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Prof. Dr. E. SCHOCKAERT
Department SBG
Limburgs Universitair Centrum
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FISH SPECIES OF THE LOWER ZEESCHELDE (BELGIUM) : A COMPARISON WITH HISTORICAL CHECKLISTS

by

PAUL A. VAN DAMME*, KRIS HOSTENS** and F. OLLEVIER*

* Catholic University of Leuven, Zoological Institute,
Laboratory of Ecology and Aquaculture,
Naamsestraat 59, B-3000 Leuven, Belgium

** University of Ghent,
Institute of Zoology, Section Marine Biology,
Ledeganckstraat 35, B-9000 Gent, Belgium

SUMMARY

In the 19th century approximately 40 fish species (excluding freshwater species) were recorded in the lower Zeeschelde between the Dutch/Belgian border and Antwerpen. In comparison with the 19th century and the first half of the 20th century the total number of fish species in the Beneden-Zeeschelde has decreased considerably. The present checklist (1991-1993) of fishes of the lower Zeeschelde (excluding freshwater species) contains only 26 species. The fish community is composed of marine species (13), catadromous species (3), estuarine residents (9) and one anadromous fish species. Besides, 6 freshwater fish species have presently been recorded. The distribution of diadromous fishes, estuarine residents and freshwater fishes is probably greatly affected by low oxygen levels in the lower Zeeschelde, whereas the disappearance of adventitious marine species is probably also the result of anthropogenic effects on a much wider geographic scale. A comparison was made with recent and historical checklists of fishes of the Westerschelde and the Oosterschelde (the Netherlands).

INTRODUCTION

The tidal area of the Schelde, which is called Westerschelde in the Netherlands and Zeeschelde in Belgium, represents one of the last remaining true estuaries in Europe which is marked by an important salinity gradient (HEIP, 1989) (Fig. 1). Research efforts have recently been undertaken to accumulate information on most compartments of this unique ecosystem (see HAMERLYNCK *et al.*, 1993a for a review) : data have become available for the functional units of the phytoplankton, the zooplankton, the hyperbenthos and the macrobenthos. Apart from DE VEEN *et al.* (1979) reliable quantitative data on the occurrence of fish in the Westerschelde estuary have only more recently been collected by HAMERLYNCK *et al.* (1993b).

However, their study area only covered marine localities (zone A in Fig. 1) and some brackish localities (up to the Belgian/Dutch border) (zone B in Fig. 1). The fish communities in the brackish water area upstream of the border (zone C in Fig. 1) and in the freshwater area have not been investigated during the last decennia. By collecting fish which were imprisoned in the cooling system of the Nuclear Power Station at Doel (Fig. 1) a recent checklist of species occurring in the lower Zeeschelde could be obtained.

The obtained checklist is compared with historical checklists of fishes of the lower Zeeschelde which were published during the last 150 years. The oldest checklist for the brackish area of the Schelde, comprising 38 species (excluding freshwater fish species), was published in 1842 by DE SELYS-LONGCHAMPS ; POLL (1945, 1947) listed 40 species in the area between Antwerpen and the Belgian/Dutch border. Checklists of freshwater fish which were published in the 19th century and in the first part of the 20th century (MAES, 1898 ; ROUSSEAU, 1915) did not contain geographical distributions. The first reliable list of freshwater fish in the lower Zeeschelde is from POLL (1945, 1947). The present checklist is further compared with a checklist of fishes captured in 1989 in the Westerschelde (HAMERLYNCK *et al.*, 1993b) and with a historical checklist for the Oosterschelde (BOTTEMANNE, 1884). Finally, preliminary information is provided on the average densities of the different fish species collected in the water intake of the nuclear power station of Doel.

MATERIAL AND METHODS

The present checklist for zone C (brackish zone of the lower Zeeschelde) (Fig. 1) was obtained by monitoring the fish which were imprisoned in the cooling circuit of the Nuclear Power Station of Doel between september 1991 and december 1993. The Nuclear Power Station at Doel is situated on the lower Zeeschelde about 5 km east of the Belgian/Dutch border. Cooling water is withdrawn from the Schelde by an intake which is located 2 m above the bottom. Fish larger than about 3 cm are retained by rotating screens and are afterwards discharged. Between 1991 and 1993 8×10^6 m^3 cooling water was sampled to obtain the present checklist.

