back within the buccal and opercular cavities (OSSE, 1969 ; ELSHOUD-OLDENHAVE and OSSE, 1976 ; VANDEWALLE, 1979). This respiratory requirement probably appears very early in fry.

As in *Barbus barbus* (VANDEWALLE *et al.*, 1992a), *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991), and many Perciforms as well (WATSON and WALKER, 1992 ; POTTHOFF *et al.*, 1987, 1988), the first ossifications of the branchial basket to appear in *Chrysichthys auratus* are the pharyngeal jaws. In all cases, they bear teeth very early. They are present before or at the time feeding on exogenous food begins. Their early ossification meets the need to grasp the food to be transformed and to be transported towards the oesophagus, a function which they perform in adults (SIBBING, 1982 ; LIEM, 1986 ; LIEM and SANDERSON, 1986 ; VANDEWALLE *et al.*, 1992b, 1995). Cartilaginous skeletal elements probably suffice to fulfill, as in *Barbus barbus*, the respiratory function of the rest of the branchial basket (VANDEWALLE *et al.*, 1992b) or, as in *Cyprinus carpio* (L., 1758), a suction feeding (OSSE, 1990).

In *Chrysichthys auratus*, the neurocranium develops more slowly than the splanchnocranium, without being as delayed as in *Barbus barbus* (VANDEWALLE *et al.*, 1992a). Except for the early ossification of the anterior region of the notochord or basioccipital, only the parasphenoid appears very early, as in the other species known in this respect (VERRAES, 1974 ; SURLEMONT and VANDEWALLE, 1991 ; VANDEWALLE *et al.*, 1992a ; WATSON and WALKER, 1992 ; OOZEKI *et al.*, 1992). As it develops, it constitutes the ceiling of the buccal cavity. It very probably closes the hypophyseal fenestra as in *Barbus barbus* (VANDEWALLE *et al.*, 1992a). and *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991). Its presence is justified by the necessity of separating, by means of a rigid bony element, the buccal cavity from the front of the braincase, thus enabling the fry to ingest solid food without it pressing on the brain.

The second step of the construction of the neurocranium is the formation of the entire cranial floor, by joining of the notochord or basioccipital with the parasphenoid and the appearance of the exoccipitals. At this time a bony roof of the braincase is totally non-existant. The same order of development has been observed in *Clarias gariepinus* (SURLEMONT and VANDEWALLE, 1991), *Barbus barbus* (VANDEWALLE *et al.*, 1992a), two haemulid species (WATSON and WALKER, 1992), and *Sillago japonica* (Temminck et Schlegel) (OOZEKI *et al.*, 1992). This most likely meets the necessity of isolating the brain from the underlying organs and structures without compromising rapid growth.

The third step is the development of the cranial roof, whereas the anterior region of the neurocranium is still almost nonexistant. This time gap in the elaboration of the neurocranium is even more marked in *Barbus barbus* (Vandewalle *et al.*, 1992a) and it seems to exist in many teleosts (Watson and Walker, 1992; Tilney and Hecht, 1993). At this stage of development, effective protection of the brain probably becomes a necessity, while the anterior region shelters no essential structure.

## CONCLUSIONS

The development of the cephalic bony skeleton in *Chrysichthys auratus* is not uniform. It is as if development had to meet survival needs which appear hierarchically in time. At hatching, the highly vascularized yolk sac fulfills the nutritional function and probably at least part of the respiratory function. The shift to ingestion of exogenous food requires the formation of buccal and pharyngeal jaws. This new type of food requires a well-delimited buccal cavity so as not to interfere with the development of other structures, notably the brain. Hence the parasphenoid, then the rest of the braincase floor, form the limit between the braincase and the buccal cavity, preventing any physical or mechanical interaction between them. The efficiency of food ingestion is reinforced by construction of the postero-ventral part of the cheek. At the same time, the dorsal protection of the cranium develops. It seems that the strengthening of the anterior portion of the neurocranium and of the splanchnocranium is not yet a necessity.

The postembryonic development of other species may not respond to the same necessities. In *Haplochromis elegans*, for instance, the frontal bone appears very early, shortly after the primordium of the parasphenoid (Verraes and Ismail, 1980; Ismail *et al.*, 1982), and in *Nerophis oequoreus*, the supraoccipital and frontal bones develop at the same time as the ethmoideal region.

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# DESCRIPTION OF *ENCENTRUM DIETERI* sp. nov. (ROTIFERA, DICRANOPHORIDAE) FROM THE HIGH ARCTIC, WITH REDESCRIPTION OF *E. BIDENTATUM* (LIE-PETTERSEN, 1906) AND *E. MURRAYI* BRYCE, 1922

by

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## SUMMARY

*Encentrum dieteri* sp. nov. (Rotifera, Monogononta : Dicranophoridae) collected from littoral marine algae of two fjords in Spitsbergen, Svalbard, is described and illustrated. *E. murrayi* Bryce, 1922 is reported for the first time since its description from Spitsbergen ; it is redescribed and illustrated. Also described and illustrated is *E. bidentatum* (Lie-Pettersen, 1906) ; *E. linnhei* Scott, 1974 is synonymised with *E. bidentatum.*

*Keywords* : Rotifera, taxonomy, *Encentrum*, new species, Arctic, Svalbard.

## INTRODUCTION

The rotifer genus *Encentrum* Ehrenberg, 1838 is, with about 90 species, the most species-rich of the Dicranophoridae. However, the validity of many of these species is questionable because of poor descriptions and illustrations. Also a considerable number of species have not been reported since their description.

The study of the genus has long been neglected due to difficulties in obtaining well-preserved specimens and insufficient sampling efforts of its habitats. As most of the dicranophorids, *Encentrum* species mainly occur in periphytic and interstitial habitats of the littoral zone, both marine and freshwater. The genus is considered to be cold stenotherm with predominantly temperate distribution.

In this paper *Encentrum dieteri* sp. nov. is described from littoral algae of a fjord on the west coast of Spitsbergen (Svalbard), *E. murrayi* Bryce, 1922 is reported for the first time since its description and redescribed, and *E. linnhei* Scott, 1974 is synonymised with *E. bidentatum* (Lie-Pettersen, 1906).

### *Encentrum dieteri* sp. nov.

Figs 1-8

### *Type locality*

Sassenfjorden near Gipshukodden, Bünsow Land, Spitsbergen, Svalbard. Coordinates : 78° 26′ 18″ N, 16° 23′ 34″ E. Obtained from marine algae (*Ectocarpus* sp., *Fucus vesiculosus* L., epilithic filamentous Cyanobacteria) growing in sublittoral fringe.

### *Material examined*

Holotype : a female in a permanent, glycerine glass slide mount deposited in the Koninklijk Belgisch Instituut voor Natuurwetenschappen (K.B.I.N.), Brussels, Belgium, N° AI.28.175.

Paratype : one female mounted in glycerine and one trophus preparation mounted in polyvinyl lactophenol, same data as holotype, in the K.B.I.N. ; 30 females in glycerine, 7 trophi preparations in polyvinyl lactophenol and 3 trophi mounted for SEM with the author in the Department of Biology, University Centre of Antwerp (R.U.C.A.).

Further material examined : 3 females collected among *Fucus vesiculosus* L., *Ectocarpus* sp. and microscopic epilithic algae from the littoral of Trygghamna, adjacent to Alkhornet, Daudmannsøyra, Spitsbergen (coordinates 78° 12′ 54″ N, 12° 50′ 42″ E).

### *Description*

Body stout, more or less parallel-sided in dorsal view, slightly curved in lateral view ; broadly oval in cross-section, higher than wide, greatest diameter near midlength. Head large, c. 1/3 total length ; neck part large, c. 1/2 head length, distincly set-off, with longitudinal folds ; anterior half of head narrower, retractable within neck part by two strong muscles attached to the corona with insertion in neck part (visible in contracted specimens as short twists in neck region) and two muscles attached to the mastax and inserted in the anterior region of the trunk. Dorsal antenna apparently paired, somewhat posterior to the middle of neck region, sunk in shallow depression. Rostrum very small, indistinct. Corona almost frontal. Trunk more or less abruptly narrowing at c. 1/4 from its posterior in dorsal view ; dorsally and laterally with a series of longitudinal folds, ventrally two short, curved folds. Tail broadly rounded. Foot with two short pseudosegments of equal length. Toes divergent, relatively long, nearly 1/4 total length, bases narrower in lateral view, slightly decurved, dorsal margins slightly curved, ventral margins slightly undulate, at c. 1/4 from the tips narrowing to tubular points ; in dorsal view more or less gradually tapering to the tubules. A pronounced terminally rounded, cylindrical papilla between toes. Eyespots absent. Retrocerebral sac long, saccate. Subcerebral glands well-developed, with globule. Salivary glands present. Gastric glands rounded to bean-shaped, short-stalked. Stomach and intestine separated, connected by distinct tube opening dorsally into intestine. Pedal glands large, clubshaped, extending into posterior part of trunk. Vitellarium with eight nuclei.

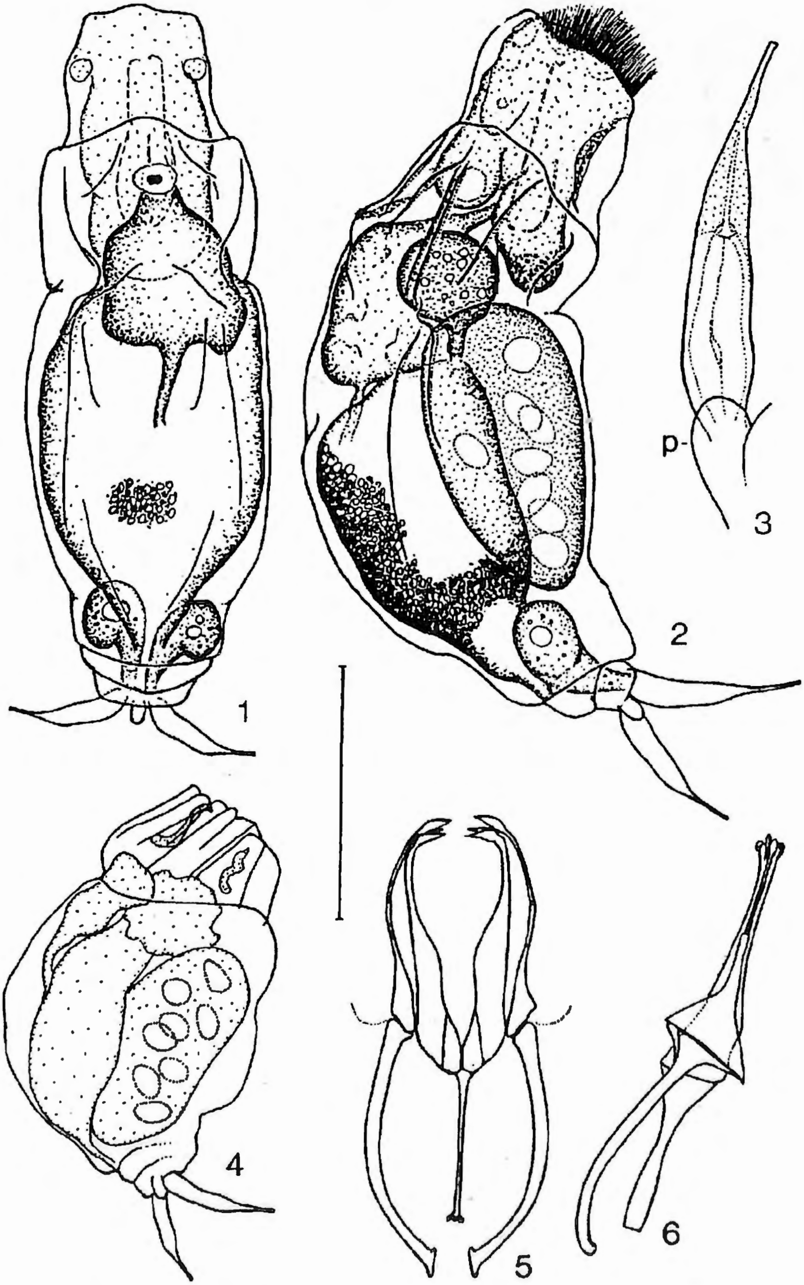
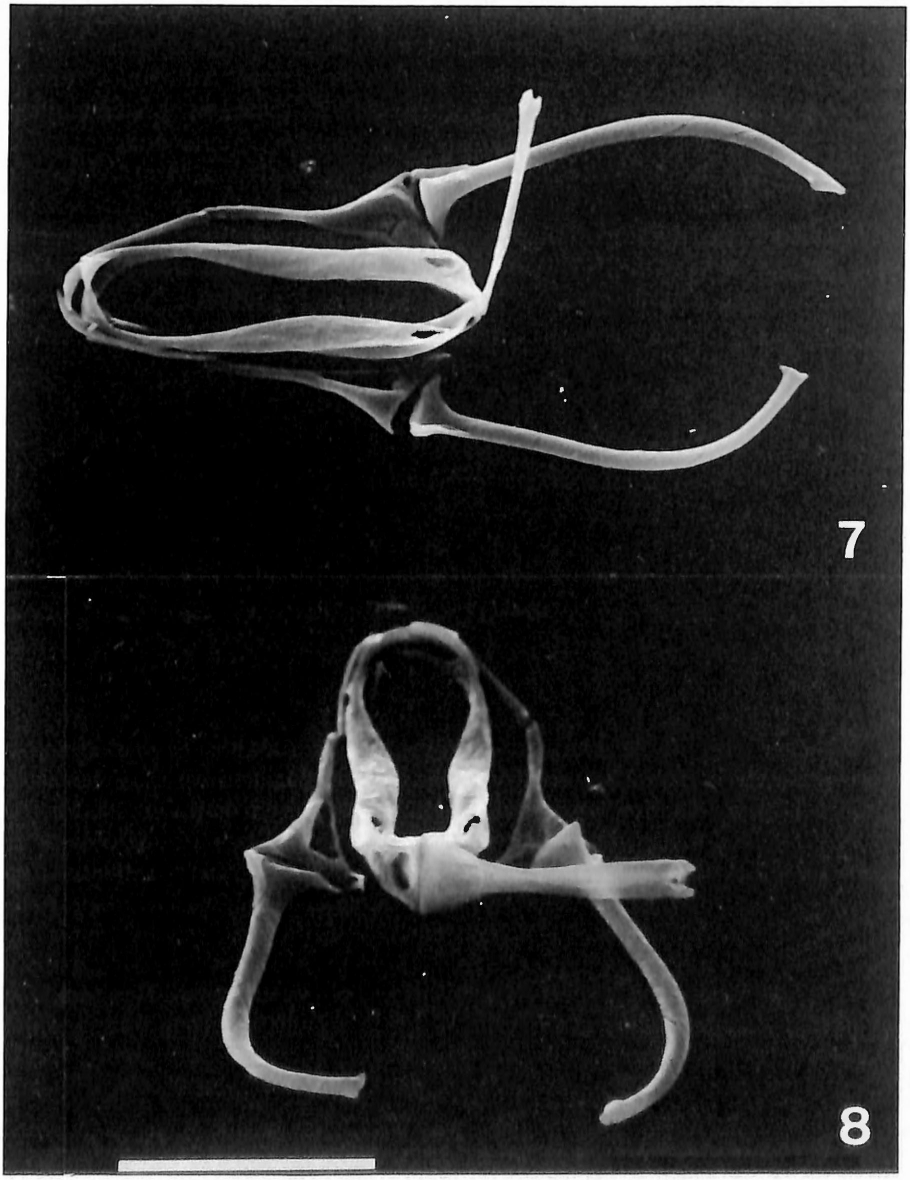


Fig. 1-6. — *Encentrum dieteri* sp. nov. — 1. Dorsal view, ♀ holotype (brain omitted). — 2. Lateral view. — 3. Toe ; p = papilla. — 4. Contracted specimen, lateral view. — 5. Trophi, dorsal view. — 6. Trophi, lateral view.
(Scale bar = 50 µm for 1,2 ; 20 µm for 3,5,6 ; 78 µm for 4).



Figs 7-8. — *Encentrum dieteri* sp. nov., SEM photographs. — 7. Trophi, dorsal view. — 8. Idem, fulcrum in lateral view.
(Scale bar = 10 µm).

Trophi elongate, very slender. Rami long, straight, outer margins parallel, median opening elongate pyriform ; each ramus terminating in a short, stout, slightly clubbed tooth, set at a right angle to the axis ; ventrally from each terminal tooth a similarly shaped and oriented pre-uncinal tooth. Fulcrum long, c. 2/3 ramus length, rod-shaped in dorsal view, posterior end slightly expanded; in lateral view with broad basis, gradually narrowing to half its length, afterwards expanding again and continuing more or less parallel-sided. Unci slender, slightly curved; head short, slightly clubbed, tips acute; shaft slightly expanded dorso-ventrally prior to basis of head. Intramallei long with broad triangular basal half and rod-shaped anterior half. Supramanubria absent. Manubria ramus length, curved in posterior half; head expanded with ventrally projecting spine, posterior end slightly crutched; head laterally with delicate, short, curved appendage that dissolves during hypochlorite treatment.

Neither males nor eggs were seen.

### *Measurements*

Total length 160-200 µm, toe 28-38 µm, papilla 5-7 µm.

Trophi 34-36 µm : ramus 18-19 µm, fulcrum 10-12 µm, uncus 8-9 µm, intramalleus 11-12 µm, manubrium 18-19 µm.

### *Derivation of name*

The species is named for my son Dieter, in recognition of his much appreciated help with sampling, field analyses and logistics.

### *Differential diagnosis*

The papilla between the toes is a rare structure of unknown function within the genus *Encentrum*. It has only been reported for *E. (Parencentrum) longipes* (Wulfert, 1936), *E. (Parencentrum) walterkostei* Jersabek, 1994, *E. sacculiforme* Tzschaschel, 1979, *E. sorex* Wulfert, 1951 and *E. valkanovi* Althaus, 1957. *Encentrum dieteri* is easily distinguished from the above mentioned papilla bearing species, by the shape of its relatively long toes. The species can not be confused with any other congener by its characteristic elongate trophi. The only other *Encentrum* with extremely slender trophi is *E. bidentatum* (Lie-Pettersen, 1906), from which *E. dieteri* is distinguished by the entirely different external morphology (Fig. 9-10) and major differences in the trophi (Fig. 11-12, 15-18), such as the elongate pyriform median opening instead of a wedge-shaped one, longer and differently shaped unci, shape of intramallei and manubria.

### *Ecology and distribution*

*Encentrum dieteri* occurred in Sassenfjorden and Trygghamna, which are side arms of the large Isfjorden in high arctic Spitsbergen. The species was collected in samples of *Ectocarpus* sp., *Fucus vesiculosus* L. and filamentous microscopic algae and Cyanobacteria growing on boulders and stones below the low water level. The highest numbers were counted among *Ectocarpus* sp.; it was not found among *Fucus vesiculosus* from the intertidal region. Temperature was 3-4° C, salinity 29.2-33.8 ‰, $Cl^-$ 16.2-18.7 $mgl^{-1}$, $SO_4^{2-}$ 2.4-5.0 $mgl^{-1}$, $Na^+$ 9.1-11.2 $mgl^{-1}$, $K^+$ 0.3-0.4 $mgl^{-1}$, $Ca^{2+}$ 0.4 $mgl^-$, $Mg^{2+}$ 1.1-1.8 $mgl^{-1}$.

The rotifer assemblages with the new species comprised *Aspelta clydona* Harring and Myers, 1928, *Colurella* spp., *Encentrum algente* Harring, 1921, *E. graingeri* Chengalath, 1985, *E. marinum* (Dujardin, 1841), *Encentrum* spp., *Keratella quadrata* (O.F. Müller, 1786), *Proales halophila* (Remane, 1929), *P. reinhardti* (Ehrenberg, 1834), and *P. theodora* (Gosse, 1827).

The analysis of the gut contents revealed a single *Colurella* sp. only, so we can say nothing definite about the feeding habits of *E. dieteri.*

## ***Encentrum bidentatum* (Lie-Pettersen, 1906)**

Figs 9-18

*Pleurotrocha bidentata* : LIE-PETTERSEN (1906), p. 32-33, Taf. II, fig. 6-7 ;

*Encentrum bidentatum* (Lie-Pettersen, 1906) after GODSKE ERIKSEN (1968), p. 26-28, fig. 2A-D ;

*E. linnhei* : SCOTT (1974), p. 247-251, fig. 1-2 ;

non *Diglena bidentata* (Lie-Pettersen) after VON HOFSTEN (1911-12), p. 210-212, fig. 5a-d ;

non *Encentrum bidentatum* (Lie-Pettersen) after REMANE (1929), p. 144, 151, fig. 176A-D.

### *Material examined*

Two permanent slide preparations labelled « *Encentrum bidentatum* (Lie-Pettersen) leg. et det. Brit Godske Eriksen, Z.M.U.B., 49.148 neotype and 49.149 paraneotype, rockpool with *Enteromorpha,* Flatevossen, Raunefjorden Tarna, 27 Nov. 1967 », in the collections of the Zoological Museum, Bergen, Norway.