The checklists of DE SELYS-LONGCHAMPS (1842) and POLL (1945, 1947) cover the fish species collected from beam trawl catches in the lower Zeeschelde and they therefore disregard species which occur in the Westerschelde only : The first author lists all the species which were observed as far as Antwerpen in the years preceding publication, whereas the samples of the second author were all collected in 1943 or 1944 between the Dutch/Belgian border and Antwerp. Further on in the text, we will refer to the year of publication rather than to the period of collection. Some species were probably overlooked by these authors (the common goby *Pomatoschistus microps* and the painted goby *P. pictus* were probably lumped with the sand goby *P. minutus* by both authors ; three-spined stickleback *Gasterosteus aculeatus* was probably not considered to be an estuarine species by DE SELYS-LONGCHAMPS, 1842) or had not yet been described at that time (for example, the

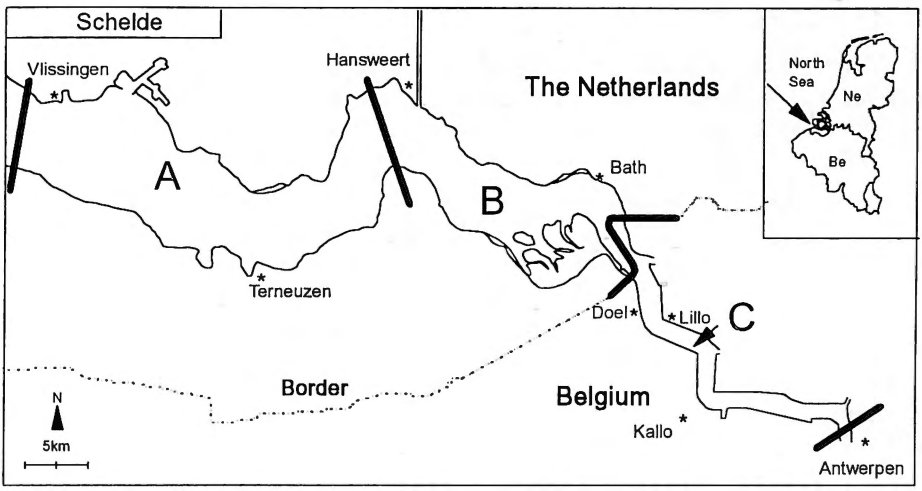

Fig. 1. — Map of the Schelde estuary, with indications of Zones A, B (Westerschelde) and C (lower Zeeschelde). Be = Belgium; Ne = the Netherlands.

smaller pipefish *Syngnathus rostellatus* was only described in 1855, lozano's goby *Pomatoschistus lozanoi* was described as a new species in 1923). These fish were quoted with a question mark in Table 1. For summation of the number of species we distinguish between recorded number of species and estimated number of species.

The common and scientific names of fish species were used according to WHEELER (1992). The species were classified in six ecological types depending on the use they make of estuarine areas (ELLIOTT and TAYLOR, 1989, COSTA and ELLIOTT, 1991, HAMERLYNCK *et al.*, 1993b) : CA stands for catadromous species, AN stands for anadromous species, MJ for juveniles of marine species that make use of the estuary as a nursery ground, MO for adventitious marine species with no estuarine requirements, ER for estuarine resident species, and FW for freshwater species. In contrast to HAMERLYNCK *et al.* (1993b), *Pomatoschistus minutus* and *P. lozanoi* were classified as juveniles of marine species (MJ) and not as seasonally occurring marine species (MS).

RESULTS AND DISCUSSION

The fish species recorded during the present study are listed in Table 1 and Table 2. The checklist contains 32 species belonging to 6 ecological types : juvenile migrant species (10), catadromous species (3), estuarine residents (9), adventitious marine species (3), freshwater species (6) and anadromous species (1). Two species, the painted goby *Pomatoschistus pictus* and the sand-smelt *Atherina presbyter*, are new records for the area.

The checklists of DE SELYS-LONGCHAMPS (1842) and POLL (1945, 1947) are listed and compared with the present checklist in Table 1. In the 19th century

TABLE 1

List of the fish species (excluding freshwater fish species) of the lower Zeeschelde, according to DE SELYS-LONGCHAMP (1842) (1), POLL (1945, 1947) (2) and the present data (3) (Ecological types are explained in Material and Methods), and approximate yearly mean density at the power station of Doel.

Species	Type	1842 (1)	1945 (2)	1991-93 (3)	1991-93 (3)
Family Petromyzontidae					
Petromyzon marinus (L.)	AN	x			
Lampetra fluviatilis (L.)	AN	x	x	x	o
Family Scyliorhinidae					
Scyliorhinus canicula (L.)	MO	x			
Family Squalidae					
Squalus acanthias (L.)	MO	(x)			
Family Squatinidae					
Squatina squatina (L.)	MO	x	(x)		
Family Rajidae					
Raja clavata (L.)	MO	x			
Raja batis (L.)	MO	x			
Family Dasyatidae					
Dasyatis pastinaca (L.)	MO		(x)		
Family Acipenseridae					
Acipenser sturio (L.)	AN	x			
Family Anguillidae					
Anguilla anguilla (L.)	CA	x	x	x	oo
Family Congridae					
Conger conger (L.)	MO	x	(x)		
Family Clupeidae					
Clupea harengus (L.)	MJ	x	x	x	ooo
Sprattus sprattus (L.)	MJ	x	x	x	oooo
Alosa alosa (L.)	AN	x			
Alosa fallax (Lacépède, 1803)	AN	x	x		
Family Engraulidae					
Engraulis encrasicolus (L.)	ER	x	x	x	o
Family Osmeridae					
Osmerus eperlanus (L.)	ER	x	x	x	o
Family Salmonidae					
Salmo salar (L.)	AN	x			
Salmo trutta (L.)	AN		(x)		
Coregonus lavaretus (L.)	AN	x			

TABLE 1 (*cont.*)

Species	Type	1842 (1)	1945 (2)	1991-93 (3)	1991-93 (3)
Family Gadidae					
Gadus morrhua (L.)	MJ	x	x		
Merlangius merlangus (L.)	MJ	x	x	(x)	o
Trisopterus luscus (L.)	MJ	x	x	x	o
Melanogrammus aeglefinus (L.)	MO	x			
Ciliata mustela (L.)	MJ		x		
Family Belonidae					
Belone belone (L.)	MO	x	x		
Family Atherinidae					
Atherina presbyter (Cuvier, 1829)	ER			x	o
Family Gasterosteidae					
Gasterosteus aculeatus (L.)	ER	?	x	x	oo
Family Syngnathidae					
Syngnathus acus (L.)	ER	x	x	x	o
Syngnathus rostellatus (Nilsson, 1855)	ER	?	x	x	ooo
Family Triglidae					
Trigla lucerna (L.)	MO	x	x	(x)	o
Eutrigla gurnardus (L.)	MO	x			
Family Cottidae					
Myoxocephalus scorpius (L.)	ER	x	x		
Family Agonidae					
Agonus cataphractus (L.)	ER	x	x		
Family Cyclopteridae					
Cyclopterus lumpus (L.)	MO		x		
Liparis liparis (Linnaeus, 1766)	ER		x		
Family Percichthyidae					
Dicentrarchus labrax (L.)	MJ		x	x	oo
Family Carangidae					
Trachurus trachurus (L.)	MO		x	x	o
Family Mugilidae					
Liza ramada (Risso, 1826)	CA		x	x	o
Family Zoarcidae					
Zoarces viviparus (L.)	ER	x	x	x	o
Family Trachinidae					
Echiichthys vipera (Cuvier, 1829)	MO		x		
Trachinus draco (L.)	MO	x			

TABLE 1 (*cont.*)