A permanent slide preparation labelled « *Encentrum linnhei* Type. Scott, 1974, Rock pools, Loch Linnhé, West coast of Scotland, N° 1973.737-739 » in the collections of the British Museum (Natural History), London.

Living and preserved specimens of *E. linnhei* Scott, 1974 from rockpool water, Loch Linnhé, Scotland. One female and trophus preparation deposited in the K.B.I.N., Brussels, Belgium (N° A.I. 28.175) ; 20 females in glycerine, 15 trophi preparations in glycerine or Faure and 5 trophi mounted for SEM with the author in the Department of Biology, R.U.C.A.

### *Description*

Body more or less parallel-sided in dorsal view, tapering posteriorly. Head c. 1/4 total length, distinctly offset by neck-fold ; a secondary faint transverse fold near mid length. Rostrum very small, indistinct. Corona almost frontal ; a long, stiff bristle laterally on each side of mouth. Dorsal antenna anterior to neck-fold. Trunk curved dorsally, flattened ventrally, slightly compressed laterally. Tail broadly rounded. Foot short, c. 1/5 total length, conical, composed of one pseudosegment, slightly decurved ventrally. Toes small, c. 1/17-1/23 total length, set close together, more or less conical, bases somewhat swollen, tips slightly decurved ventrally in lateral view (occasionally outcurved laterally), with more or less offset tubules. Salivary glands present. Oesophagus relatively long ; stomach and intestine weakly

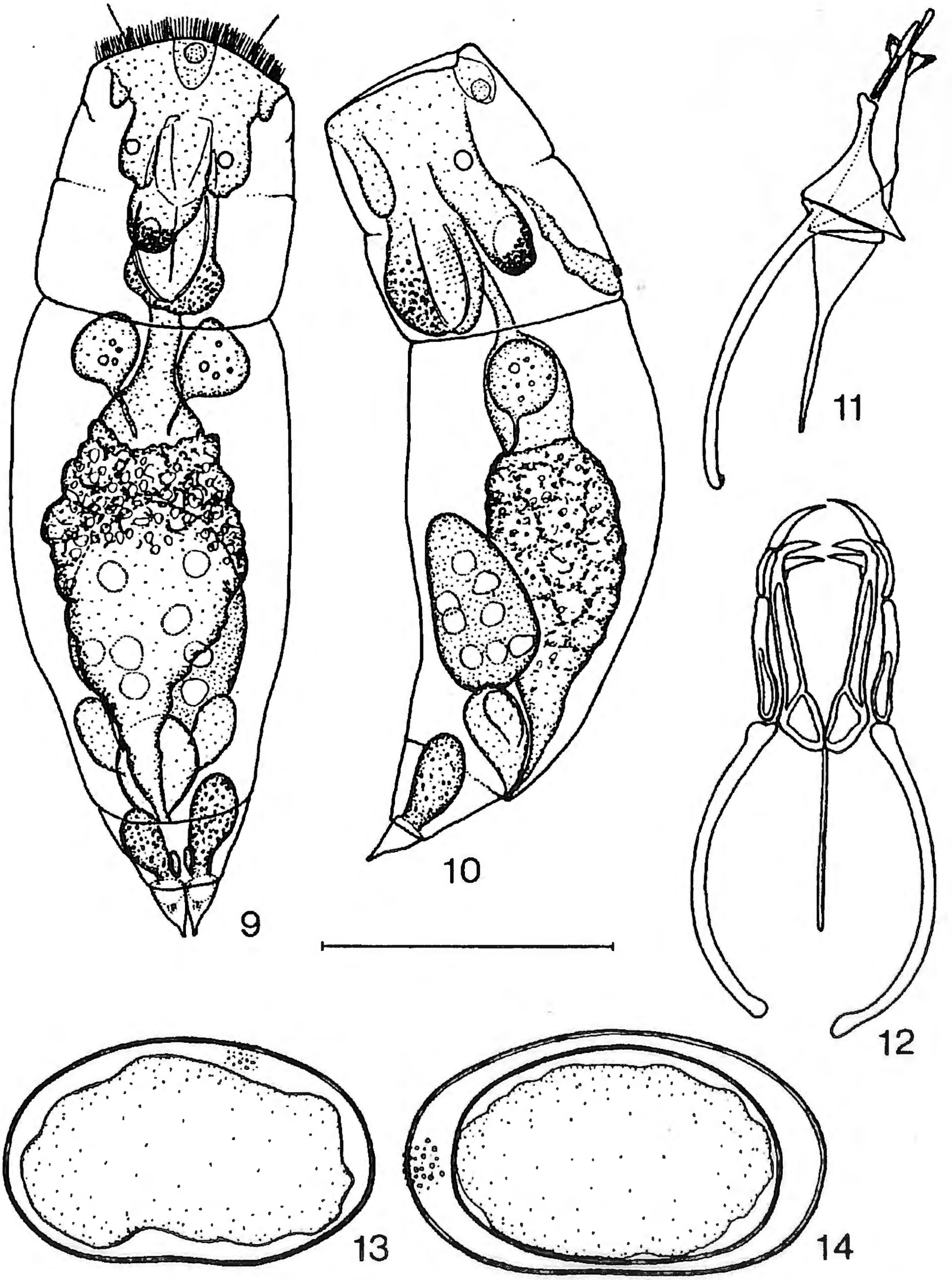


Fig. 9-14. — *Encentrum bidentatum* (Lie-Pettersen, 1906). — 9. Specimen in dorsal view. — 10. Specimen in lateral view. — 11. Trophi, lateral view. — 12. Trophi, dorsal view. — 13. Subitaneous egg. — 14. Resting egg.
(Sale bar = 50 µm for 9,10,13,14 ; 20 µm for 11,12).

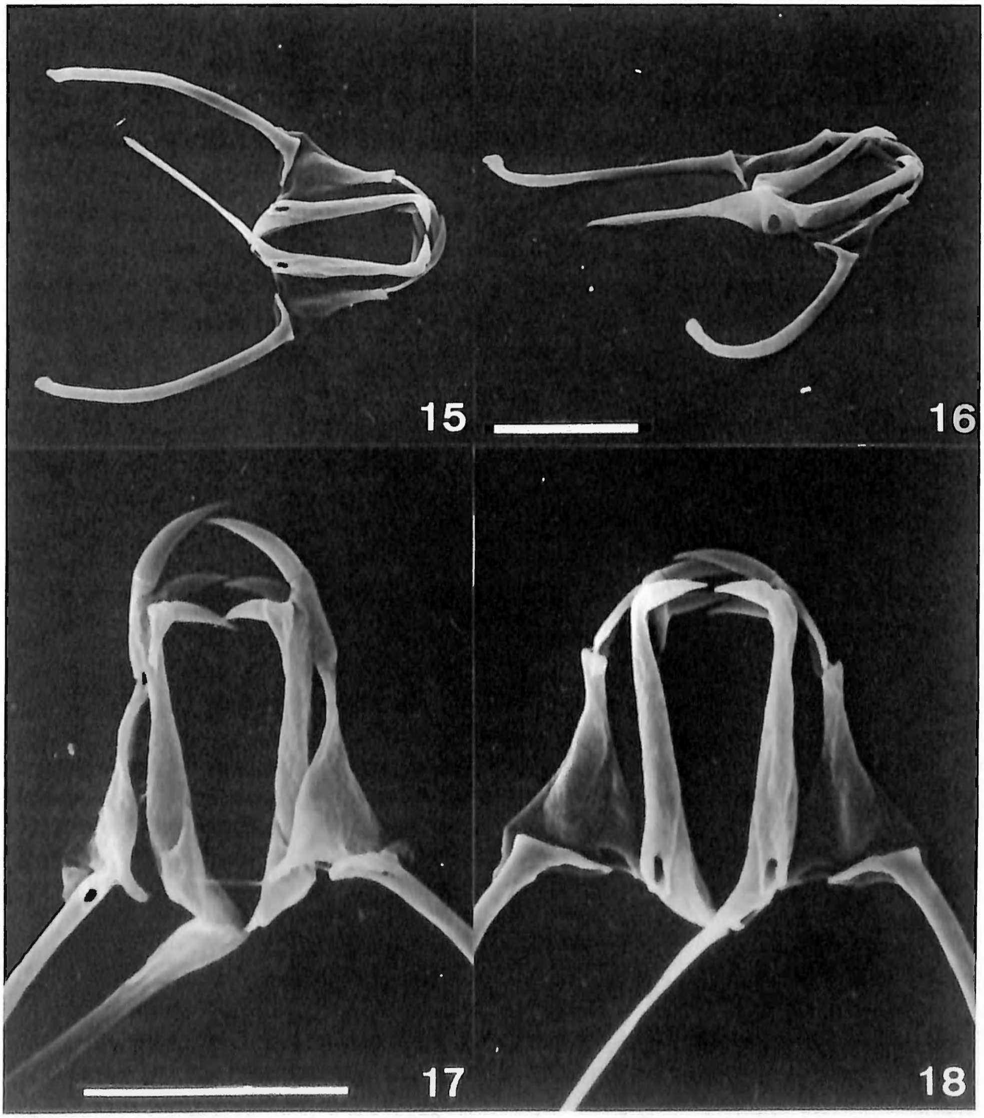


Fig. 15-18. — *Encentrum bidentatum* (Lie-Pettersen, 1906), SEM photographs. — 15. Trophi, dorsal view. — 16. Idem, fulcrum in lateral view. — 17. Trophi detail, ventral view. — 18. Idem, dorsal view.
(Scale bar = 10 µm).

separated. Gastric glands prominent, rounded to broad fusiform, with thin medium-long stalks. Pedal glands foot length, pyriform. Eyespots absent. Retrocerebral sac and subcerebral glands present. Two light refracting globules laterally from mastax. Vitellarium with eight nuclei.

Trophi large, elongate, slender. Rami nearly straight, broader at bases, outer margins slightly diverging anteriorly, median opening wedge-shaped; each ramus terminating in a sharp, inwardly projecting tooth, set at a right angle to the axis; at the base of each terminal ramus tooth ventrally a pre-uncinal element with at a right angle an inwardly projecting tooth. Fulcrum long, nearly ramus length, rod-shaped in dorsal view; in lateral view broad at base, gradually tapering till mid-length, continuing elongate-lanceolate. Unci slender, curved, acutely pointed, head c. 1/2 uncus length. Intramallei long, with broad triangular basal part and short, more or less rod-shaped anterior third. Supramanubria absent. Manubria c. 3/4 incus length, curved, both ends slightly expanded in dorsal view, head with acute projection ventrally.

Male unknown.

Subitaneous and resting eggs ovate, one long side slightly flattened, covered with short, fairly close-set pustules; pustules of resting eggs coarser.

### *Measurements*

Total length 130-220 µm, toe 10-18 µm.

Trophi 30-34 µm : ramus 13-14 µm, fulcrum 12 µm, uncus 7-8 µm, intramalleus 8-9 µm, manubrium 19-21 µm.

Subitaneous egg 51-66 µm x 38-42 µm; resting egg 65-80 µm x 44-47 µm.

### *Distribution*

So far the species has only be reported from rockpools in Scotland and Norway.

### *Comments*

The study of the type material of *E. bidentatum* (Lie-Pettersen, 1906) and *E. linnhei* Scott, 1974 showed that both species are conspecific.

The shape of the body and toes, and the morphology of the inner organs of the specimens studied agree fairly well with the description given by LIE-PETTERSEN (1906) of *Pleurotrocha bidentata.* As mentioned already by GODSKE ERIKSEN (1968), LIE-PETTERSEN's drawing of the trophi is rather inaccurate. One can obtain his figure however, if the trophi are studied *in situ* at a certain orientation of the body.

The specimens collected among Fucaceae from the Swedish west coast by VON HOFSTEN (1911-12) and identified as *Diglena bidentata* (Lie-Pettersen) definitely do not belong to this species. His species shows longer and more slender toes, the foot is long and slender, the corona is distinctly ventral, there is a pronounced rostrum, light refracting bodies are absent and the rami outline is circular. The records of *E. bidentatum* by REMANE (1929), who takes over VON HOFSTEN's (1911-12) figures, from shore pools in the Bay of Kiel and by SICK (1933) who reported it from the same area, likewise do not concern the species described by LIE-PETTERSEN (1906).

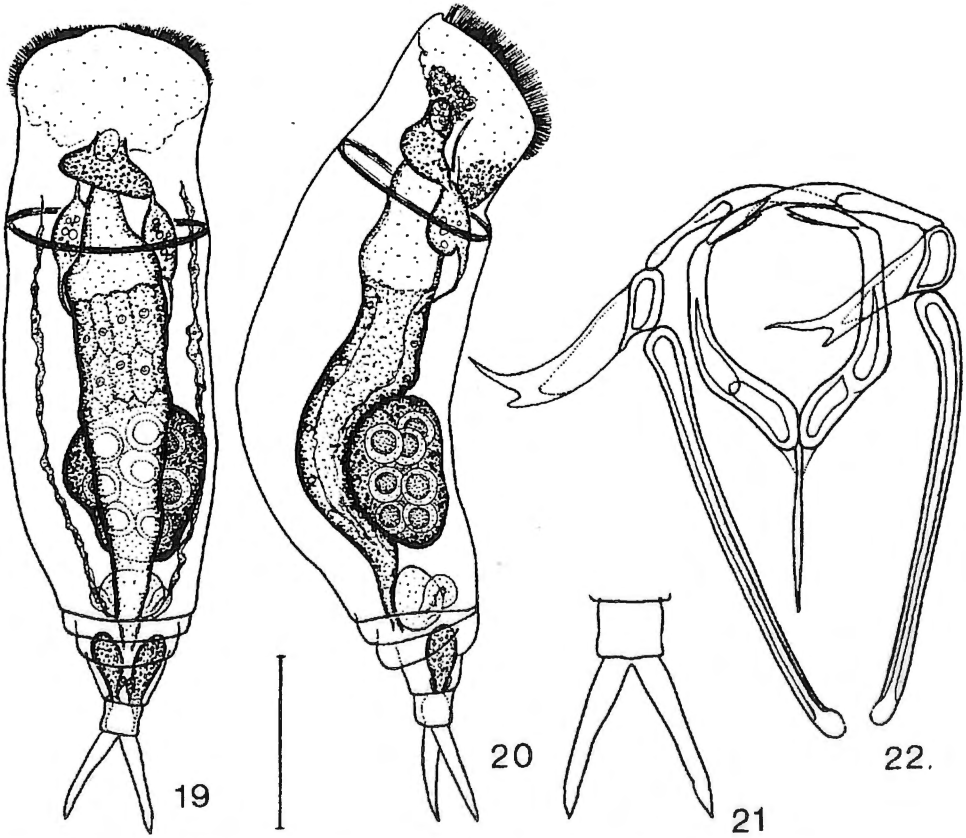
## *Encentrum murrayi* Bryce, 1922
Figs 19-26

### *Material examined*

Five females collected on 29.07.1994 from temporarily submerged mosses in frost crack bordering tundra polygon on strandflat adjacent to Alkhornet, Daudmannsøyra, Spitsbergen, Svalbard ; coordinates 78° 12′ 54″ N, 12° 50′ 42″ E. One female deposited in the K.B.I.N., Brussels, Belgium (N° A.I. 28.175) ; two females in glycerine and two trophi mounted for SEM with the author in the Department of Biology, R.U.C.A.

### *Description*

Body rather slender, elongate ; in dorsal view tapering to conical foot ; in lateral view gibbous dorsally. Head c. 1/4-1/5 total length, offset by indistinct shallow neck-fold and pronounced circular muscle. Rostrum small and narrow, rounded.



Figs 19-22. — *Encentrum murrayi* Bryce, 1922. — 19. Dorsal view. — 20. Lateral view. — 21. Toes, detail. — 22. Trophi, dorsal view.
(Scale bar = 83 µm for 19,20 ; 50 µm for 21 ; 20 µm for 22).

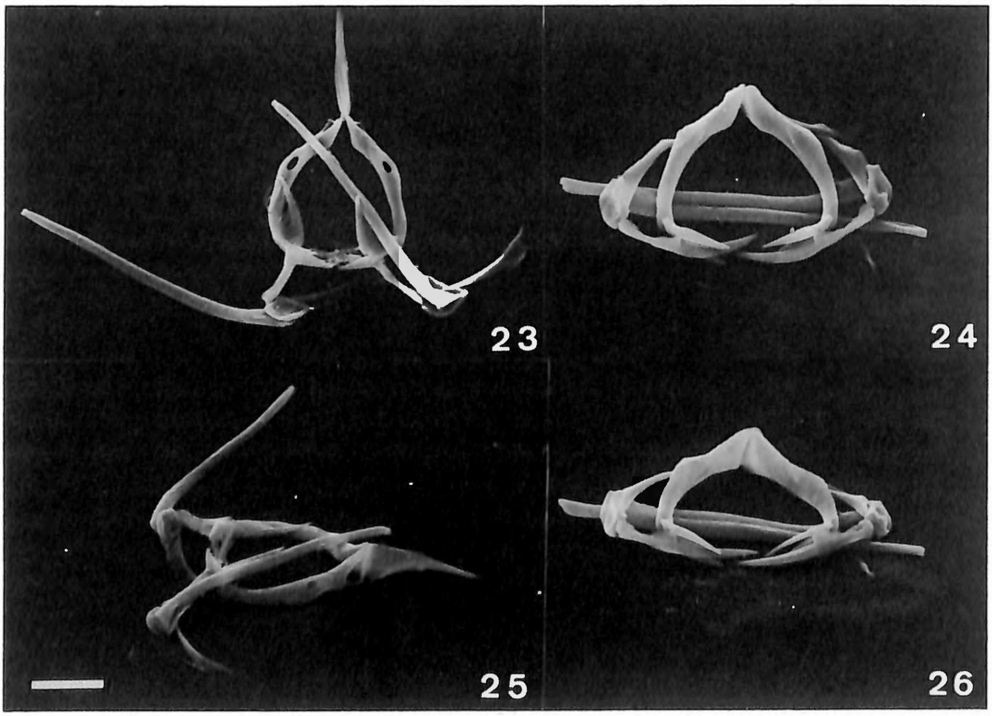


Fig. 23-26. — *Encentrum murrayi* Bryce, 1922, SEM photographs. — 23. Trophi, dorsal view. — 24. Trophi, ventral view. — 25. Trophi, lateral view. — 26. Trophi, oblique frontal view.
(Scale bar = 10 µm).

Corona slightly oblique. Foot with two pseudosegments, the posterior sometimes appearing two-jointed due to an additional faint transverse fold; anterior pseudosegment with dorsal fold overlying basal part of posterior one. Toes very stout, relatively short, c. 1/8 total length, strongly divergent, bases set close together, apparently fused; slightly decurved ventrally, almost parallel-sided in lateral view, very gradually tapering in dorsal view, tips short, slightly set off, with short tubules. Salivary glands present. Gastric glands oval; stalks thin, gland length, apparently connected with retrocerebral sac. No distinct constriction between stomach and intestine. Two pairs of pedal glands, outer pair almost as long as foot, inner pair much smaller; with reservoir in posterior foot pseudosegment. Eyespots absent. Retrocerebral sac expanded laterally. Vitellarium with eight nuclei.

Trophi large, rami lyrate, each ramus terminating in robust, incurved, lanceolate acute tooth; at base of terminal tooth ventrally a pair of prominent, inwardly projecting lanceolate pre-uncinal teeth; ventral pre-uncinal tooth largest, as large as terminal ramus tooth; anterior 2/3 of outer margins of rami more or less parallel-sided, posterior 1/3 tapering towards fulcrum, median opening obovoid; inner marginal teeth and alulae absent. Fulcrum 3/4 ramus length, elongate lanceolate in dorsal view; in lateral view with broad base, rapidly tapering towards posterior end, slightly curved dorsally, dorsal margin more strongly curved. Unci long, single-toothed, curved, in frontal view laterally broadened in posterior half, with ventral and dorsal expansions near mid-length. Manubria somewhat longer than incus, slightly incurved anteriorly, head slightly clubbed. Intramallei small, more or less drop-shaped. Supramanubria long, on dorsal margin of intramallei, at more or less right angles to incus, parallel-sided, free end bifid with long acute part and short blunter part, anterior margin and free end reinforced. Two epipharyngeal fans with very thin and long rays.

### *Measurements*

Total length 390-568 μm, toe 47-55 μm.

Trophi 49-64 μm : ramus 22-30 μm, fulcrum 15-20 μm, uncus 18-24 μm, pre-uncinal tooth 10-11 μm, intramalleus 6-10 μm, manubrium 38-52 μm.

The specimens seen by BRYCE (1922) were 300 to 375 μm long, the variation being to some extent dependent upon the length of the toes which measured about 25 μm to 48 μm; for the manubria he reported a length of about 33 μm.