Species	Type	1842 (1)	1945 (2)	1991-93 (3)	1991-93 (3)
Family Ammodytidae					
Ammodytes tobianus (L.)	ER	x	x	x	o
Hyperoplus lanceolatus (Sauvage, 1824)	MO		x		
Family Callionymidae					
Callionymus lyra (L.)	MO	x	(x)		
Family Gobiidae					
Pomatoschistus microps (Kroyer, 1838)	ER	?	x	x	oooo
Pomatoschistus minutus (Pallas, 1770)	MJ	x	x	x	oooo
Pomatoschistus lozanoi (deBuen, 1923)	MJ	?	?	x	ooo
Pomatoschistus pictus (Malm, 1865)	MO			(x)	o
Aphia minuta (Risso, 1810)	MO		x		
Family Bothidae					
Arnoglossus laterna (Walbaum, 1792)	MO		x		
Scophthalmus maximus (L.)	MO	x			
Scophthalmus rhombus (L.)	MO	x	x		
Family Pleuronectidae					
Pleuronectes platessa (L.)	MJ	x	x	x	o
Pleuronectes flesus (L.)	CA	x	x	x	o
Limanda limanda (L.)	MJ			(x)	o
Family Soleidae					
Solea solea (L.)	MJ	x	x	x	oo
Recorded number of species		38	40	26	
Estimated number of species		(42)	(41)		

x present
(x) only 1 record
? probably present but overlooked or not known at the time
o $< 0.1/1000\ m^3$
oo $> 0.1/1000\ m^3 < 1/1000\ m^3$
ooo $> 1/1000\ m^3 < 10/1000\ m^3$
oooo $> 10/1000\ m^3$

approximately 40 marine, anadromous, catadromous or brackish water species inhabited the brackish water between the Dutch/Belgian border and Antwerpen. De Selys-Longchamps (1842) listed 38 species, but the three-spined stickleback *Gasterosteus aculeatus*, Nilsson's pipefish *Syngnathus rostellatus*, the common goby *Pomatoschistus microps* and Lozano's goby *P. lozanoi* were probably overlooked or

TABLE 2

List of the freshwater fish species of the Lower Zeeschelde according to POLL (1945, 1947) (1) and according to the present data (2)

	1945	1993
Species	(1)	(2)
Family Esocidae		
Esox lucius (L.)	x	
Family Cyprinidae		
Cyprinus carpio (L.)	x	x
Abramis brama (L.)	x	x
Abramis bjoerkna (L.)	x	
Rutilus rutilus (L.)	x	x
Rutilus erythrophtalmus (L.)	x	
Family Cobitidae		
Misgurnus fossilis (L.)	x	
Family Percidae		
Perca fluviatilis (L.)	x	x
Stizostedion lucioperca (L.)	x	x
Family Centrarchidae		
Lepomis gibbosus (L.)	x	
Family Gasterosteidae		
Pungitius pungitius (L.)	x	x
Number of species	11	6

were not known at that time. POLL (1945, 1947) listed 40 species (*P. lozanoi* was probably overlooked), with one striking absence : the sturgeon *Acipenser sturio* had all but disappeared from the Schelde estuary by then, probably due to both overfishing (REDEKE, 1941) and habitat destruction.

There is a marked historical decrease in total number of fish species recorded in the brackish water in the last decennia (Fig. 2). In comparison to the checklists of DE SELYS-LONGCHAMPS (1842) and POLL (1945) more than 15 species have disappeared from the lower Zeeschelde in 1994.

The fish community in the lower Zeeschelde is dominated by a small number of fish species. Sixteen species were found in densities lower than 0.1/1000 m^3 (Table 1).

Most apparent is the absence of some typical estuarine resident species, such as the bull-rout *Myoxocephalus scorpius*, the hook-nose *Agonus cataphractus* and the sea-snail *Liparis liparis*. These species were recorded by HAMERLYNCK *et al.* (1993b)

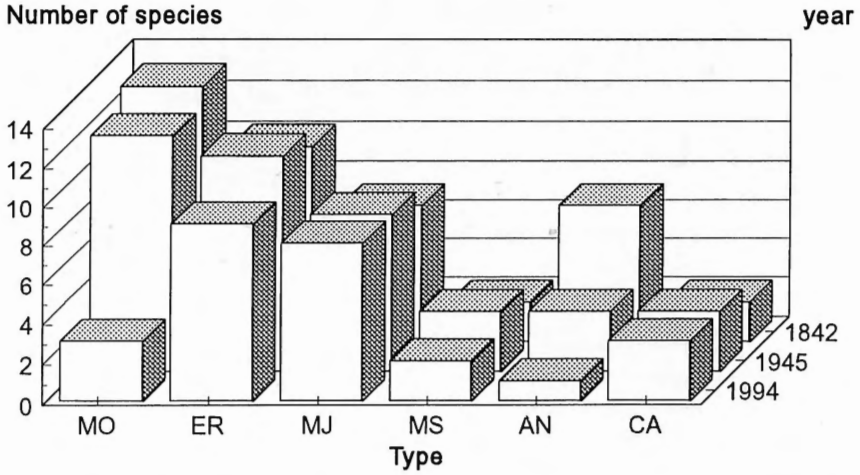

Fig. 2. — Number of fish species belonging to the different ecological types in 1842 (DE SELYS-LONGCHAMPS), 1945 and 1947 (POLL) and 1994 (the present data). For the abbreviations of the ecological types see Material and Methods.