### *Differential diagnosis*

*Encentrum murrayi* is characterized by its overall dimensions (300-568 μm) and stout, diverging, almost parallel-sided toes (25-55 μm). The species is closest to *Encentrum lutra* Wulfert, 1936, *E. permolle* (Gosse, 1886) and specimens described as *Dicranophorus permollis giganthea* by DARTNALL and HOLLOWDAY (1985) on the basis of the virtually identical trophi. *Encentrum lutra* and *E. permolle* are usually smaller (257-380 μm and 195-396 μm respectively) and display shorter, more or less conical toes (16-23 μm and 13-22 μm respectively). *Dicranophorus permollis giganthea* is a large species (overall length 446 μm, toe length 36 μm) known from several lakes at Signy Island (South Orkney Islands), Antarctica; it shows a frontal eyespot (absent in *E. murrayi*), a single foot pseudosegment (two in *E. murrayi*), apparently more strongly curved and tapering toes, rami terminating in simple incurved points (not lanceolate) and apparently absent pre-uncinal teeth.

### *Ecology*

The species was found among temporarily submerged mosses. Water temperature 4.2° C, conductivity 54 $\mu Scm^{-1}$, pH 7.5, alkalinity 1.04 mmole $l^{-1}$, oxygen 10.0 $mgl^{-1}$, $Cl^-$ 4.02 $mgl^{-1}$, $SO_4^{2-}$ 10.8 $mgl^{-1}$, $PO_4^{3-}$ < 40 $\mu gl^{-1}$, $NO_3^-$ 0.8 $mgl^{-1}$, $NO_2^-$ 0.0 $mgl^{-1}$, $NH_4^+$ 0.0 $mgl^{-1}$, Si 0.35 $mgl^{-1}$, $Na^+$ 4.33 $mgl^{-1}$, $K^+$ 0.33 $mgl^{-1}$, $Ca^{2+}$ 18.3 $mgl^{-1}$, $Mg^{2+}$ 1.5 $mgl^{-1}$.

The accompanying rotifer fauna mainly consisted of numerous bdelloid species and the monogononts *Bryceella stylata* (Milne, 1886), *Colurella uncinata* (O.F. Müller, 1773), *Lepadella ovalis* (O.F. Müller, 1786), *Encentrum lutra* Wulfert, 1936 and *E. mucronatum* Wulfert, 1936.

Analysis of the gut contents showed that *E. murrayi* feeds on bdelloids.

*Comments*

The species described here is certainly identical with the *Encentrum murrayi* described by BRYCE (1922) and never reported since. BRYCE (1922) hatched « about a dozen living examples » from washings of dry ground mosses collected at the strandflat near Brycebyen, Billefjorden (Bünsow Land, Spitsbergen). Our specimens were collected from a similar type of habitat in the same great fjord area of Isfjorden.

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I am very grateful to Dr. J.M. Scott (Dunstaffnage Marine Laboratory) for providing live specimens of *E. bidendatum.* Drs. C.G. Hussey (British Museum, Natural History) and E. Willassen (Museum of Zoology, Bergen) are thanked for the loan of type material of *E. linnhei* and *E. bidentatum.* Thanks are due to Mr. A. Das for the chemical analyses and Mrs. S. Pooters for typing the manuscript. I am very much indebted to the Department of Human Anatomy, University Centre of Antwerp for access to the scanning electron microscope. The field expedition was financially supported by the University Centre of Antwerp.

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# THE GENUS *FILENCHUS* ANDRASSY, 1954 (NEMATA : TYLENCHIDAE) FROM IRAN

by

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## SUMMARY

Seven known species of the genus *Filenchus* were found in soil samples collected from the rhizosphere of wild and agricultural plants in the central, western, and northern parts of Iran. *F. facultativus* (Szczygiel, 1970) Raski and Geraert, 1987 was found in two types : finely rounded tail tip and bluntly rounded tail tip. *F. acris* (Brzeski, 1986) Raski and Geraert, 1987 was found for the first time since its description. These species along with *F. baloghi* (Andrássy, 1958) Siddiqi, 1986, *F. discrepans* (Andrássy, 1954) Raski and Geraert, 1987, *F. misellus* (Andrássy, 1958) Raski and Geraert, 1987, *F. sheri* (Khan and Khan, 1978) Siddiqi, 1986 and *F. vulgaris* (Brzeski, 1963) Lownsbery and Lownsbery, 1985 are reported for the first time from Iran.

*Key words* : taxonomy, morphology, Tylenchida, *Filenchus*, Iran.

## INTRODUCTION

Nematology in Iran has only recently received attention. Only about 20 species of the family Tylenchidae have been identified (KHEIRI, 1970 ; KHEIRI, 1972 and some unpublished reports and studies). An attempt to identify some species of the family Tylenchidae has been carried out on the basis of soil samples collected since 1988, mostly in 1993, from natural and agricultural lands in the following areas : Lahijan in the north, Yazd and Varamin in the centre, and mostly Hamadan Province in the west. The species of the genus *Filenchus* will be dealt with here.

## MATERIAL AND METHODS

Nematodes were extracted by the centrifugal-flotation method, killed and fixed by hot FAP, transferred to anhydrous glycerine by the modified Seinhorst method (DE GRISSE, 1969). The nematodes were mounted on aluminium slides with double cover slips (COBB, 1917), and examined by light microscope (LM) and scanning electron microscope (SEM). For SEM, glycerine embedded nematodes in the permanent slides were first transferred into a drop of glycerine in a small embryo dish. Then distilled water was added drop by drop until nematodes were in pure distilled water. Ultrasonic treatment for about 8 minutes was used to remove adhering particles. The nematodes then were initially dehydrated by passing through a gradual ethanol concentration of 25, 50, 75, 95, and 100 % at two hourly intervals, followed by an overnight dehydration in 100 % ethanol. The standard critical point drying procedure was used with $CO_2$ as a drying liquid. Finally, dried nematodes were placed on a self-adhesive conducting aluminium tape and coated with gold. These gold coated specimens were studied under the scanning electron microscope.

## RESULTS AND DISCUSSION

### *Filenchus acris* (Brzeski, 1986) Raski and Geraert, 1987

(Figs. 1 G-J ; 2 A-D)

*Measurements*

Females (n = 3) : L = 0.409 ± 0.02 (0.385-0.425) mm ; a = 35 ± 1.5 (32-35) ; b = 5.7 ± 0.7 (4.9-6.7) ; c = 4.1 ± 0.2 (3.9-4.4) ; c' = 13 ± 1.2 (12-15) ; V = 61.2 ± 1.5 (59.3-62.8) ; V' = 81.1 ± 1.1 (79.6-82.1) ; VL = 250 ± 6.8 (241-257) µm ; Stylet = 5-6 µm ; Excretory pore = 58 ± 0.9 (57-59) µm ; Oesophagus = 73 ± 6.2 (64-78) µm ; MB = 43 ± 1.5 (42-45) ; V-a = 57 ± 4.7 (54-64) µm ; L' = 309 ± 9.9 (295-318) µm ; Tail = 101 ± 9.1 (88-109) µm.

*Description*

Female : Cuticle thin, with flat and wide annuli ; 1.8 (1.6-1.9) µm near mid body. Lateral field as a single ridge uncrenated. SEM photos show fine annuli on the head ending in a squarish cephalic plate with rounded corners, slightly indented on dorsal and ventral borders, circumoral plate set off by depression, approximately rounded. Amphidial apertures begin at cephalic plate, continue as simple, oblique slits posteriorly. Stylet delicate, knobs elongated and backwardly directed. Dorsal gland opening near stylet knobs. Metacorpus fusiform, muscular. Isthmus slender, long, crossed by nerve ring at its middle. Basal bulb pyriform.

Gonad outstretched ; oocytes in one row ; spermatheca small, ovate, without sperm. Uterus with four rows of four cells. Post-vulval-uterine sac rounded, 8-10 µm long, 0.7-0.9 times of VBD. Vulva slit, about one third of VBD, with small lateral membranes. Vagina straight with thin walls. Anus indistinct. Tail elongated conical, annulation disappears on posterior part of tail. Tail tip finely rounded.

Male not found.

*Discussion*

This population comes close to *Filenchus neoparvus* Raski and Geraert, 1987, *F. facultativus* (Szczygiel, 1970) Raski and Geraert, 1987, and *F. acris* (Brzeski, 1986) Raski and Geraert, 1987. It differs from the first species by having a shorter

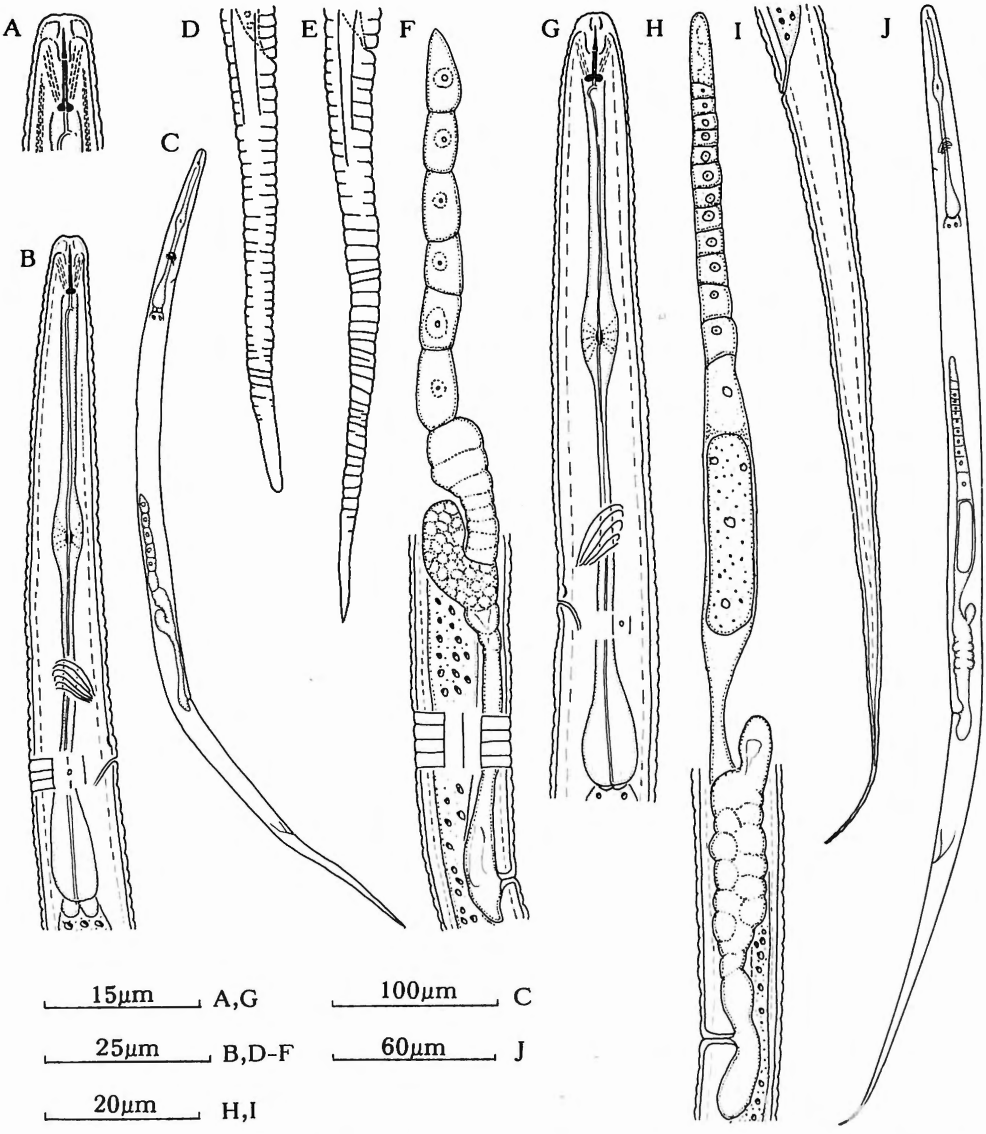


Fig. 1. — A-F. *Filenchus baloghi* — A. Anterior end - B. Oesophagus region - C. General view - D and E. Tail - F. Reproductive system - G-I. *Filenchus acris* - G. Oesophagus region - H. Reproductive system - I. Tail - J. General view.

stylet and genital tract, and striation on the head (stylet = 7-8 µm, ovary extending up to basal oesophageal bulb and the striation of the head is not clear in *F. neoparvus*). The second species has a longer stylet (stylet = 6-8 µm in various populations of *F. facultativus versus* 5-6 µm). It differs from *F. acris* by having different V, V' and MB ratios : V = 67 (66-69), V' = 84 (83-86), MB = 37 (35-38). In spite of these morphometrical differences, this population is considered as *F. acris*.

### *Habitat and locality*

This population was found in natural grassland, Cheshmeh Farshe, Hamadan, Iran.This is the first record since the original description.

## ***Filenchus baloghi*** **(Andrássy, 1958) Siddiqi, 1986**

(Figs1 A-F, 2 E)

### *Measurements*

Females (n = 4) : L = 0.511 ± 0.022 (0.480-0.540) mm ; L' = 0.433 ± 0.015 (0.415-0.450) mm ; a = 38 ± 2.9 (36-43) ; b = 5.7 ± 0.27 (5.3-6.0) ; c = 6.7 ± 0.39 (6.2-7.3) ; c' = 10 ± 1 (8.7-11.4) ; V = 64-65 ; V' = 75.8 ± 0.8 (75-77) ; stylet = 7-8 µm ; oesophagus = 91 ± 7.8 (80-102) µm ; MB = 47 ± 1.6 (46-50) ; V-a = 106 ± 3.2 (102-111) µm ; tail = 77 ± 7.5 (66-87) µm ; T/V-a = 0.72 ± 0.06 (0.65-0.82) ; annuli = 1.85 ± 0.09 (1.7-1.9) µm.

Male : not found.

### *Description*

The annulation of the cuticle is irregular, flat from anterior end to vulva and more rounded from vulva to tail end ; some annuli 2-3 times wider than the others ; 2-3 annuli anterior and posterior to vulva, at ventral side, are about twice as wide as the adjoining ones. Lateral field consists of three lines, the outer ones are crenate ; ends slightly posterior to anus. Cephalic region bluntly rounded, almost hemispherical outline, continuous with body contour. SEM photos show fine annuli continue onto head ending at squarish cephalic plate with rounded corners, indents on dorsal and ventral borders. Stylet delicate with small but distinct knobs. Metacorpus weakly developed, ovate, 43 ± 5 (37-51) µm from the anterior end. Excretory pore 78.3 ± 5.5 (69-83) µm from the anterior end, hemizonid 1-2 annuli in front of it ; deirids at level of excretory pore. Gonad outstretched ; ovary with few cells in one row ; spermatheca small to large, elongate, filled with sperm. Post vulval-uterine sac rounded, 6-11 µm long. Vagina short, at right angle to body axis. Tail conoid with annulated and finely or broadly rounded terminus.

### *Discussion*

This population very closely corresponds with the original description. In comparison with an Argentinean population (Torres and Geraert, 1996), it has smaller stylet, more posterior median bulb, and longer oesophagus : stylet = 7-8 µm, MB = 47 ± 1.6 (46-50), and oesophagus = 91 ± 7.8 (80-102) µm *versus* 8-10 µm, 41-42, and 81.4 ± 3.3 (77-87) µm, respectively in that population.

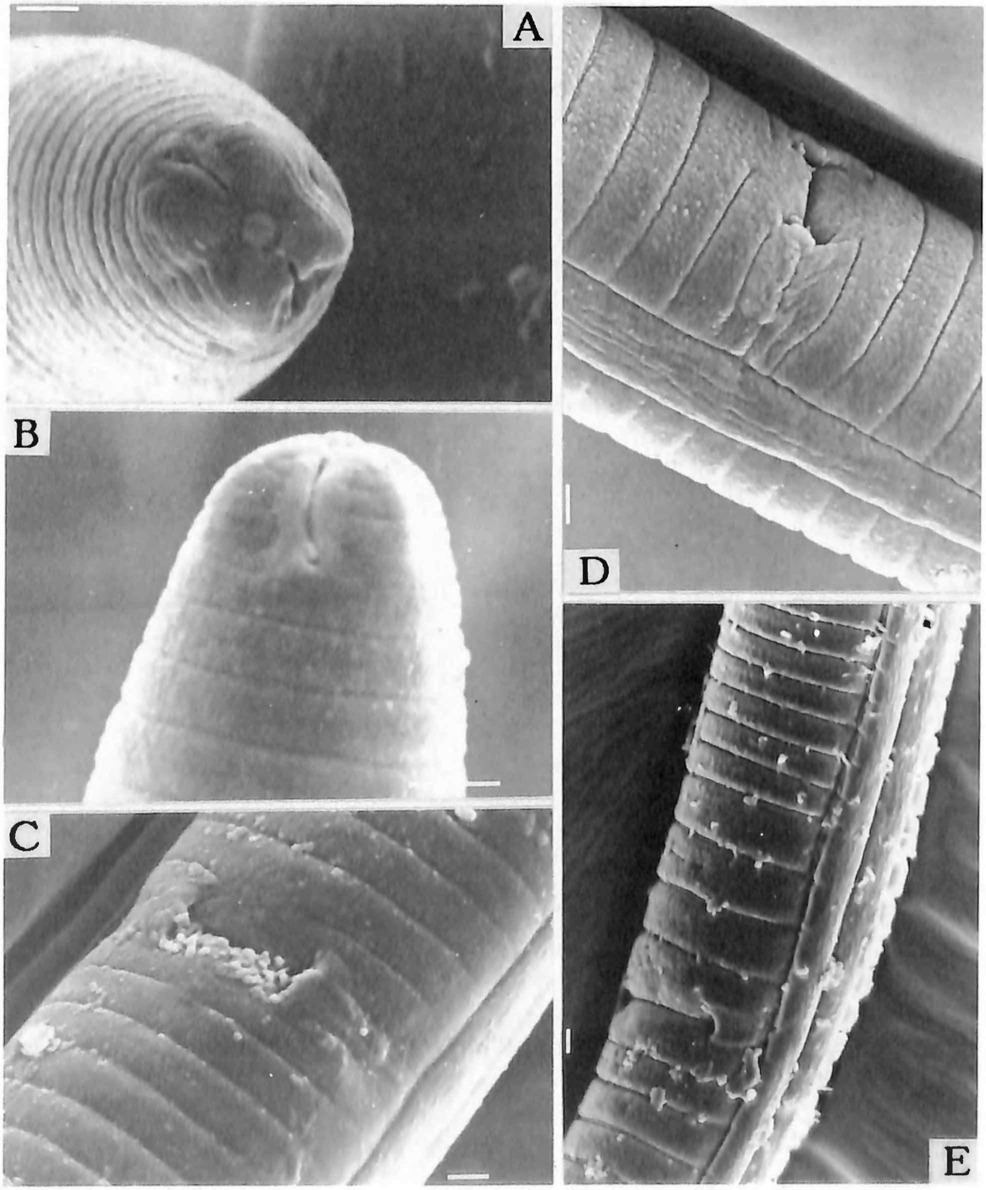


Fig. 2. — A-D. *Filenchus acris*, Female — A. Face view - B. Lateral view of head - C and D. Vulva with lateral field - E. *F. baloghi* - Lateral field and annulation at vulva. Bars equal 1 μm on A-E.

*Habitat and locality*

This population has been collected in the soil around *Equisetum arvensis* from « Darahe Morad Bayke », Hamadan.

### *Filenchus discrepans* (Andrássy, 1954) Raski and Geraert, 1987
(Figs 3, 4)

*Measurements*

Population No. 1 : Females (n = 6) : L = 0.530 ± 0.02 (0.505-0.565) mm ; L' = 0.390 ± 0.017 (0.370-0.420) mm ; a = 45.6 ± 2.4 (43-53) ; b = 5.6 ± 0.2 (5.3-6) ; c = 3.8 ± 0.1 (3.6-4.0) ; c' = 16.8 ± 1.7 (14.4-19.6) ; V = 60.4 ± 1.3 (59-63) ; V' = 82 ± 2.9 (79-88) ; stylet = 6.5-7 µm ; oesophagus = 93.8 ± 2.9 (89-98) µm ; MB = 37.6 ± 1.1 (36-39) ; V-a = 76.2 ± 3.8 (71-82) µm ; tail = 138.4 ± 6.2 (125-143) ; T/V-a = 1.8 ± 0.1 (1.6-2) ; annulation = 0.8 ± 0.1 (0.7-0.9) µm.

Male (n = 1) : L = 0.535 mm ; L' = 0.405 mm ; a = 46 ; b = 5.2 ; c = 4.2 ; c' = 15.7 ; T = 24 ; stylet = 6.5 µm ; oesophagus = 103 µm ; MB = 36 ; tail = 127 µm ; spicula = 15.5 µm ; gubernaculum = 4 µm ; annulation = 1 µm.

Population No. 2 : Females (n = 10) ; L = 0.530 ± 0.048 (0.435-0.600) mm ; L' = 0.388 ± 0.039 (0.320-0.450) mm ; a = 42.2 ± 4.2 (33.3-47.7) ; b = 5.8 ± 0.5 (4.9-6.5) ; c = 3.7 ± 0.2 (3.4-4.0) ; c' = 16.5 ± 1.8 (12.5-18.5) ; V = 58.2 ± 1.6 (55-61.2) ; V' = 79.5 ± 1.3 (78-82.3) ; stylet = 6-7 µm ; oesophagus = 91.3 ± 5.9 (79-100) µm ; MB = 38.6 ± 2 (35-41) ; V-a = 77.7 ± 11.4 (56-94) µm ; tail = 142.5 ± 11 (111-154) µm ; T/V-a = 1.9 ± 0.2 (1.6-2.1) ; annulation = 1 ± 0.1 (0.9-1.3) µm.

Male : not found.

*Description*

Female (based on population No. 1) : cuticle marked with delicate transverse striae ; lateral field in form of plain band ; SEM photos show some faint, interrupted inner lines in the band. Cephalic region continuous with body contour, almost truncate, about 4 µm wide and 2 µm high ; SEM shows fine annuli continuing onto head ending at squarish cephalic plate with rounded corners ; circumoral plate set off by depression, rounded and raised. Amphidial apertures big clefts beginning at the middle of labial plate, continuing posteriorly with slight curvature along the four head annuli ; cephalic framework moderately sclerotized.

Female reproductive system outstretched, spermatheca small to moderate, axial to offset (based on the size) ; offset part consisted of cells with globular nucleus ; with or without sperm ; post-uterine sac 7-10 µm long, 0.6-1.0 VBD. Vagina perpendicular to body axis.

Male : similar to female. Body narrows markedly at level of cloacal opening, cloacal lips make a short protruded tube. Caudal alae low rounded, adanal, beginning slightly after the spicule head, extending an equal distance posterior to cloaca.

*Discussion*

The two populations are similar except small differences in V and V' values, population No. 2 having lower values. These populations with lateral field as a plain band set off by two lines, short stylet, and fine annuli come close to *F. neonanus* Raski and Geraert, 1987, *F. discrepans* (Andrássy, 1954) Raski and

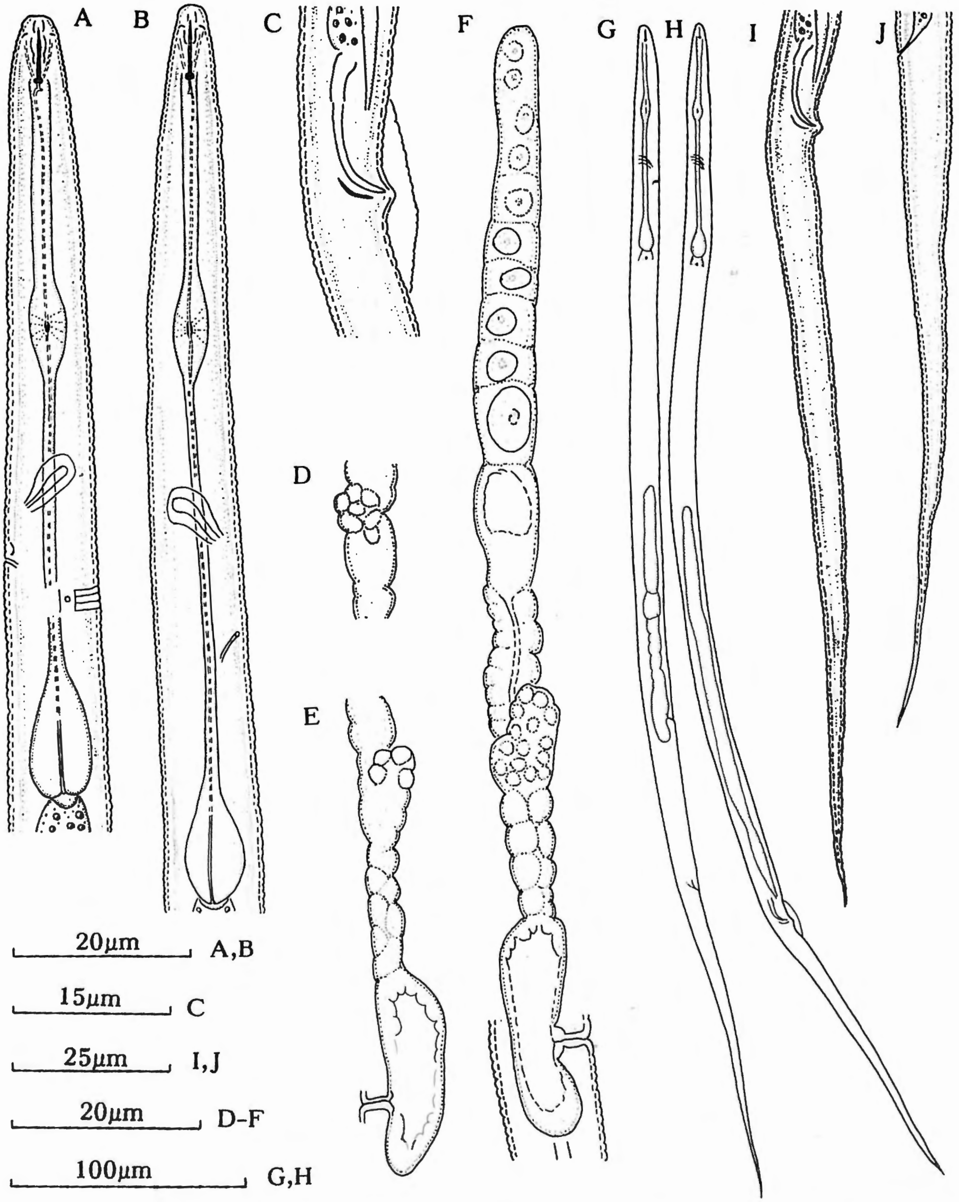
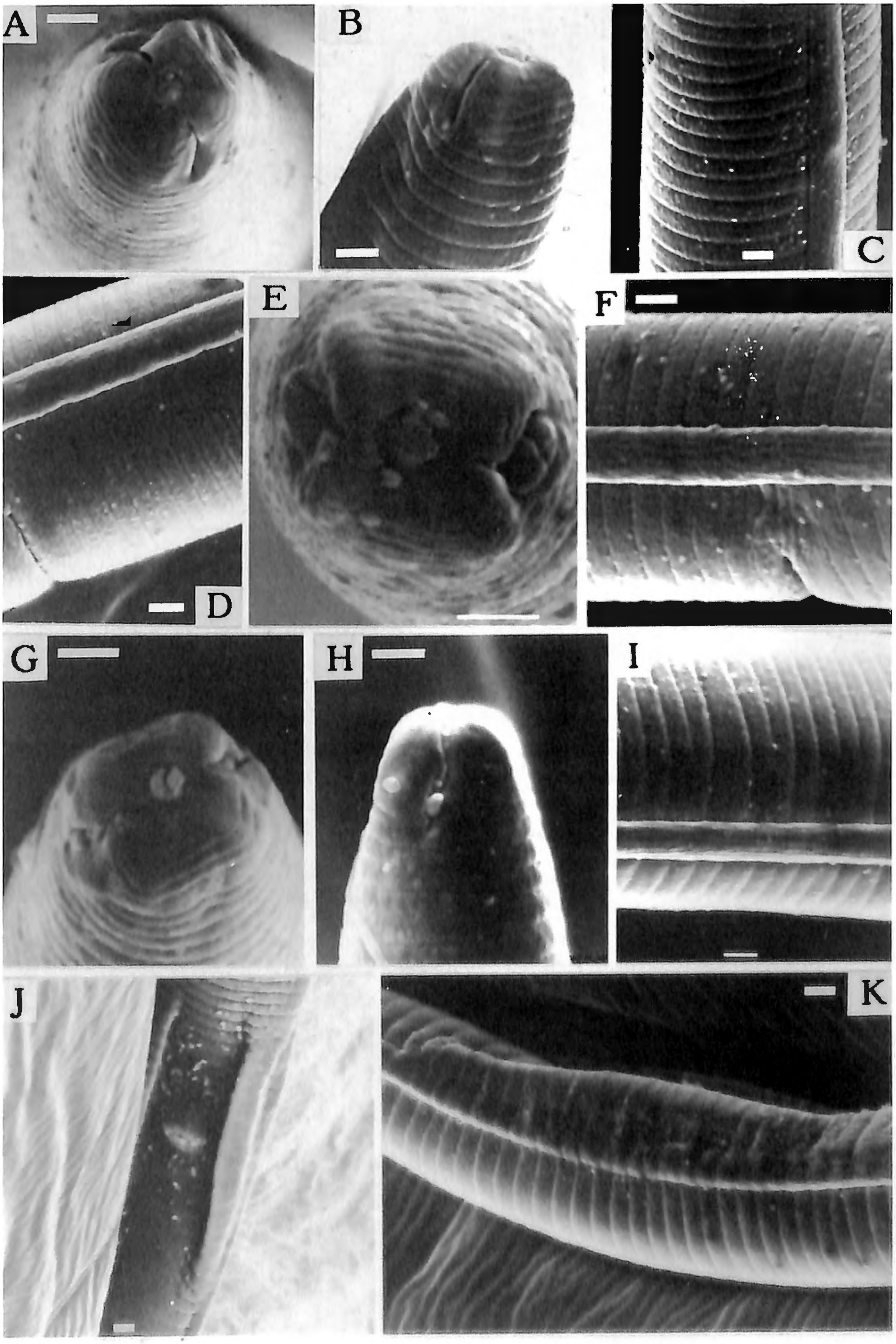


Fig. 3. — *Filenchus discrepans* — A,D-F,G,J. Female — A. Anterior end - D-F. Reproductive system - G. General view - J. Tail — B,C,H,I. Male — B. Anterior end. - C. Cloacal region - H. General view - I. Tail.


A
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Geraert, 1987, and *F. helenae* (Szczygiel, 1969) Raski and Geraert, 1987. *F. neonanus* has shorter tail (higher c value) longer stylet, more posterior metacorpus and vulva, and shorter post-vulval-uterine sac and tail : stylet = 7-8.5 µm, MB = 47 (44-51), V = 63 (62-65), tail = 90-113 µm. The other two species are not easy to differentiate from each other : *F. discrepans* is described with males, *F. helenae* without; *F. discrepans* has a vulva position of 61-64 %, *F. helenae* 53-61 % (Geraert, 1991). So, according to vulva position, our populations are *F. helenae*, but population No. 1 has a male. On the other hand Mizukubo (1994), after studying some Japanese populations (one population with male) as *F. helenae* has come to the conclusion that both species are the same, and suggested that *F. helenae* is a junior synonym of *F. discrepans*. We consider our populations as *F. discrepans*.

### *Habitat and locality*

These populations were found in grasslands from different sides of Alvand Mountain in Hamadan.

## ***Filenchus facultativus* (Szczygiel, 1970) Raski and Geraert, 1987**

(Figs 5, 6)

### *Measurements*

Type I; finely rounded tail tip :

Females (n = 9) : L = 0.460 ± 0.03 (0.415-0.510) mm; a = 35 ± 2 (32-38); b = 5.6 ± 0.5 (5.3-6.1); c = 5.1 ± 0.3 (4.2-5.4); c' = 10.1 ± 1.2 (9.2-13.2); V = 70 ± 1 (68-71); V' = 88 ± 1 (86-89); VL = 325 ± 26 (270-365) µm; stylet = 6-7 µm; median bulb = 34.6 ± 1.3 (33-38) µm; MB = 42 ± 1.5 (41-45); tail = 91 ± 6 (81-100) µm; V-a = 45 ± 4 (39-52) µm; T/V-a = 2 ± 0.2 (1.8-2-3).

Males (n = 3) : L = 0.410 ± 0.02 (0.380-0.430) mm; a = 34 ± 3 (31-38); b = 5.2 ± 0.3 (4.9-5.6); c = 4.8 ± 0.1 (4.7-5); c' = 10 ± 1 (9-11); MB = 44 ± 1.3 (43-46); stylet = 6 (5-7) µm; T = 40 ± 4 (36-46); spicules = 13 ± 1 (12-14) µm; gubernaculum = 3-4 µm; tail = 85 ± 4.6 (80-91) µm.

Type II; bluntly rounded tail tip :

Females (n = 4) : L = 0.460 ± 0.017 (0.445-0.490) mm; a = 35 ± 2.5 (32-38); b = 5.1 ± 0.1 (4.9-5.3); c = 5.8 ± 0.4 (5.3-6.1); c' = 9.3 ± 1 (7.8-10.7); V = 70 ± 1 (68-71); V' = 84-85; VL = 320 ± 17 (300-340) µm; stylet = 6-6.5 µm; median bulb = 37.5 ± 1.5 (35-39) µm; MB = 42 ± 2 (39-44); V-a = 58 ± 2 (56-61) µm; tail = 81 ± 2.5 (77-84) µm; tail/V-a = 1.4 ± 0.1 (1.3-1.5).

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Fig. 4. — *Filenchus discrepans* — A-F. Female — A,E. Face view - B. Ventro-lateral view of head - C. Lateral field at level of deirid and excretory pore - D,F. Lateral field at vulva. (E and F, population without male) — G-K Male — G. Face view - H. Lateral view of head - I. Lateral field - J. Ventral view of caudal alae - K. Lateral view of caudal alae. Bars equal 1 µm on A-K.

Male (n = 1) : L = 0.395 mm ; a = 34 ; b = 4.7 ; c = 5.3 ; c' = 8.5 ; MB = 40 ; stylet = 6.5 µm ; T = 46 ; spicules = 12 µm ; gubernaculum = 3 µm ; tail = 74 µm.

### *Description*

Female

Type I : body 13 ± 1 (11-15) µm wide ; cylindrical in shape from vulva to base of stylet then narrows gradually to bluntly rounded at anterior end. Cuticular annuli flat, 1.5 ± 0.2 (1.2-1.7) µm wide. Lateral field a prominent band set off by two sharp lines. SEM photos show one or two irregular shallow incisures in the band. Cephalic region with three annuli ; continuous with body countour, 4.5-5 µm wide and 2-2.5 µm high. Labial plate almost rectangular with rounded corners ; oral plate is concave oval. Amphidial apertures begin near oral plate with closed anterior end, and sinuous outline cutting through 2-3 annuli beyond labial plate. Stylet slender with rounded basal knobs. Oesophagus 82 ± 3 (76-86) µm long. Excretory pore situated at 67 ± 3 (61-72) µm from anterior end. Hemizonid just anterior to excretory pore. Deirids 2-4 annuli posterior to the excretory pore.

Reproductive tract with one row of oocytes ; spermatheca offset with long pocket, 31 ± 7 (22-41) µm, extending anteriorly parallel to body axis, filled with rounded sperm. Vagina more than half of the body diameter, slightly anteriorly tilted. Vulva a simple indented transverse slit without lateral membranes. Post-vulval-uterine sac 5.5 ± 1.5 (3-8) µm, shorter than VBD ; P.V.S./VBD = 0.5 ± 0.1 (0.3-0.7). Tail narrowly conoid ending in finely rounded tip. The annulation of posterior part of the tail is irregular.

Type II : Similar to type I, but with the following differences. Cuticular annuli 1.8 ± 0.2 (1.6-2) µm wide. SEM doesn't show any incisure in the lateral fields. Cephalic region with one or two annulations ; labial plate squarish with rounded corners, indented on dorsal and ventral borders. Oesophagus is longer ; 90 ± 2.4 (88-94) µm. The V-a distance is larger ; 59 ± 2 (56-61) µm versus 45 ± 4 (39-52) µm in type I, but the tail is shorter ; 80.5 ± 2.5 (77-84) µm versus 90.5 ± 6.1 (81-100) µm, and tail shape is narrowly cylindroid with bluntly rounded terminus.

Males

Type I : Similar to female in general outline of head except for two prominent, button-like sensilla in a small depression on ventral side that gives an asymmetrical pattern to face view (agreeing with Raski & Geraert, 1987). The ventral side of the head and labial plate is slightly depressed. SEM shows one or two irregular shallow incisures in the lateral field, as in females. Ventral line of lateral field disappears on 4-5 annuli posteriad to beginning of caudal alae.

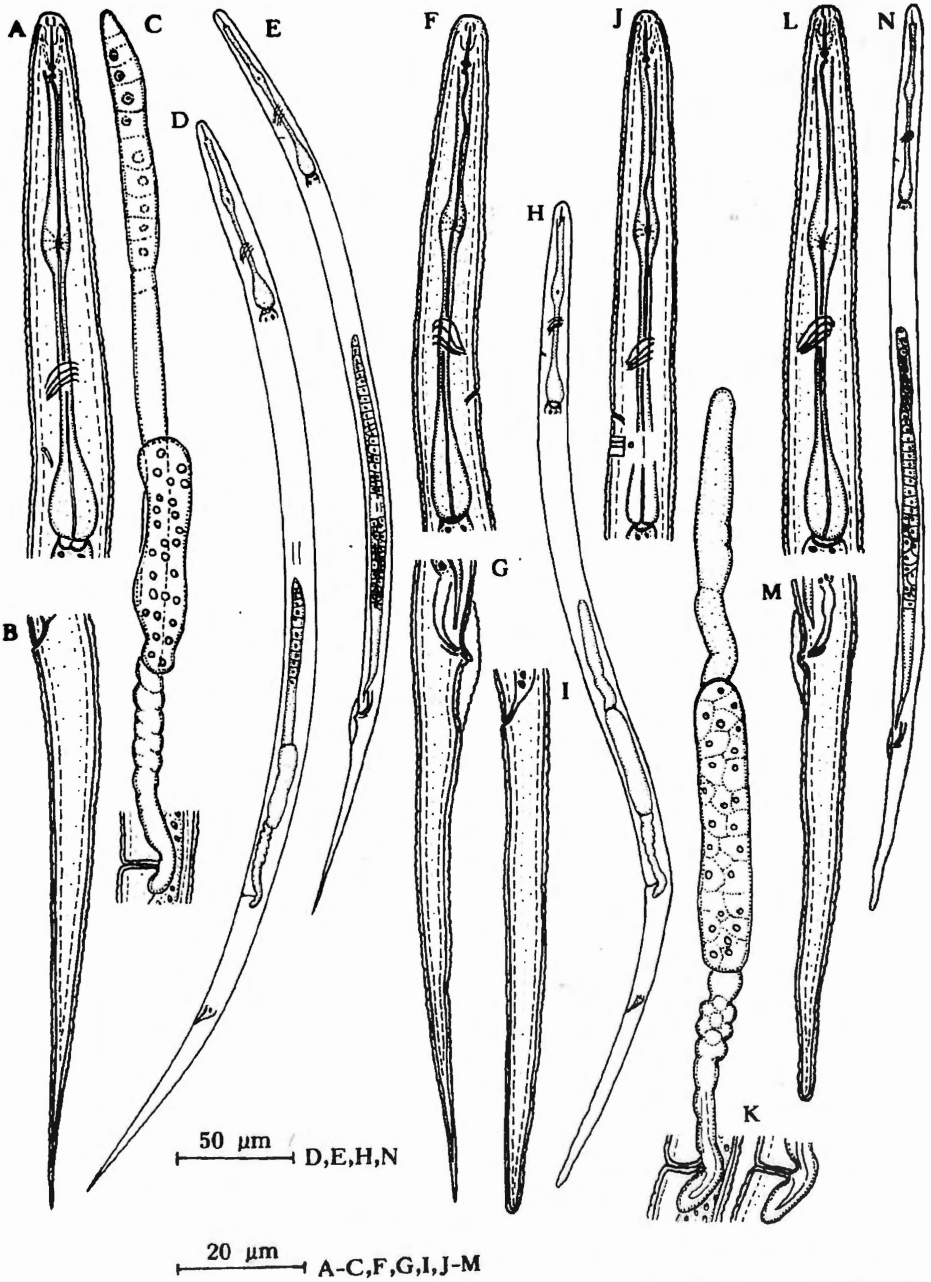
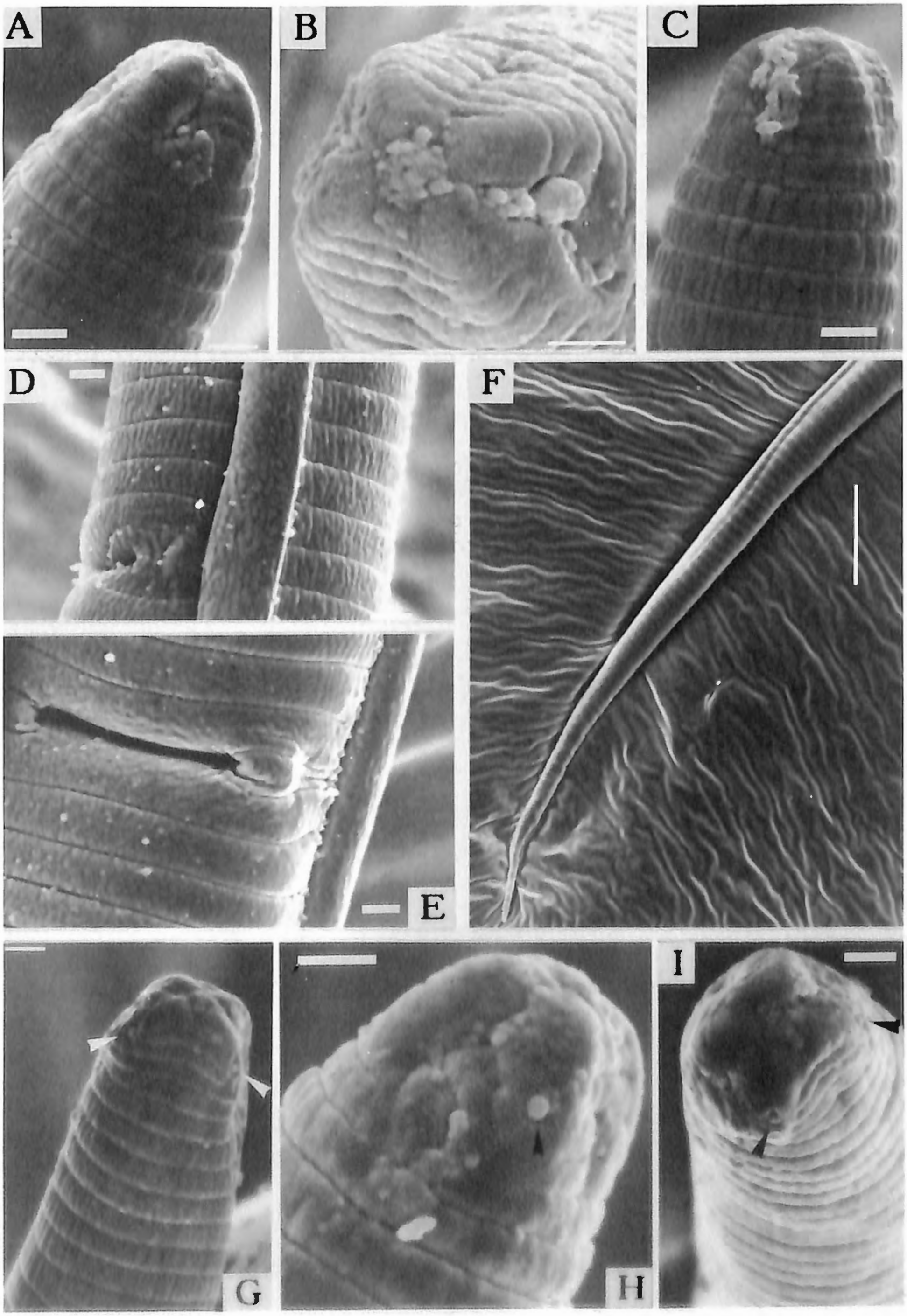