both in the marine and the brackish zone of the Westerschelde. Possibly, they do not penetrate to the lower Zeeschelde due to reduced oxygen levels in this area.

Some marine species which occasionally occurred in the Zeeschelde in the 19th century, such as the monkfish *Squatina squatina* and the brill *Scophthalmus rhombus*, have not been recorded in this study. However, the local disappearance of these species may be a result of the overall decrease in abundance of these species in the North Sea, due to overfishing.

Furthermore, the almost complete absence of anadromous fishes is noteworthy, such as the sea lamprey *Petromyzon marinus,* the allis shad *Alosa alosa*, the twaite shad *Alosa fallax,* the sturgeon *Acipenser sturio*, the schelly *Coregonus lavaretus* and the salmon *Salmo salar*. These fish species were recorded by DE SELYS-LONGCHAMPS (1842), but all (except twaite shad) had already disappeared in the middle of this century (POLL, 1945). At present, all these species seem to be absent, probably due to anthropogenic effects (*e.g.* migration barriers in the middle and upper courses of the river). Though the three latter species may have been abundant before the 18th century (VAN NEER and ERVYNCK, 1993) they were rare in the 19th century in the Oosterschelde which at that time was still connected with the Westerschelde (BOTTEMANNE, 1884). The lamprey *Lampetra fluviatilis*, which presently is a protected species in Belgium, is the only anadromous species which has persisted in the lower Zeeschelde till now (Table 1).

Finally, the number of freshwater fish species was reduced to 6. Among these, the carp *Cyprinus carpio*, the roach *Rutilus rutilus* and the bream *Abramis brama* were rarely found in the present study. The other three species, the perch *Perca fluviatilis*, the pikeperch *Stizostedion lucioperca* and the nine-spined stickleback *Pungitius pungitius*, represented less than 0.7 % of the total number of fish found

between 1991 and 1993 (VAN DAMME, unpubl.). Notwithstanding the low water quality in the lower Zeeschelde, it is noteworthy that some freshwater fish species are still present in this area. However, it is not clear whether they can survive in summer when oxygen concentrations regularly fall below 2 mg/l (VAN DAMME, unpubl.). Exchange of fish individuals between the Schelde and adjacent channels, docks or affluents might help to sustain the freshwater fish populations. BRUYLANTS *et al.* (1989) recorded a number of catadromous and freshwater fish species in small rills which are connected with the Schelde by docks and sluices. Some of these species, such as the eel *Anguilla anguilla*, the stone loach *Noemacheilus barbatulus*, the bullhead *Cottus gobio*, the roach *Rutilus rutilus*, the silver bream *Abramis bjoerkna*, ten-spined stickleback *Pungitius pungitius* and perch *Perca fluviatilis* may occasionally venture in the Schelde and may then be caught by the water intake of the Power Station. Other possible sources of freshwater fish are the Albert canal which is connected with the Schelde by a sluice and which contains a rather rich fish fauna (VERREYCKEN, unpublished), and a channel at Bath, which connects the Zoommeer (a freshwater lake) with the Westerschelde.

The fish fauna in more upstream parts of the Schelde (upper Zeeschelde) has not been studied in the past years. Most authors assume that fish are absent in this area due to low oxygen levels and pollution stress (DE VEEN *et al.*, 1979; HAMERLYNCK *et al.*, 1993b). Though temperature and salinity normally play the dominant role in structuring estuarine fish communities (COSTA and ELLIOTT, 1991) community structure in the upper regions of strongly polluted estuaries such as the Schelde is also strongly affected by reduced oxygen levels. In the more upstream part of the Schelde estuary nowadays all hyperbenthic life has disappeared because of hypoxia (MEES *et al.*, 1993). Furthermore, macrobenthic communities have a low diversity and a low density upstream of Doel (YSEBAERT *et al.*, 1993). The absence of the hyperbenthic and macrobenthic compartments, normally containing the main food items for fish populations in the tidal area, further reduces the chance that stable populations of fish might be formed in this zone.

We should be aware that the completeness of a checklist is dependent on the collection efficiency and intensity. It is beyond all doubt that there are differences in catch efficiency among the different authors cited : DE SELYS-LONGCHAMPS (1842) and POLL (1945, 1947) collected fish qualitatively from an unspecified number of beam trawl catches of commercial fish trawlers, whereas *e.g.* HAMERLYNCK *et al.* (1993b) used a research vessel equipped with a 3m beam trawl, which is thought to have a lower catch efficiency than a commercial beam trawl. For extensive discussions on the catch efficiency of beam trawls we refer to KUIPERS *et al.* (1992). The efficiency of the method of collection of imprisoned 0+ juvenile and adult fish in cooling systems has been discussed by VAN DENSEN and HADDERING (1982). Typically pelagic fish, such as twaite shad, allis shad, sprat and herring may be caught inefficiently with this method.

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SYNDESMIS LONGICANALIS SP. NOV., AN UMAGILLID TURBELLARIAN (PLATHELMINTHES) FROM ECHINOIDS FROM THE KENYAN COAST

by

JOZEF B. MOENS *, ELS E. MARTENS ** and ERNEST R. SCHOCKAERT *
* Zoology Research Group, Dept. SBG,
Limburgs Universitair Centrum, B-3590 Diepenbeek, Belgium
** Departement of Zoology, University of Nairobi,
P.O. Box 30197, Nairobi, Kenya

SUMMARY

A new species of umagillid rhabdocoel is described from echinoids from the Kenyan coast. *Syndesmis longicanalis* sp. nov. is found in the intestine of both *Tripneustes gratilla* and *Toxopneustes pileolus* collected near Mombasa. The most striking characteristic, which distinguishes this new species from all known species of the *Syndesmis-Syndisyrinx* group is the very long sclerotic bursal canal and the three ventral glandular papillae. A more detailed comparison between the specimens from the two different hosts demonstrates that they belong to the same species although some differences are statistically significant.

Keywords : Syndesmis longcanalis n. sp., Umagllidae, commensal, turbellarians, Plathelminthes, Echinoidea.

INTRODUCTION

The majority of species of symbiotic turbellarians in echinoderms, descibed until now, belongs to the family Umagillidae (Rhabdocoela) ; only a few species are acoels (JANGOUX, 1990). They occur in the coelom and/or in the intestine of various echinoderms and some in sipunculids as well.

All umagillids found in echinoids belong to the *Syndesmis-Syndisyrinx* group. Although it is a cosmopolitan group, most species are known from relatively few well studied parts of the world : N.E. Atlantic and Brasil, N.E. Pacific and Australia. Only a few species are reported from the W. Indian Ocean (Madagascar) by HYMAN (1960). We presently carry out an inventorisation of commensal turbellarians of the E. African coasts. This is a first report on a representative of the Umagillidae from this region with the detailed description of a new species found in the intestine of two echinoids, *Tripneustes gratilla* L., 1758 and *Toxopneustes pileolus* LAMARCK, 1816. Specimens of both hosts are compared to demonstrate that only one species is concerned.

MATERIALS AND METHODS

The echinoids *Tripneustes gratilla* and *Toxopneustes pileolus* were collected in the lagoons at Nyali and Bamburi, N. of Mombasa (Kenya). The animals were kept for several days in running and continuously aerated sea water. The test was opened by carefully cutting out a disc at the aboral surface. Coelomic fluid and the washings with sea water of the test were examined under a stereoscopic microscope. Then the intestine was opened and the content washed out with sea water and examined as well. Many specimens were studied alive and then mounted in lactophenol. For permanent whole mount preparations specimens were fixed in FAA (Formol-Alcohol-Acetic) (JOHANSEN, 1940) or Bouin's, flattened under a coverglass. For parafine sectioning the worms were fixed in warm Bouin's or Stieve's fixative. Specimens for whole mounts were stained with borax carmine ; 5 µm serial parafine sections were stained with iron hematoxylin and eosin or with Mallory's, modified after Casson (fixatives and stains : see ROMEIS, 1968). Measurements were obtained from photographs of living specimens or from camera lucida drawings from whole mounts or sections. They are given as mean ± standard deviation, range and number of observations. The statistical analysis of the data was carried out according to SEBER (1984) using the statistical procedure Proc GLM (Manova statement) from SAS (1988).