Fig. 5. — *Filenchus facultativus* — A-G. Type I, finely rounded tail tip — A-D. Female — A. Anterior end - B. Tail - C. Reproductive system - D. General view — E-G. Male — E. General view - F. Anterior end - G. Tail — H-N. Type II, rounded tail tip — H-K. Female - H. General view - I. Tail - J. Anterior end - K. Reproductive system - L-N. Male - L. Anterior end - M. Tail - N. General view.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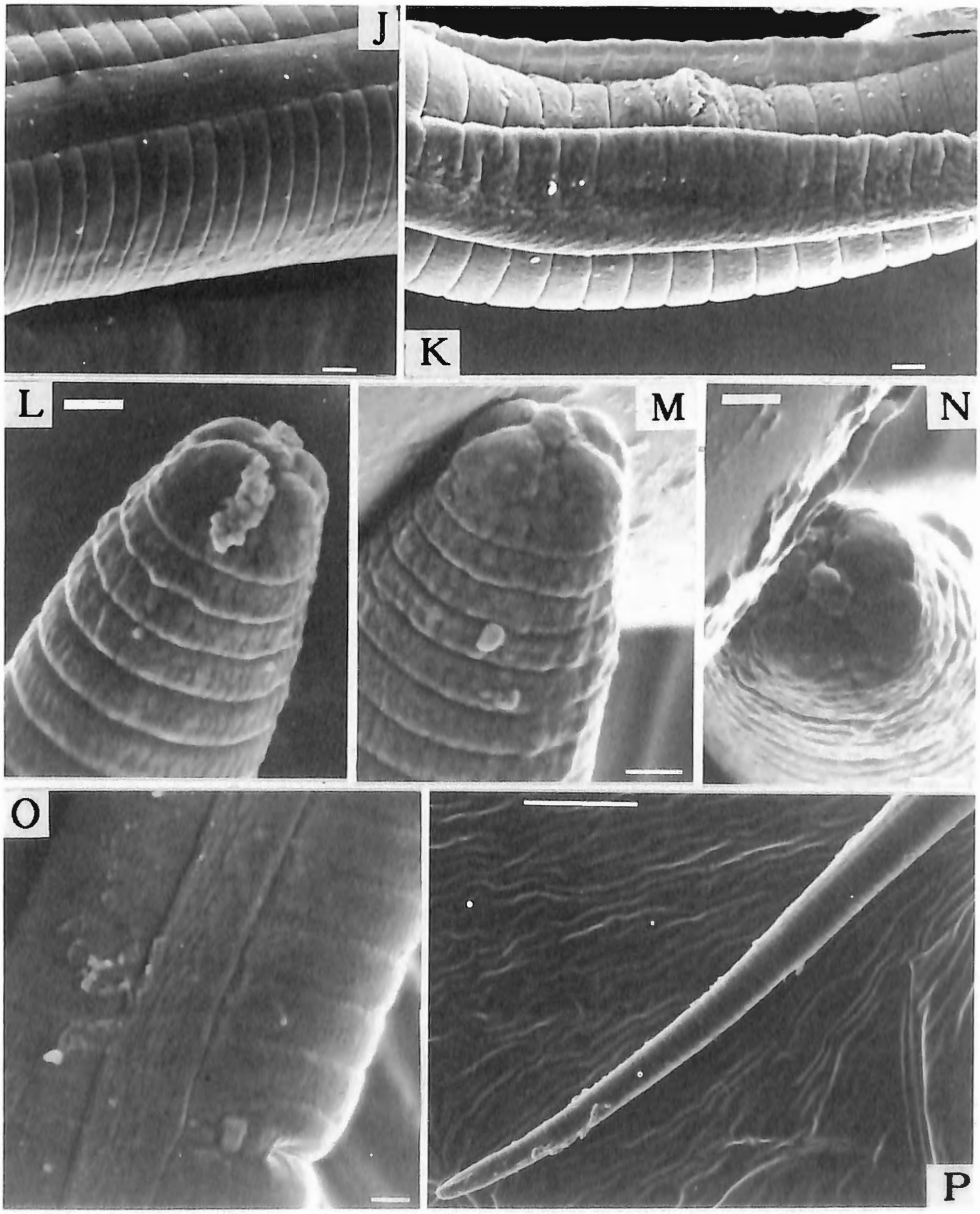

Fig. 6. — *Filenchus facultativus* — A-K. Type I, finely rounded tail tip — A-F. Female — A and C. Lateral views of head - B. Face view - D. Lateral field at vulva - E. Vulva - F. Tail — G-K. Male — G. Ventral view of head - H and I. Ventro-lateral view of head - J. Lateral field - K. Caudal alae — L-P. Type II, rounded tail tip, Female — L. Lateral view of head - M. Ventral view of head - N. Face view - O. Lateral field at vulva - P. Tail. Bars equal 1 µm on A-E, G-O ; 10 µm on F and D. Arrows indicate paired subventral cephalic papillae.

Type II : There are some differences between the males of this type and the first type but they are consistent with the females : tail is shorter, 74 µm versus 85 ± 5 (80-91) µm ; oesophagus is longer, 84 µm against 78 ± 1.2 (77-80) µm, and the tail end is bluntly rounded.

*Discussion*

The two types were compared with several populations of *Filenchus facultativus*. Type I with pointed tail tip is close to a Sudanese population (Zeidan and Geraert, 1991), but both types have shorter stylet and tail ; stylet = 8 ± 0.5 (7.5-8.5) and tail = 126 ± 9 (112-140) µm in Sudan population, also the ratios c, c', and V are smaller in type II : c = 4.2 ± 0.4 (3.8-4.8), c' = 12.3 ± 1.1 (11.2-13) and V = 63 ± 1 (62-65). They differ from an Argentinean population (Torres and Geraert, 1996) by having shorter stylet and tail in females ; stylet = 8 ± 0.5 (7.5-9) µm and tail = 141.5 ± 12 (127-161) µm. Two populations from California (Raski and Geraert, 1987) and the original description (Szczygiel, 1969) show no differences.

As a whole, the morphometrics of our populations are within the range studied until now, but it is necessary to point out that approximately all studied populations, except the type materials (Szczygiel, 1970) were mixed and have had pointed to rounded tail ends. It seems that there is a correlation between tail shape and oesophagus length and maybe these two types represent two species or one dimorphic species.

*Habitat and locality*

This population was found at the rhizosphere of cotton, *Gossypium sp.* in Varamin, Iran.

### ***Filenchus misellus* (Andrássy, 1958) Raski and Geraert, 1987**

(Figs 7 A-F, 8)

*Measurements*

Females (n = 5) : L = 0.365 ± 0.01 (0.350-0.380) mm ; L' = 0.310 ± 0.012 (0.295-0.325) mm ; a = 28.8 ± 2.2 (27-33) ; b = 5 ± 0.2 (4.7-5.4) ; c = 6.3 ± 0.3 (5.9-6.6) ; c' = 7 ± 0.8 (5.6-8.2) ; V = 69 ± 1.6 (67-72) ; V' = 82.2 ± 1.6 (80-85) ; head-anus (VL) = 255 ± 13 (240-275) ; stylet = 6.5-7 µm ; oesophagus = 73.4 ± 4.5 (67-80) µm ; MB = 45.2 ± 2.9 (40-49) ; tail = 58.8 ± (56-62) µm ; V-a = 54.8 ± 3.4 (51-59) µm ; T/V-a = 1.0-1.1.

Male : not found.

*Description*

Females : Cuticle with very fine striation, about 0.9 µm apart. Lateral field with four lines, SEM photo shows two outer bands wider than the middle one, and aerolated. Cephalic region rounded, with three or four incomplete annuli ; labial plate rectangular with rounded corners. Amphidial aperture sinuous, continues to the first head annulus. Oesophagus with oval metacorpus, situated at 33 ± 3.2 (30-39) μm from anterior end. Excretory pore at 56.6 ± 1.9 (53-58) μm from anterior end. Deirid not distinct. Reproductive system outstretched ; ovary with one row of oocytes. Vagina short, about 1/3 of VBD, in a right angle to body axis. Vulva-anus distance as long as tail length. Tail conical with pointed terminus ; annulation continues to tail end ; the latter shows some variation.

### *Discussion*

This population comes close to *F. magnus* (Husain and Khan, 1977) Siddiqi, 1986 and *F. misellus*. The first one has a shorter stylet, 5-6 μm, and the tail is longer than vulva-anus distance. In comparison with a Sudanese population of *F. misellus* (Zeidan and Geraert, 1991) it shows some differences. That population has a slightly shorter stylet, longer tail, more anterior vulva and higher T/V-a value : stylet = 5.5-6.5 μm, tail = 66 ± 4 (60-71) μm, V = 65 ± 1 (63-66), and T/V-a = 1.39 ± 0.17 (1.13-1.57). We consider our population as *F. misellus*.

### *Habitat and locality*

This population was found in the soil around roots of pomegranate, *Punica granatum*, in Yazd.

## ***Filenchus sheri* (Khan and Khan, 1979) Siddiqi, 1986**

(Fig. 7, G-N)

### *Measurements*

Females (n = 4) : L = 0.515 ± 0.019 (0.490-0.535) mm ; L' = 0.380 ± 0.015 (0.360-0.395) mm ; a = 35.3 ± 3.3 (31.1-39.9) ; b = 5.6 ± 0.3 (5.3-6.1) ; c = 3.8 ± 0.1 (3.6-3.9) ; c' = 14.8 ± 0.9 (13.6-15.8) ; V = 58.1 ± 1.7 (56.1-60.7) ; V' = 79 ± 1.8 (76.8-81.5) ; Stylet = 7.5-8.5 μm ; oesophagus = 92 ± 2.9 (88-95) μm ; MB = 40.4 ± 1.7 (38.9-43.2) ; V-a = 80.5 ± 2.2 (78-84) μm ; tail = 136 ± 5.8 (127-142) μm ; tail/V-a = 1.7 ± 0.1 (1.5-1.8).

Males (n = 2) : L = 0.495-0.500 mm ; L' = 0.385-0.390 mm ; a = 33.6-39.1 ; b = 5.6-5.7 ; c = 4.5-4.6 ; c' = 11.4-12.9 ; T = 22.1-40.6 ; stylet = 9 μm ; oesophagus = 87-90 μm ; MB = 44.4-44.8 ; tail = 109-112 μm ; spicula = 14.5 μm ; gubernaculum = 4-6 μm.

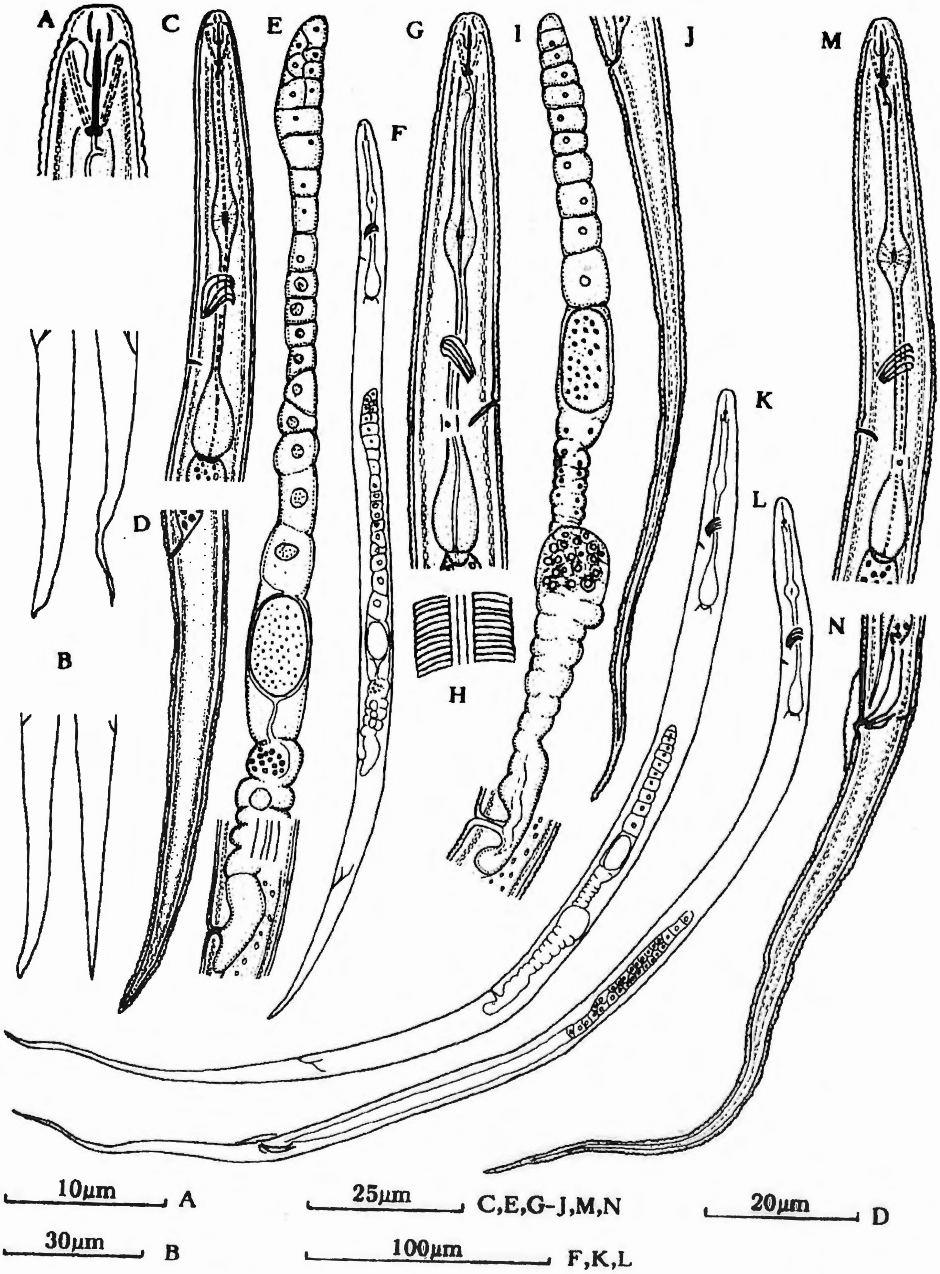

Fig. 7. — A-F. *Filenchus misellus* — A Anterior end - B. Variation in tail shape - C. Oesophagus region - D. Tail - E. Reproductive system - F. General view — G-N. *Filenchus sheri* — G-K. Female — G. Oesophagus region - H. Annulation and lateral field at mid body - I. Reproductive system - J. Tail - K. General view — L-N. Male — L. General view - M. Oesophagus region - N. Tail.

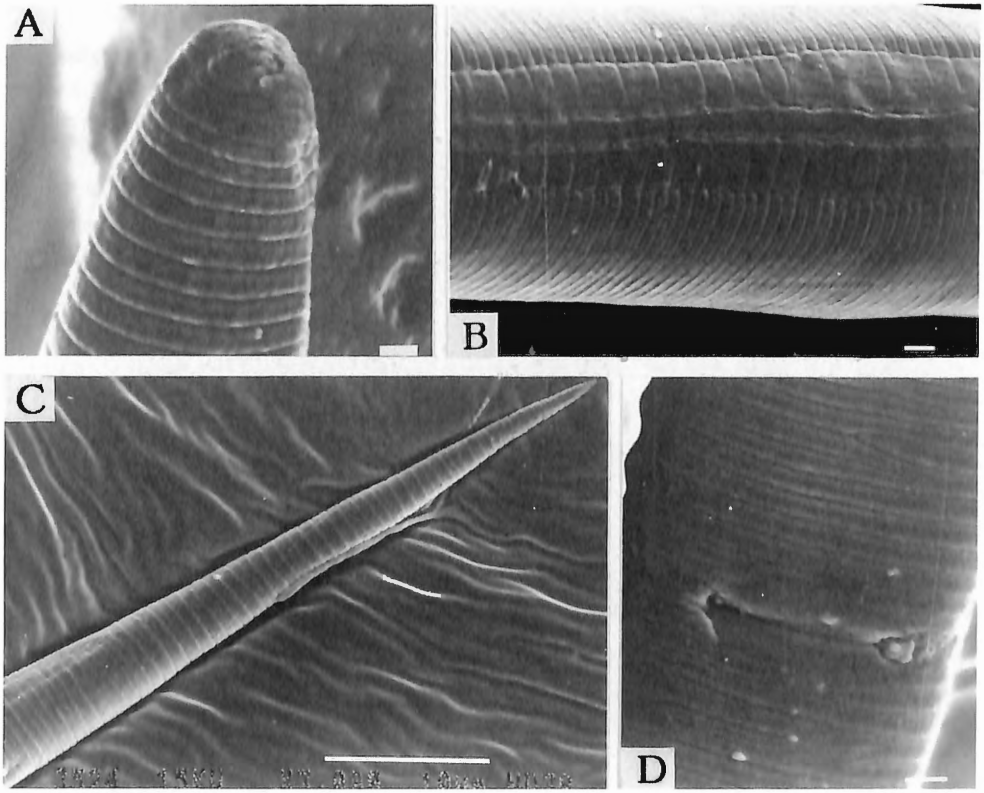

Fig. 8. — *Filenchus misellus* — A. Lateral view of head - B. Lateral field - C. Tail - D. Vulva. Bars equal 1 µm on A, B, D ; 10 µm on C.

*Description*

Female : Cuticle with fine annuli 1-1.1 µm wide ; lateral field with four incisures at midbody, the inner ones difficult to see by light microscope. Head region continuous with body contour, not set off, bears three to four fine annuli up to labial plate. Stylet delicate, knobs well-developed. Metacorpus ovate, with well-developed valvular apparatus, situated at 37 (36-38) µm from anterior end. Isthmus slender ; posterior, glandular region bulb-like pyriform, about 1.5 times the metacorpus. Excretory pore and hemizonid at the same level, 72.5 (66-77) µm from anterior end. Deirids 2-3 annuli posterior to excretory pore.

Gonad outstretched, spermatheca offset, small with rounded sperms. Post-vulval-uterine sac rounded, 8-11 µm long, 0.6-0.9 VBD. Vulva-anus distance shorter than tail length. Tail elongate-conoid, tapering evenly to a finely rounded terminus ; annulation continues to tail end.

Male : corresponds to female except small differences in stylet, tail length, and c ratio : males have slightly longer stylet, shorter tail and higher c value. Spicula ventrally curved ; gubernaculum simple, trough shaped ; bursa adanal.

### *Discussion*

This population with four lines in lateral field comes close to *F. afghanicus* (Khan & Khan, 1978) Siddiqi, 1986 and *F. sheri* (Khan & Khan, 1978) Siddiqi, 1986. *F. afghanicus* has slightly longer stylet, 8-10 µm. Morphometrically our population corresponds to *F. sheri*, but in this species annuli are wider (1.4 µm), and c ratio is slightly higher (4-5), nevertheless, we consider our population as *F. sheri.*

Both species were first found in Afghanistan and described by KHAN and KHAN (1979) as *Tylenchus* species. The original descriptions do not show any big difference between these two. *F. afghanicus* has slightly longer stylet (8-10 µm *versus* 7-8 µm in *F. sheri*), and more posterior excretory pore, but a Sudanese population of *F. afghanicus* has shorter stylet, 8-8.5 µm long (ZEIDAN and GERAERT, 1991), and in our population excretory pore is like in *F. afghanicus*, and the stylet in males is 9 µm long. So it seems that these two species could be the same, and it is suggested, that for synonymization, the original material is reexamined.

### *Habitat and locality*

Our population was collected from the soil around *Equisetum arvensis* in « Darahe Morad Bayke » Hamadan.

## ***Filenchus vulgaris*** **(Brzeski, 1963) Lownsbery and Lownsbery, 1985**

### *Measurements*

Females (n = 5) : L = 0.640 ± 0.06 (0.580-0.730) mm ; L' = 0.485 ± 0.05 (0.430-0.570) ; a = 35 ± 2.2 (31.6-37.2) ; b = 6.1 ± (5.9-6.4) ; c = 4.1 ± 0.2 (3.9-4.5) ; c' = 15.1 ± 1.5 (13.4-17.4) ; V = 57.1 ± 2 (54.6-60.2) ; V' = 75.8 ± 1.5 (73.6-77.5) ; head-vulva = 360 ± 47 (325-440) µm ; stylet = 9.2 ± 0.9 (8.1-10.5) µm ; oesophagus = 105 ± 7.7 (96-115) µm ; MB = 40.8 ± 2.7 (38.1-45.8) ; Vulva-anus = 114 ± 5.4 (105-122) µm ; tail = 156 ± 9.5 (145-172) µm ; annuli = 1.4 ± 0.1 (1.3-1.6) µm ;

Males (n = 6) : L = 0.660 ± 0.034 (0.595-0.670) mm ; L' = 0.505 ± 0.032 (0.445-0.540) mm ; a = 37.6 ± 3 (33.5-42.6) ; b = 6.1 ± 0.2 (5.8-6.4) ; c = 4.3 ± 0.4 (3.9-5.2) ; c' = 12.9 ± 1.7 (9.8-15.3) ; T = 36.2 ± 2.5 (33.5-40.4) ; stylet = 9.3 ± 0.4 (8.5-10) µm ; oesophagus = 109 ± 5.9 (100-119) µm ; MB = 42.2 ± 2.1 (39.6-46.2) ; tail = 154.3 ± (128-177) µm ; Spicula = 16.7 ± 1 (15.5-18.5) µm ; gubernaculum = 4.4 ± 0.7 (3.8-5.8) µm ; annuli = 1.2 ± 0.1 (1-1.5) µm.

### *Habitat and locality*

This population that very closely corresponds with the original description and several populations of *F. vulgaris* (Raski and Geraert, 1987) was found in the soil around tea, *Thea sp.* in Tea Research Centre, Lahijan.

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# A PRELIMINARY ANALYSIS OF THE CERCOPOD SETATION PATTERN OF ALGERIAN ANOSTRACA (*CRUSTACEA*) SPECIES

by

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## SUMMARY

The position, number and length of the setae on the cercopods of Anostraca species are graphically represented and analysed. All species found in Algeria are used as examples. This revealed significant differences among the representatives of the genera *Artemia, Branchinella, Branchipus, Chirocephalus, Streptocephalus* and *Tanymastigites*, and between the related congeners *Streptocephalus torvicornis* and *S. rubricaudatus*, and *Tanymastigites perrieri* and *T. mzabica.*

*Key words* : Anostraca, cercopod armature, morphometric analysis, Algeria.

## INTRODUCTION

Description of anostracans traditionally includes an illustration of the telson with the cercopods. However, the setation pattern on the cercopods has never been used as a character of any major taxonomic importance. Even LINDER (1941) did not mention the cercopods in his monograph on morphology and taxonomy of Anostraca.

Recently, BELADJAL *et al.*, 1995 described the setation on the limbs in some Anostraca, quantifying morphological differences among genera and species, and

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explored the possibility of using these data taxonomically. In the present study we demonstrate that such analysis is also applicable to the cercopod morphology. As far as we know this technique has not been used in other crustacean taxa.

## MATERIAL AND METHODS

The cercopod material analysed herein was obtained from specimens collected in their natural habitats in Algeria and preserved in 4 % formalin (Table 1). As far as possible the same material was used as for the limb analysis in Beladjal *et al.* (1995). All data are derived from the cercopods from one male of each species, except for the parthenogenetic *Artemia* sp. population (female).

TABLE 1

*Names, sampling locality (province), coordinates and dates of collection of the species used as material for this paper.*

| *Species* | *Locality* | *Coordinates* | *Date* |
|---|---|---|---|
| *Streptocephalus torvicornis* | Dider<br>(Djanet) | 24° 34′ N<br>09° 30′ E | 30.10.1991 |
| *Streptocephalus rubricaudatus* | Bei Bei<br>(Djanet) | 24° 38′ N<br>09° 26′ E | 09.06.1978 |
| *Branchipus schaefferi* | Sidi Makhlouf<br>(Djelfa) | 34° 14′ N<br>03° 14′ E | 02.11.1991 |
| *Branchinella spinosa* | Boughzoul<br>(Medea) | 35° 42′ N<br>02° 51′ E | 02.11.1991 |
| *Chirocephalus diaphanus* | Theniet El Had<br>(Tissemsilt) | 35° 47′ N<br>02° 01′ E | 20.05.1989 |
| *Tanymastigites perrieri* | Sidi Makhlouf<br>(Djelfa) | 34° 14′ N<br>03° 14′ E | 02.11.1991 |
| *Tanymastigites mzabica* | Tilrhemt<br>(Laghouat) | 33° 10′ N<br>03° 21′ E | 13.05.1990 |
| *Artemia* spec. | Tougourt<br>(Tougourt) | 33° 06′ N<br>06° 07′ E | 08.02.1977 |

After dissection, cercopods were mounted on slides in such a way that all setae were extended. To avoid overlap of setae, the left cercopod was separated from the right by cutting the telson in two.

A video camera, fixed on a microscope (Leitz Laborlux 5) was connected to a video-printer. A series of video prints provided the elements for an accurate com-

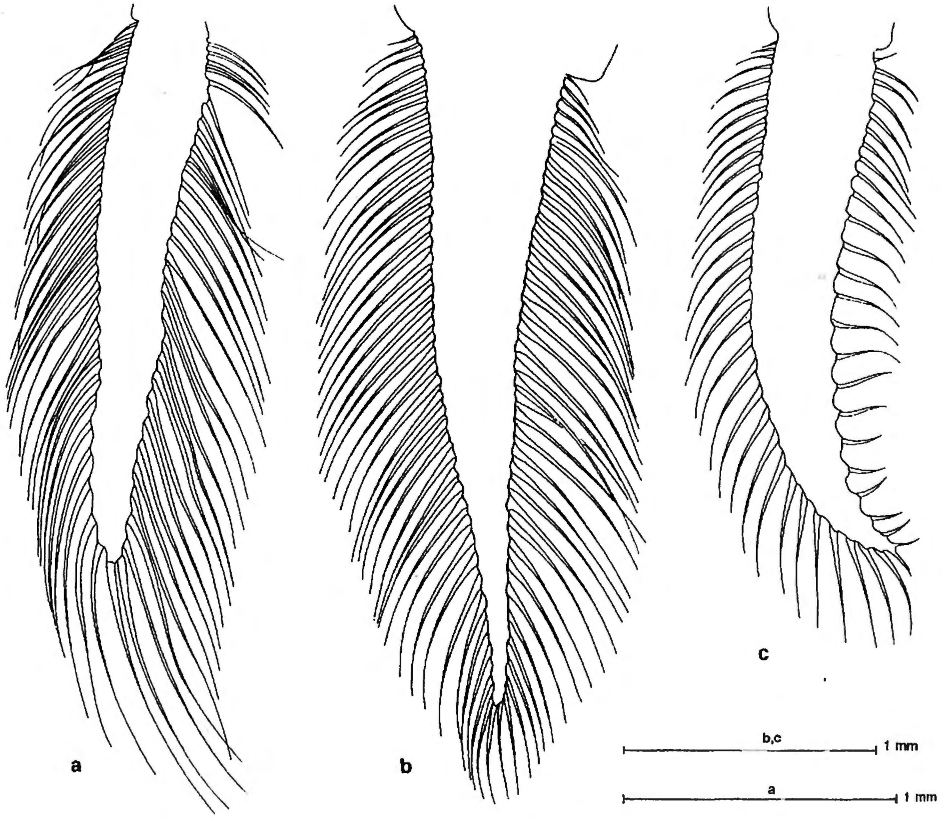


Fig. 1. — Left cercopod of (**a**) *Tanymastigites mzabica* (**b**) *Streptocephalus torvicornis* and (**c**) *Branchipus schaefferi.*

pound picture of the cercopod at high magnification. The length and distance between the successive setae were measured on that picture using a relative pointing device of graphics tablet (Summasketch III professional) and stored in the memory of the computer.

The arrangement of the setae on the cercopods of the three species is visualized in Fig. 1. In order to compare different species of different age classes, we converted the above measurements to relative values using the lengths of the cercopod as the standard length. The setae are numbered from the lateral outer basis of the cercopod near the telson, to the top and back on the inner side to the medial inner basis near the telson (Fig. 2). Fig. 3 shows the relative length of the setae, arranged according to their insertion from lateral to median on the cercopod. These values are summarised in Table 2.

## TABLE 2

*Numerical analysis of the cercopod structure of the different species : m = mean relative length of setae ; N = number of setae ; other explanations in the text.*

| | *Parameters* | *− curve* | *+ curve* | | *− curve* | − curve |
|---|---|---|---|---|---|---|
| | | *(outer)* | *1* | *2* | *(apical)* | (inner) |
| *S. torvicornis* | start | 0.000 | 0.190 | 1.247 | 0.810 | 1.886 |
| m = 0.236 | length | −0.190 | 0.620 | 0.639 | 0.437 | 0.113 |
| N = 85 | max. height | −0.187 | 0.054 | 0.091 | −0.094 | −0.158 |
| | eccentricity | −1.000 | −0.426 | −0.047 | −0.192 | 1.000 |
| | n (setae) | 12 | 26 | 25 | 16 | 6 |
| *S. rubricaudatus* | start | 0.000 | 0.080 | 1.269 | 0.633 | 1.878 |
| m = 0.218 | length | 0.080 | 0.553 | 0.610 | 0.636 | 0.122 |
| N = 86 | max. height | −0.158 | 0.055 | 0.090 | −0.112 | −0.094 |
| | eccentricity | −1.000 | −0.238 | 0.042 | 0.038 | 1.000 |
| | n (setae) | 6 | 24 | 26 | 26 | 4 |
| *B. schaefferi* | start | 0.000 | 0.141 | 1.708 | 1.054 | 1.904 |
| m = 0.157 | length | 0.141 | 0.913 | 0.196 | 0.654 | 0.096 |
| N = 57 | max. height | −0.135 | 0.094 | 0.015 | −0.124 | −0.112 |
| | eccentricity | −1.000 | 0.654 | 0.735 | −0.957 | 1.000 |
| | n (setae) | 8 | 25 | 14 | 6 | 4 |
| *Artemia* spec. | start | 0.000 | 0.376 | | | 1.380 |
| m = 1.282 | length | 0.376 | 1.004 | | | 0.620 |
| N = 16 | max. height | −0.360 | 0.508 | — | — | −0.956 |
| | eccentricity | −1.000 | −0.018 | | | 1.000 |
| | n (setae) | 3 | 9 | | | 4 |
| *T. perrieri* | start | 0.000 | 0.321 | | | 1.733 |
| m = 0.356 | length | 0.321 | 1.411 | | | 0.228 |
| N = 64 | max. height | −0.310 | 0.192 | — | — | −0.270 |
| | eccentricity | −1.000 | 0.133 | | | 1.000 |
| | n (setae) | 17 | 37 | | | 10 |
| *T. mzabica* | start | 0.000 | 0.264 | | | 1.801 |
| m = 0.336 | length | 0.264 | 1.537 | | | 0.200 |
| N = 53 | max. height | −0.201 | 0.099 | — | — | −0.220 |
| | eccentricity | −1.000 | 0.025 | | | 1.000 |
| | n (setae) | 12 | 32 | | | 9 |
| *B. spinosa* | start | 0.000 | 0.216 | | | 1.860 |
| m = 0.302 | length | 0.216 | 1.644 | | | 0.139 |
| N = 49 | max. height | −0.246 | 0.095 | — | — | −0.228 |
| | eccentricity | −1.000 | −0.156 | | | 1.000 |
| | n (setae) | 9 | 33 | | | 7 |
| *C. diaphanus* | start | 0.000 | 0.247 | | | 1.613 |
| m = 0.262 | length | 0.247 | 1.366 | | | 0.388 |
| N = 61 | max. height | −0.176 | 0.111 | — | — | −0.184 |
| | eccentricity | −1.000 | −0.026 | | | 1.000 |
| | n (setae) | 11 | 36 | | | 14 |

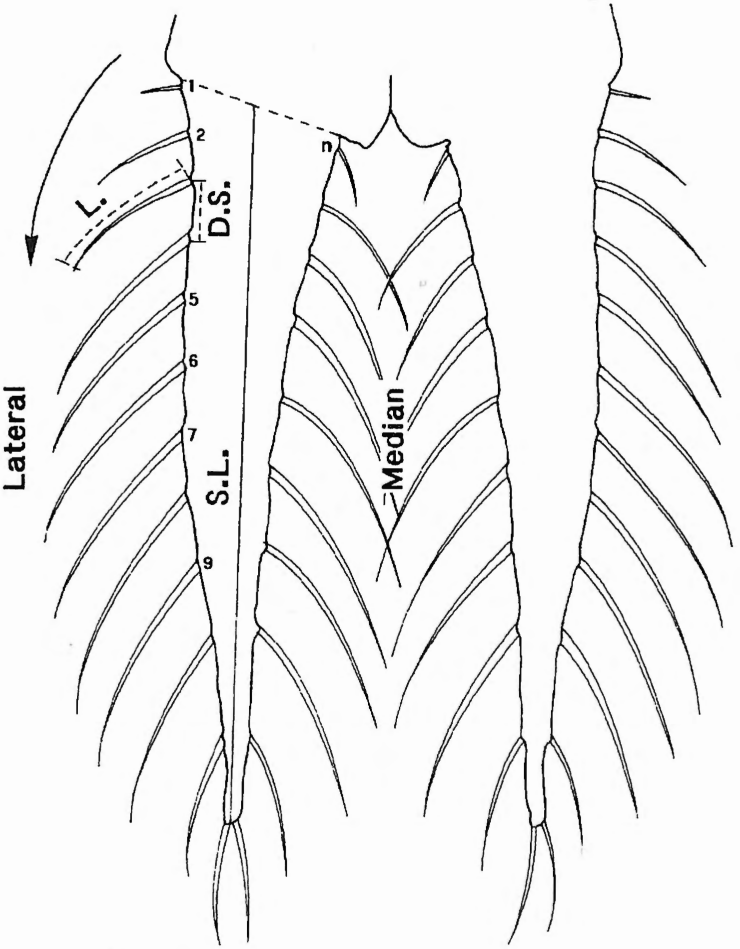


Fig. 2. — Outline of the different symbols and values used in the morphometric analysis of the setation on the cercopods. S.L. = standard length of the cercopod ; L. = length of setae, *D.S.* = distance between setae ; 1,2....n = number of setae (arrow indicates the direction).

It is desirable to relate the length of each seta x to the mean length m of all setae, total number = N, as follows : $m = \sum x/n$. Taking the difference between the mean length m and the length x of the setae successively, we obtain a distribution $(x - m)$, as presented in Fig. 4, which follows the turning value $x = m$ on the abscissa. Thus all lengths of the setae smaller than m, give negative x values and vice versa, and $x = 0$ (turning value) corresponds to the mean setae length. Now these data can be analysed as follows : the distribution above can be split into in series of positive $(x > m)$ and negative $(x < m)$ deviations from the mean m or x = 0, corresponding to the different columns in Table 2. Each curve has a starting and an end point intersecting the mean m or x-axis, so defining the length of that curve. This is represented in the first row of Table 2 (starting point) and the second row (length of the curve), for each species analyzed. All curves have a maximum value (third row in Table 2), corresponding to the longest ($x > m$), or shortest seta ($x < m$) in the positive curves ($x - m > 0$) or negative curves ($x - m < 0$). Geometrically this maximum value can be situated in the middle (0) between the extremes ($-1$ or $+1$), where the curve joins the x-axis. This eccentricity is quantified in the fourth row of Table 2. The bottom row, gives the number of setae building up each curve.

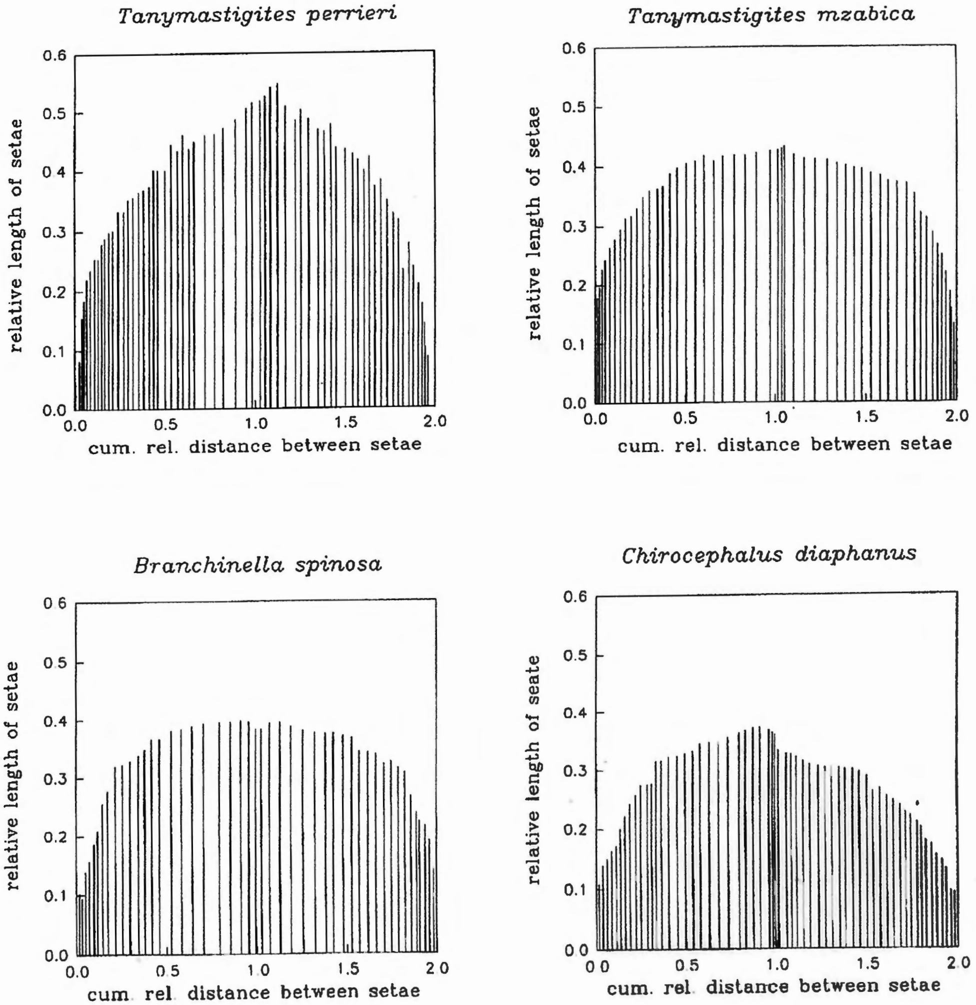
Finally, the relative distance between setae is calculated by dividing the absolute distance between these setae by the total absolute length of the cercopod. Thus, the relative length of the cercopod equals one, and the total setal insertion zone on the cercopod (lateral + medial) equals 2, being the sum of the relative distances of the setae.

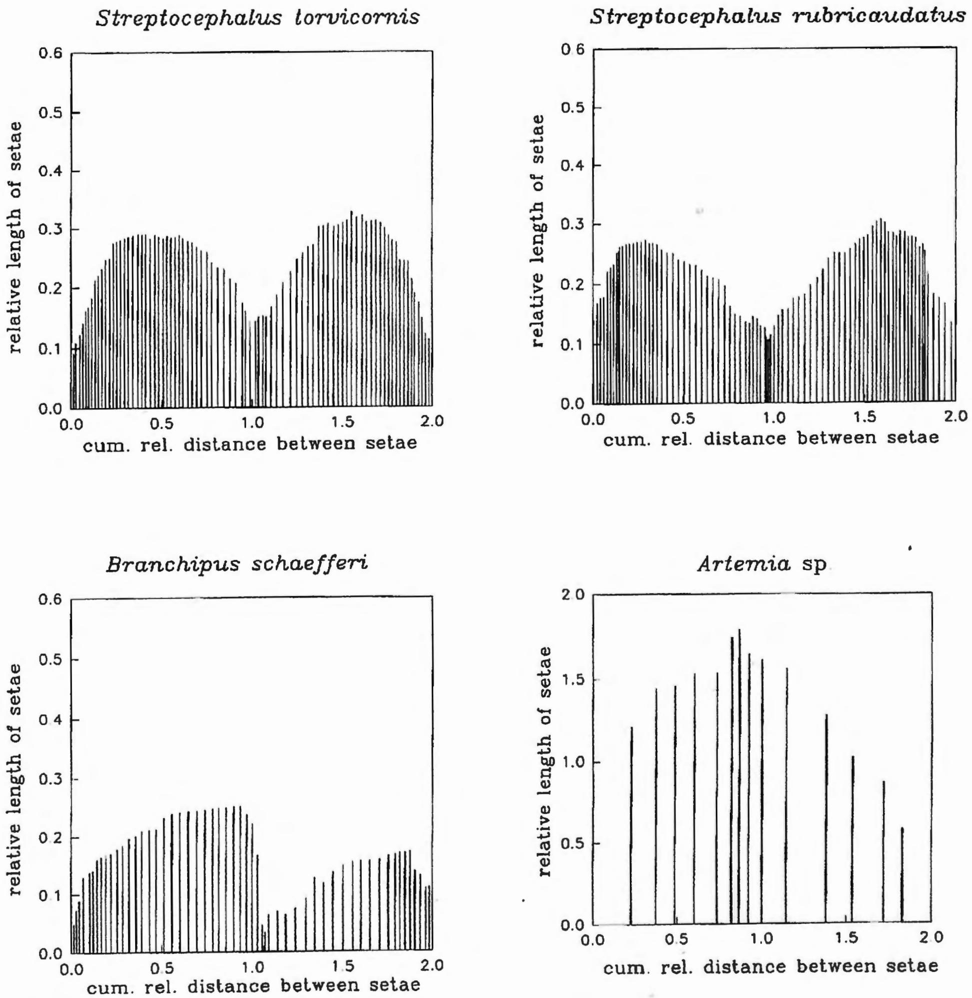
## RESULTS AND DISCUSSION

*Artemia* sp. differs profoundly from all other fairy shrimps. It has few (16) extremely long setae (the mean is 1.282 times the length of the cercopod; max. 2.286, min. 0.906). The other species can be divided in two major groups : the first group (containing *Tanymastigites perrieri* (Daday, 1910), *T. mzabica* (Gauthier, 1928), *Chirocephalus diaphanus* Prévost, 1803 and *Branchinella spinosa* (Milne-Edwards, 1840)) shows only one positive curve ; the second group has two positive curves separated by an apical negative curve (*Streptocephalus torvicornis* (Waga, 1842), *S. rubricaudatus* (Kulunzinger, 1867) and *Branchipus schaefferi* (Fisher, 1834)).

Amongst members of the first group, *B. spinosa* is the simplest representative. The lengths of its setae are quite homogeneously distributed. Only few setae (9 and 7) are shorter than the mean, giving the positive curve a very broad basis (1.644). In *C. diaphanus*, the outer negative curve is shorter, and contains less setae than the inner negative curve. In *Tanymastigites* the inverse situation is seen : the positive curve is shorter (1.366 versus 1.411 and 1.537) and the setae are not as long (max 0.373, mean 0.262 versus max 1.767, mean 0.356, and max 1.873, mean 0.336). Although both species present the same *Tanymastigites* basic pattern of setation, specific differences can be pointed out. In *T. perrieri* the negative curves are wider (0.321, 0.228) than in *T. mzabica* (0.264, 0.200). Since the shortest setae in

*T. perrieri* (−0.310, −0.270) are smaller than in *T. mzabica* (−0.201, −0.220), and the longest seta is much bigger in *T. perrieri* (0.192) than in *T. mzabica* (0.099), the difference between the shortest and the longest seta is 0.502 in *T. perrieri* while only a difference of 0.300 is found in *T. mzabica*. This is seen in Fig. 3a as a rounded profile for *T. mzabica*, in contrast to a rather pointed profile in *T. perrieri*.

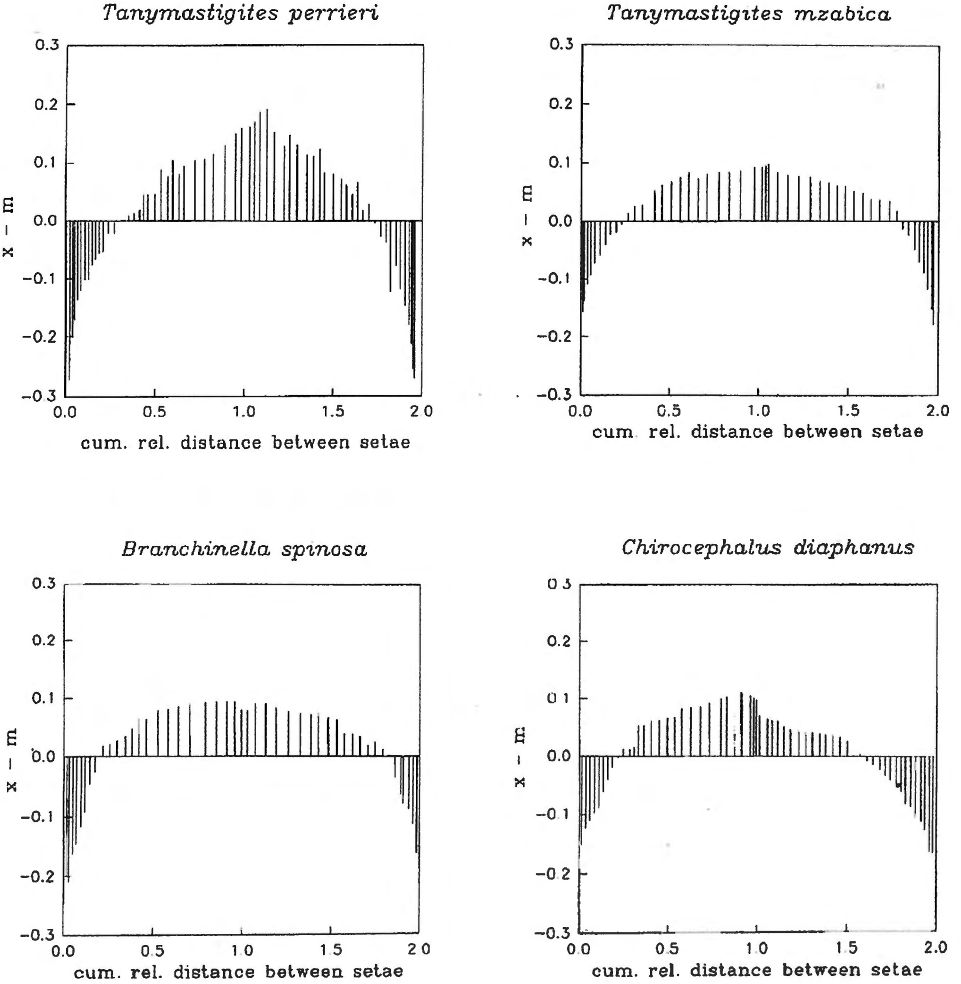




Figs 3a-b. — The relative length of the setae arranged according to their insertion from lateral to median on the cercopod.

The two genera representing the second group are extremely different. In *B. schaefferi* the second positive curve is very small, separated from the first positive curve by a highly asymmetric (0.957) apical curve. In *Streptocephalus* two well developed positive curves alternate with a normal (symmetrical) apical curve. However, as for *Tanymastigites*, this basic pattern shows discriminative features for both species. In *S. torvicornis* the inner curve is wider (0.190) and the apical negative curve shorter (0.437) than in *S. rubricaudatus* (0.080 and 0.636, respectively).

The data for the analysis presented in this paper are based on calculations derived from a single male of each species (except for *Artemia*). The species-specific setation pattern of the cercopods presented in Fig. 3 and Table 2 is striking and the methodology appears to be promising. It must, however, be examined in a number of individuals of each species and statistical analyses must be performed before its taxonomic value can be assessed.

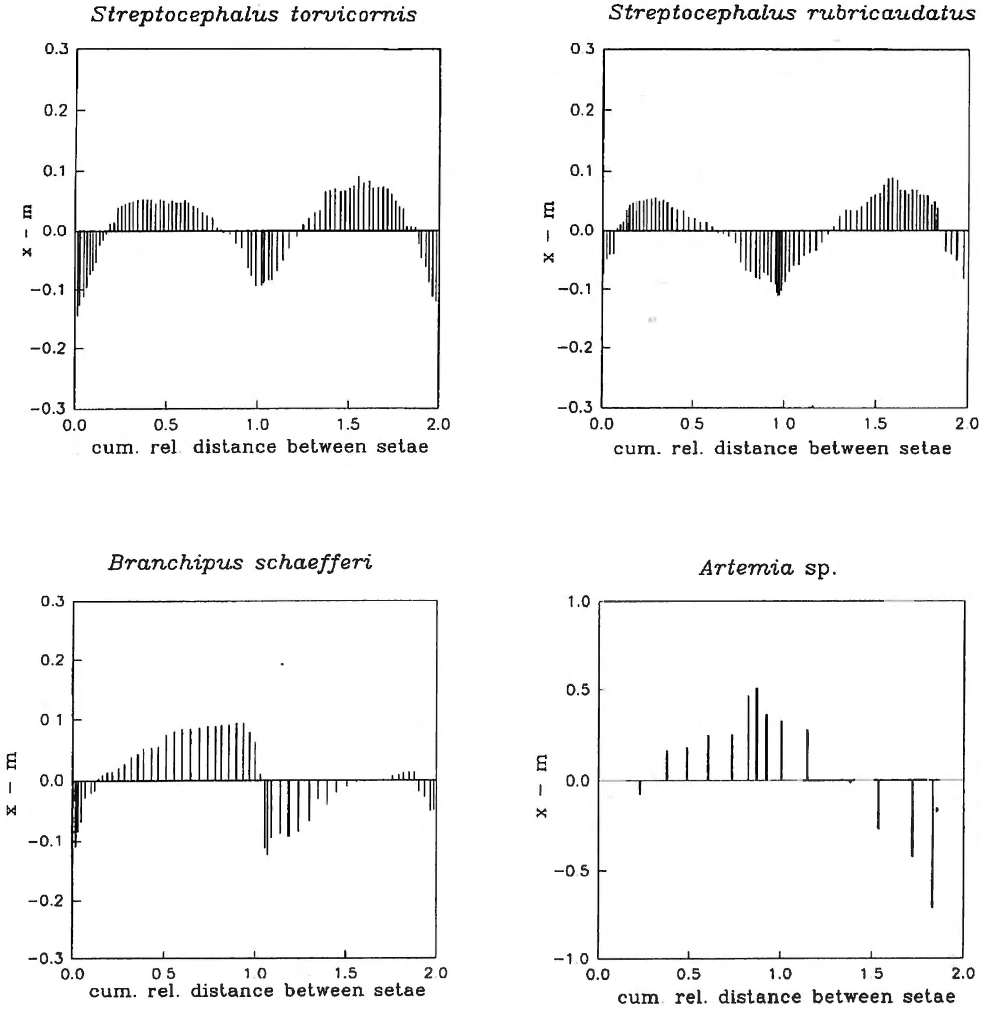


*Tanymastigites perrieri*

*Tanymastigites mzabica*

*Branchinella spinosa*

*Chirocephalus diaphanus*



Figs 4a-b. — The length differences of the setae ($\underline{x}-m$) in relation to the mean length m, arranged according to their insertion from lateral to median on the cercopod.

## ACKNOWLEDGMENTS

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# TWO NEW SPECIES OF KALYPTORHYNCHIA (PLATHELMINTHES) FROM THE N. AMERICAN ATLANTIC COAST

by

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## SUMMARY

The kalyptorhynchs (Platyhelminthes, Rhabdocoela) *Gnathorhynchus riseri* sp.n. (Gnathorhynchidae) and *Placorhynchus doei* sp.n. (Placorhynchidae) are described from coarse sandy shores in Massachusetts, U.S.A.. *G. riseri* and its probable sister species *G. rostellatus* Brunet, 1973 have similar copulatory bulbs with prostatic fascicles enclosing the ejaculatory duct, in the former species differentiated to an eversible penis papilla. *P. doei* is identified by its pointed sclerotic copulatory stylet, dissolved by acid fixatives.

*Key words* : Plathelminthes, Kalyptorhynchia, N. America, Atlantic coast.

## INTRODUCTION

The two species described here are part of the free-living Platyhelminthes material collected and preliminarily studied by the author in the summer 1972 when working in the Marine Science Institute at Nahant belonging to the Northeastern University in Boston. The material is deposited in the Swedish Museum of Natural History in Stockholm, Sweden (SMNH).

The north west Atlantic kalyptorhynch Platyhelminthes are poorly known, especially compared with the European fauna (see *e.g.* KARLING, 1963, 1992 ; NOLDT, 1989a,1989b). Only twenty species of Kalyptorhynchia have been recorded so far from the north west Atlantic coastal areas, the first one being *Phonorhynchus helgolandicus* (Mecznikoff, 1865) (GRAFF, 1911). More recently *Florianella bipolaris* was described by RIEGER and STERRER (1975) and *Carolinorhynchus follubeachensis* by NOLDT (1987). Nine were found in Canadian brackish water areas by AX and ARMONIES (1987) : *Parautelga bilioi* Karling, 1964, *Acrorhynchides robustus* (Karling, 1931) *Phonorhynchus helgolandicus* (Mecznikoff, 1865), *Phonorhynchoides carinostylis* n. sp., *Gyratrix hermaphroditus* Ehrenberg, 1831 (previously known from fresh water), *Prognathorhynchus eurytuba* n. sp., *Placorhynchus octaculeatus* Karling, 1931, *Placorhynchus dimorphis* Karling, 1947, *Placorhyncus* ? *echinulatus*

Karling, 1947, *Baltoplana magna* Karling, 1949, *Tylacorhynchus vicarus* Boaden, 1963, an unidentified *Prognathorhynchus* species and a presumed species of the Polycystidae. In addition *Utelga heinckei* (Attems, 1897), *Itaipusa scotica* (Karling, 1954), *Zonorhynchus seminascatus* Karling, 1956, *Drepanorhynchides hastatus* (Meixner,1929) and *Gnathorhynchus conocaudatus* Meixner, 1929 were reported by KARLING (1980, 1992). With the two new species descibed below, *Gnathorhynchus riseri* n. sp. and *Placorhynchus doei* n. sp. the total number of Kalyptorhynchia observed on the N. American Atlantic coast is 22, 19 Eukalyptorhynchia and 3 Schizorhynchia.

## DESCRIPTIONS AND DISCUSSION

### **Gnathorhynchus riseri** sp.n.

(Figs 1-5)

*Material* : : Holotype : SMNH 4674 a specimen sectioned parasagittally. Other material : live specimens and one specimen (paratype) sectioned transversaly (*leg.* the author).

*Type locality* : Phillips Beach (USA, Mass.), coarse sandy shore 27 June 1972.

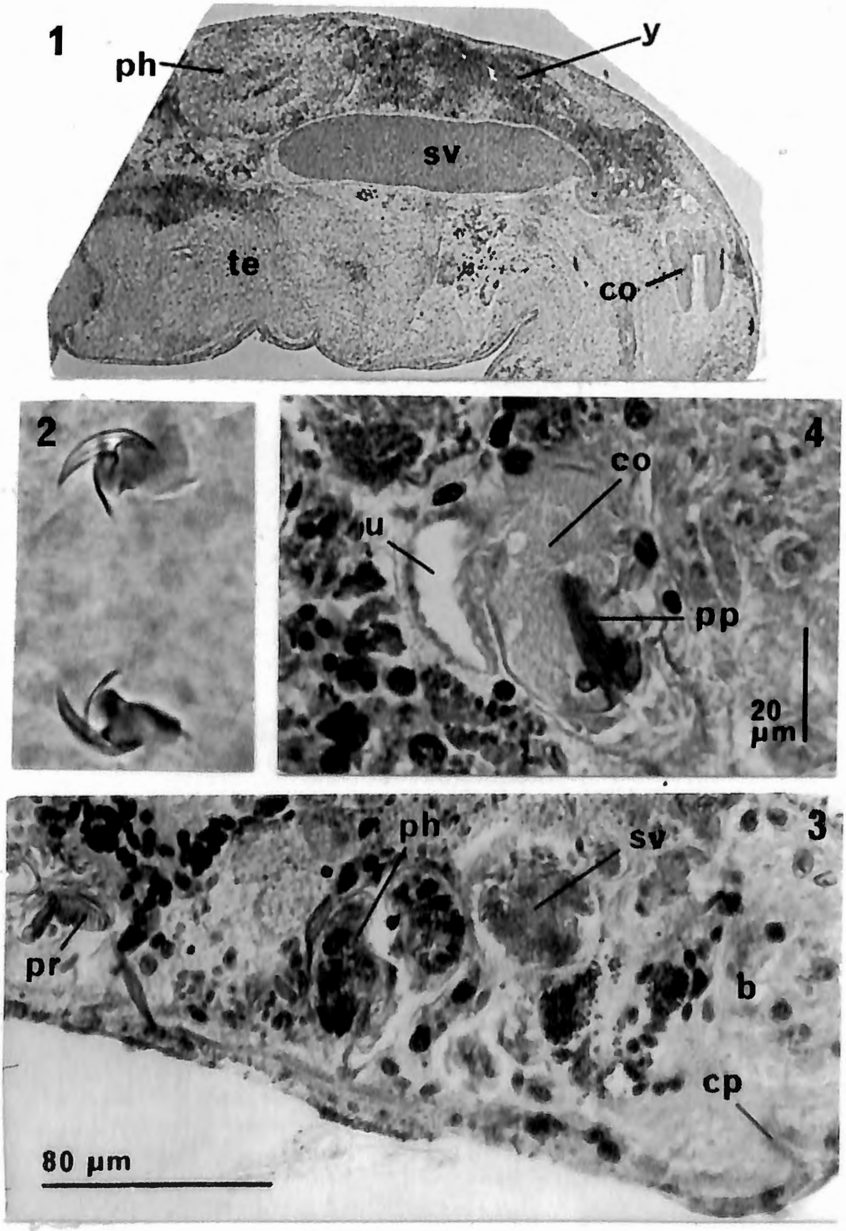
*Etymology* : species name in honour of Dr. Nathan W. Riser, Director of the Marine Science Institute at Nahant.

#### *Description*

Filiform, 1-1.5 mm, transparent, yellowish, paired pigmented eyes. Proboscis hooks (Figs 2-3) 30 µm including the basal cups based on short muscular pads. Rosulate pharynx in about half body length. Unpaired gonads, testis and yolk gland beside the pharynx, ovary caudally, embedded in bursal tissue. Elongate seminal vesicle (Fig. 1) opening by a tubular seminal duct in the cylindrical copulatory bulb (Figs 1, 4, 5) containing five (?) tubular prostatic fascicles with two kinds of secretion enclosing the eversible ejaculatory duct. No male sclerotic structures. Long tubular common atrium, opening terminally (Fig. 3) with proximally associated uterus and copulatory bulb. Oviduct not observed.

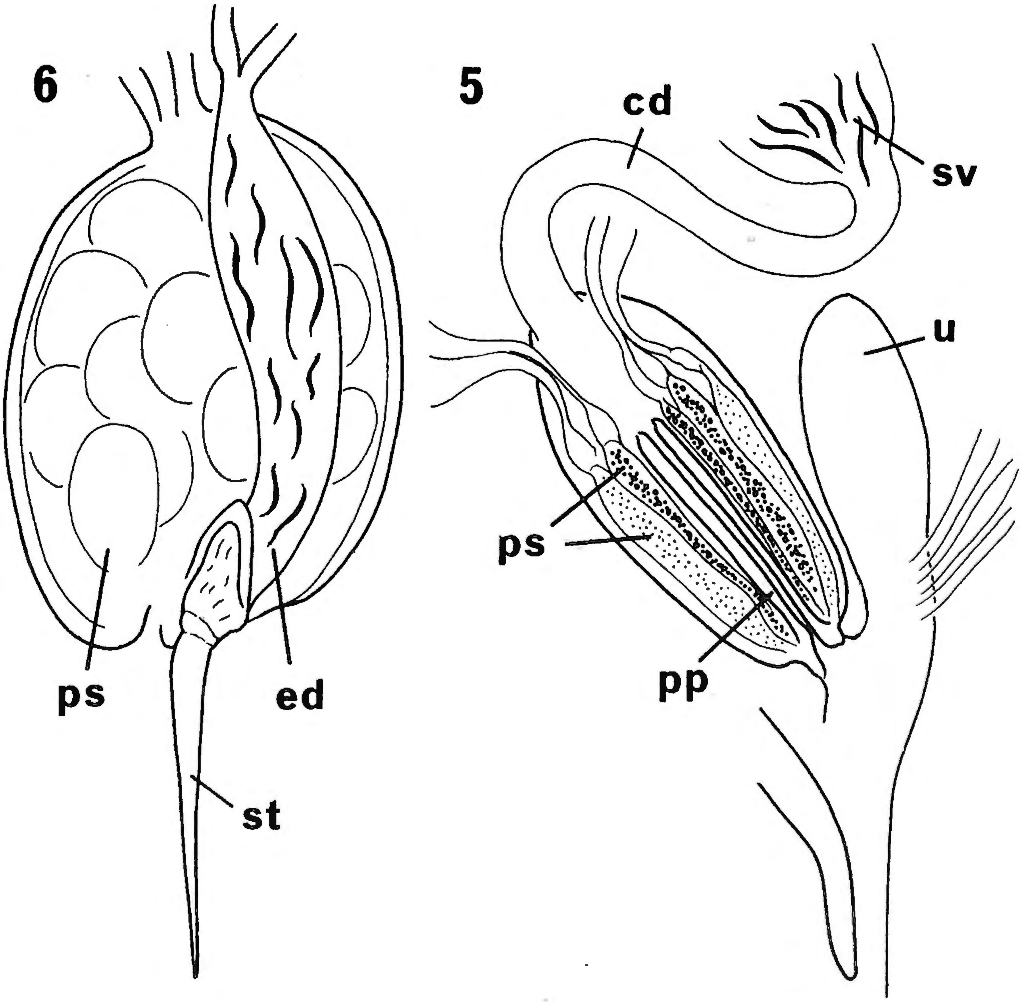
#### *Discussion*

The original diagnosis (MEIXNER, 1929, p. 778) of the genus *Gnathorhynchus* and the taxonomic key to the genera in Gnathorhynchidae (DEN HARTOG 1968, pp. 330-340) do not conflict with the structural traits of *G. riseri.* In the related species *G. rostellatus* Brunet, 1973 the copulatory bulb contains two kinds of secretion in 4-5 prostatic fascicles, enclosing the straight, evidently non-eversible ejaculatory duct. This feature is considered a synapomorphy with *G. riseri.* The two species further agree in the topography of the pharynx and the genital organs, but differ in the lack of pigmented eyes and in the differentiation of a proximal filiform out-



Figs 1-4. — *Gnathorhynchus riseri* sp.n. — 1. Part of squeezed live specimen — 2. Proboscis hooks, live specimen — 3. Part of holotype, parasagittal section — 4. Male copulatory organ, the same section.

growth of the proboscis hooks in *G. rostellatus*; in *G. riseri* the structure is replaced by a minute hook (Fig. 2).



Figs 5-6. — Male copulatory organ, drawings from live specimens — 5. *Gnathorhynchus riseri* sp.n. — 6. *Placorhynchus doei* sp.n.

### **Placorhynchus doei** sp.n.
(Figs 6-10)

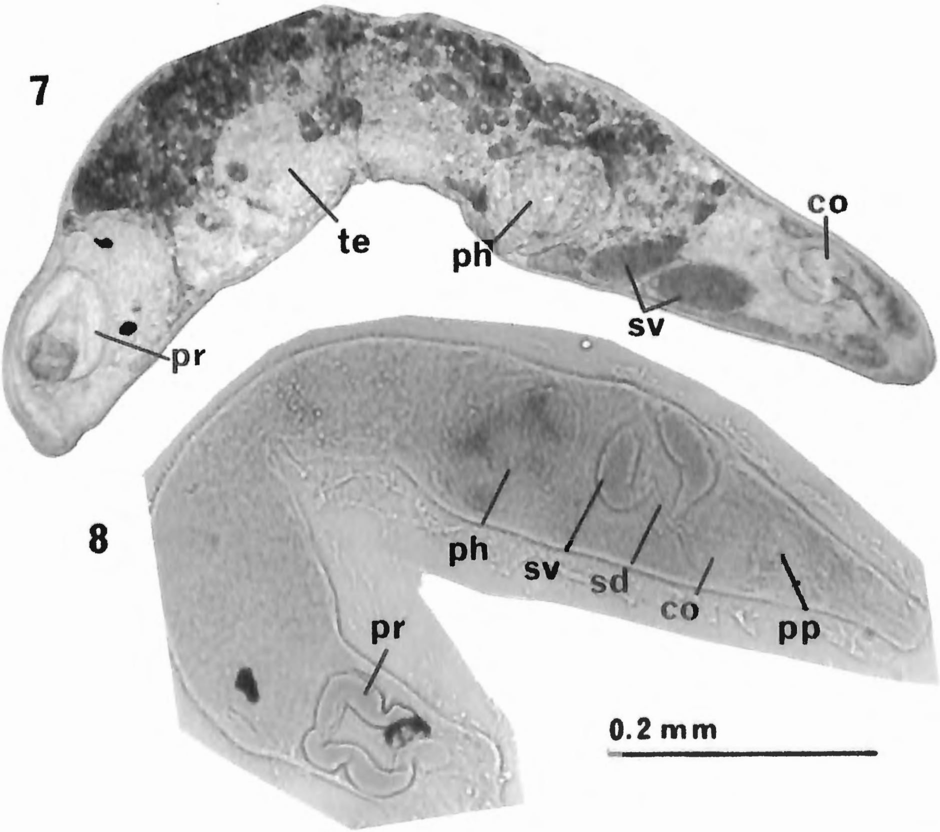
*Material*: Holotype: SMNH 4675 a whole-mounted specimen. Other material: live specimens from the type locality and the near-by Nauset Beach.

*Type locality*: Cockle Cobe Beach, coarse sandy shore (USA, Mass.), 2.7.1972.

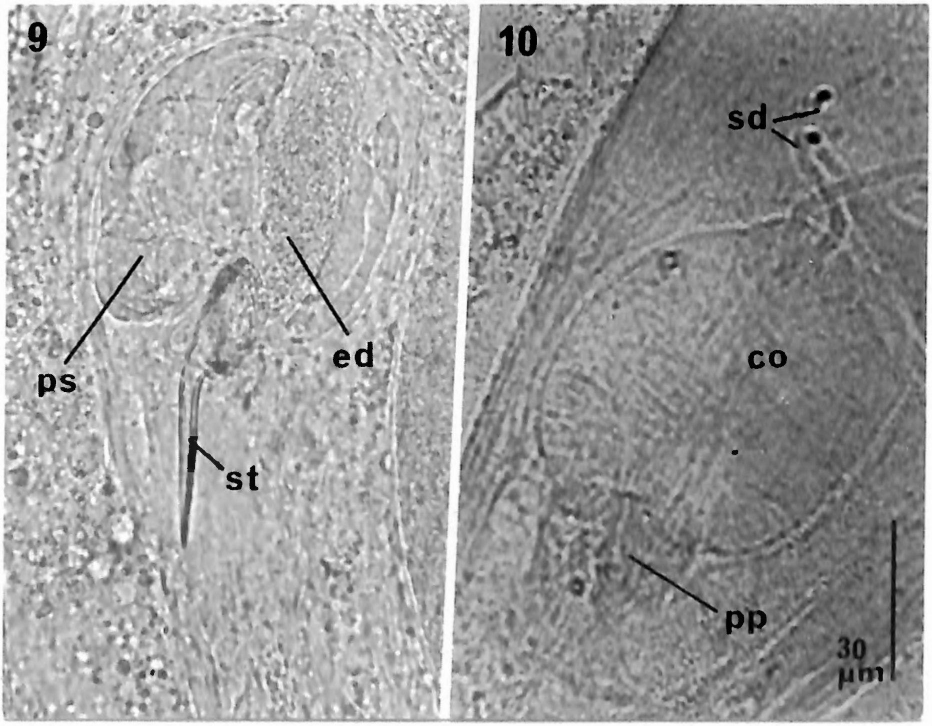
*Etymology*: species name in honour of Dr. David Doe, collector of the material.

*Description*

Filiform, 2 mm, paired pigmented eyes. Muscular plates of proboscis proximally separate. Rosulate pharynx slightly behind the mid-body. Paired testes in front and paired large seminal vesicles behind the pharynx. Yolk glands dorsally, paired ovaries beside and in front of the globular caudally situated copulatory bulb. Sperm is discharged from the seminal vesicles through filiform seminal ducts (Fig. 10) into the tubular internal ejaculatory duct, embedded in prostatic fascicles within the copulatory bulb. In live specimens (Figs 7, 9) sperm was seen discharged through the straight, proximally widened, distally pointed, approximately 100 µm long sclerotic stylet and the prostatic secretion through a separate pore beside the stylet. In preserved specimens (Figs 8, 10) the stylet is absent, the copulatory bulb distally forming a soft irregular papilla, arisen by eversion of the prostatic outlet of the bulb, evidently combined with the basal funnel of the stylet. Apparently the sclerotic wall of the stylet is dissolved by the acid fixative.



Figs 7-8. — *Placorhynchus doei* sp.n. — 7. Squeezed live specimen — 8. Squeezed preserved specimen, holotype.



Figs 9-10. — *Placorhynchus doei* sp.n., male copulatory organ — 9. Squeezed live specimen — 10. Squeezed preserved specimen.

### *Discussion*

In the abscence of a phylogenetic analysis of the genera within the Placorhynchidae Meixner, 1938 (*Placorhynchus* Karling, 1931, *Clyporhynchus* Karling, 1947, *Harsa* Marcus, 1951, *Oneppus* Marcus, 1954), the generic position of *Placorhynchus doei* is provisionally determined on the general structural conformity with the type species *P. octaculeatus* Karling, 1931.

Karling (1989, p. 21) considered sclerotic penial stylets as transformed cirrus hooks in *Harsa obnixa* Marcus, 1951 and as a sclerotized basement membrane of the penis papilla in *Placorhynchus pacificus* Karling, 1989. Penial structures of « aragonite », soluble in acid fixatives, like the stylet of *Placorhynchus doei*, have been described in the planarian *Dendrocoelopsis spinosipenis* Kenk, 1973 and in the polycystidid *Acrorhynchides styliferus* Schockaert and Karling, 1975 (see also discussion in Schockaert and Karling, 1975, p. 134). Aragonite structures in the shape of spicular skeletons are known from several plathelminths (Rieger and Sterrer, 1975).

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The author thanks Dr. Nathan W. Riser, Director of the Marine Science Institute at Nahant for working facilities at the institute and Dr. David Doe for live material of one of the species, further Ms Christine Hammar for her help with micrographs and the drawings of the figures and Mrs Ann-Marie Sundstrom for typing the manuscript. Dr. Ulf Jondelius and Dr. Ernest Schockaert are aknowledged for their help in finalising the manuscript.

## ABREVIATIONS IN THE FIGURES

| | | | |
|---|---|---|---|
| b | bursal tissue | pr | proboscis |
| cd | common seminal duct | ps | prostatic secretion |
| o | male copulatory organ | st | stylet |
| co | common genital pore | sv | seminal vesicle |
| ed | ejaculatory duct | te | testis |
| ph | pharynx | u | uterus |
| pp | penis papilla | y | yolk glands |

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## SHORT NOTE

# THE PHYLOGENY OF SOME AFRICAN MUROIDS (RODENTIA) BASED UPON PARTIAL MITOCHONDRIAL CYTOCHROME *b* SEQUENCES

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*Key words* : *African Muridae, mtDNA, cytochrome b, phylogeny.*

Almost 50 % of all extant mammal species are rodents and much of the taxonomic confusion in this group concerns the Muroidea. Immunological data, DNA/DNA hybridization experiments, amino acid sequences, distribution of highly amplified Lx fragments and mitochondrial DNA sequences disagree with the morphology based systematics and suggest that the genus *Acomys* does not belong to the Murinae Illiger, 1814 (1, 2, 3, 4, 5, 6, 7, 8, 9). If the « acomyines » (*Acomys* Geoffroy, 1838, *Uranomys* Dollman, 1909 and *Lophuromys* Peters, 1874) and the Murinae are found to be separated by at least two nodes in the cladogram, the similarity between the cranial and dental morphologies of these two clades could be the result of convergent evolution.

To test recently published phylogenies based on different molecular data we analyzed the nucleic acid sequences of portions of the mitochondrial cytochrome *b* gene (cyt *b*). In order to evaluate the potential importance of biological sampling on phylogenetic inference, we studied the relations among a number of African genera instead of *Mus L.*, 1758 and *Rattus* Fisher, 1803 often used as the representatives of the Murinae. We present parsimony analyses of cyt *b* from species of six genera traditionally allocated to the Murinae (*Mastomys natalensis* (Smith, 1847) ; *Dasymys incomtus* (Sundevall, 1846) ; *Arvicanthis nairobae J.A.* Allen, 1909 ; *Acomys spinosissimus* Peters, 1852 ; *A. wilsoni* Thomas, 1892 ; *Hybomys univittatus* (Peters, 1876) ; a yet undescribed *Hybomys* species and *Lophuromys flavopunctatus* Thomas, 1888), one species of the Gerbillinae Gray, 1825 (*Tatera valida* (Bocage, 1890)), species of two genera of Cricetomyinae Roberts, 1951 (*Cricetomys gambianus* Waterhouse, 1840 and *Beamys hindei* Thomas, 1909) and sequences from the literature of species from three genera of the Sigmodontinae Wagner, 1843 (10). Throughout this contribution we use the taxonomy of Musser and Carleton (11) in which the Muroidea contain only the family Muridae Illiger, 1814 subdivided into 17 subfamilies.

DNA was isolated from frozen or ethanol-preserved muscle tissue samples from the collections of the Department of Biology of the University of Antwerp (RUCA). The primers used to amplify a 402 base pairs (bp) long cyt *b* gene segment were L13724 (5′-CGAAGCTTGATATGAAAAACCATCGTTG-3′ and H14139 (5′-AAACTGCAGCCCCTCAGAATG ATATTTGTCCTCA-3′) (12). PCR-reactions were performed in three vials containing 25 µl of Tris buffer (10 mM, pH 9.0) containing

50 mM KCl, 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.4 μM of each primer, 50-500 ng template DNA, and *Taq* polymerase (0.65 units : 30 cycles, 94°C : 60s, 49°C : 60s and 72°C : 90s). The double-stranded PCR product was cleaned on a Millipore Ultrafree-MC 30,000 spin column to remove unincorporated nucleotides and cycle sequenced on an ALF-DNA Sequencer according to the manufacturer's protocol, using 0.8 μM primer, 2.5 units of *Tth* polymerase and both primers (Pharmacia). The mtDNA sequences were analysed using the parsimony method (PAUP 3.1.1 : 13). Transversions (TV) were considered to be ten times more important than transitions (TS) and cyt *b* sequences of the marsupial *Didelphis virginiana* Kerr, 1792 and/or the Geomyidae Bonaparte, 1845 *Cratogeomys* Merriam, 1895, *Geomys* Rafinesque, 1816 and *Papageomys* Merriam, 1895 (14, 15) were used as outgroup sequences. Statistical support for the branching patterns was estimated using the bootstrap method under the same TS/TV settings (100 replications) in PAUP.

We analysed 357 bp of the mitochondrial cyt *b* fragment. In total 172 sites were variable and 152 sites were parsimony informative. A high number of amino acid replacements were observed of which 33 of the 119 sites were informative for parsimony analysis. Pairwise comparisons among the cyt *b* sequences indicated that TS/TV ratios are low, suggesting that the studied taxa have diverged long ago or have undergone unusual rapid mutation rates in comparison with other mammals (16, 17). Finally, the overall base compositions within the muroids showed a strong anti-G bias at third positions in cyt *b*. (A : 41 %, T : 21 %, C : 36 % and G : 2 %). Because of the degenerate nature of the amino acid code, many third codon positions and some first positions are less constrained and evolve at a higher rate (16). In accordance with observations on the cyt *b* sequences of arctic carnivores many third codon positions were found to be completely consistent with the obtained phylogeny ; therefore we did not delete these characters (17).

Parsimony analysis yielded a single most parsimonious tree whose branching pattern was subsequently evaluated using the bootstrap method. The clades agreed with the subfamily grouping of most of the species studied (Fig. 1). Analyses that did not take the observed TS/TV ratio into account never resulted in trees in agreement with the (morphology based) classification of the studied species. The Cricetomyinae is the only subfamily in our dataset that was not supported by enough characters to yield a bootstrap value higher than 50 %. *Tatera valida*, the only representative of the Gerbillinae in our data set, did not cluster with any of the other subfamilies.

Our cyt *b* phylogeny does not exclude the possibility that the « acomyines » and the Murinae are a monophyletic group and the *Acomys-Lophuromys* clade may be a sister-clade to the African murines as has been suggested by immunological data (9). In addition, cyt *b* sequences of *Uranomys ruddi* Dollman, 1909 (not shown) confirm the existence of an *Acomys-Lophuromys-Uranomys* clade (4, 9, 18, 19). Our data did not allow us to evaluate whether or not the « acomyines » are closely related to the genus *Tatera* as suggested by recent DNA hybridization and amino acid sequence data (5, 6, 9).

Our study illustrates the limitations of partial cyt *b* sequences for phylogenetic studies within and among muroid subfamilies. The only phylogenetic statement at the « subfamily level » that is supported by our data is the inclusion of the Sigmodontinae within the Muridae. Although our cyt *b* phylogeny is consistent

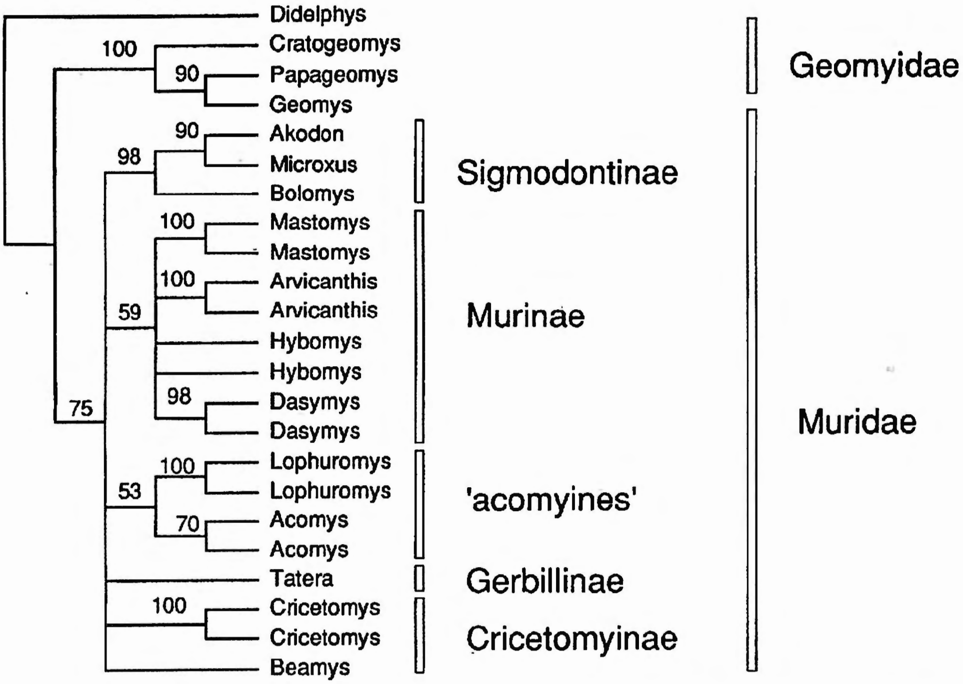

Fig. 1. — Cladogram produced by parsimony analyses of a partial mitochondrial cyt *b* gene (357 aligned sites) of representatives of twelve murid genera (see text). Numbers at nodes are bootstrap values obtained after 100 replicates (C.I. = 0.28). The Cricetomyinae is not supported by enough characters to yield a bootstrap value > 50 %.

with the subfamily groupings within the muroids, more sequence information will be required to establish the relationships between the Murinae and the « acomyines » or to determine the phylogenetic relations among muroid subfamilies. Consequently, a portion of the 16S rRNA mitochondrial gene is presently being sequenced on more taxa of various African subfamilies of the Muridae to be added to our data-base. Confirmation from our cyt *b* sequences of *Otomys lacustris* Allen and Loveridge, 1933 (subfamily Otomyinae Thomas, 1897 ; data not shown) that this genus belongs to the Murinae — as was recently suggested by immunological data (9) — illustrates the need to include taxa of all subfamilies in such analyses.

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