RESULTS

Occurrence in hosts

The worms were only observed in the intestine of the hosts. In 34 specimens of *Tripneustes gratilla* , 0 to 247 worms per host were found with a frequency of 65 %. The distribution of *S. longicanalis* is very patchy : some sea urchins have a high infection rate while specimens from places at a relative short distance (± 100 m) are totally negative. In the four specimens of *Toxopneustes pileolus* a maximum of 2 to 35 worms was found. Here the frequency was 100 %.

Description of *Syndesmis longicanalis* sp. nov. (Figs 1-7)

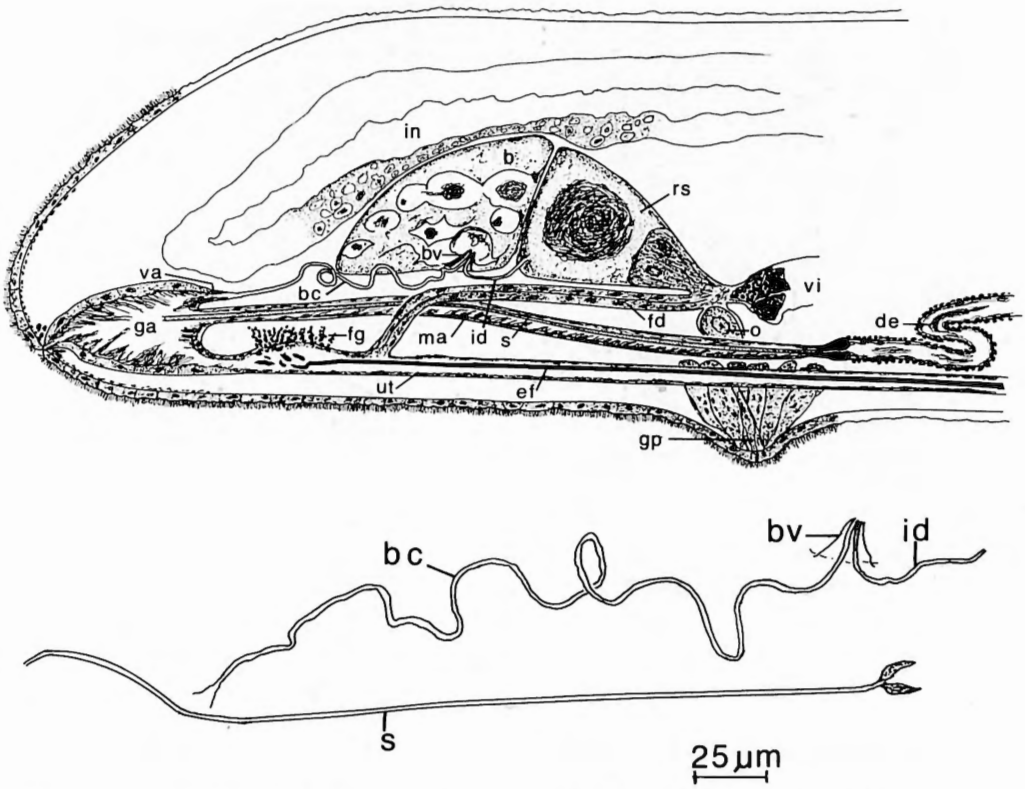
Material studied : many living animals and whole mounts ; several specimens sectioned.

Holotype : permanent mount stained with boraxcarmine.

Type locality : Nyali , N. of Mombasa (Kenya), in intestine of *Toxopneustes pileolus* (Febrary 1992) from a depth of 2-5 m.

Other localities : Nyali and Bamburi, N. of Mombasa, in the intestine of *Tripneustes gratilla* and *Toxopneustes pileolus* at depths of 2-5 m. (February 1992 and October 1992).

Type material is deposited in the zoological collection of the Limburg University Center, Diepenbeek, Belgium.



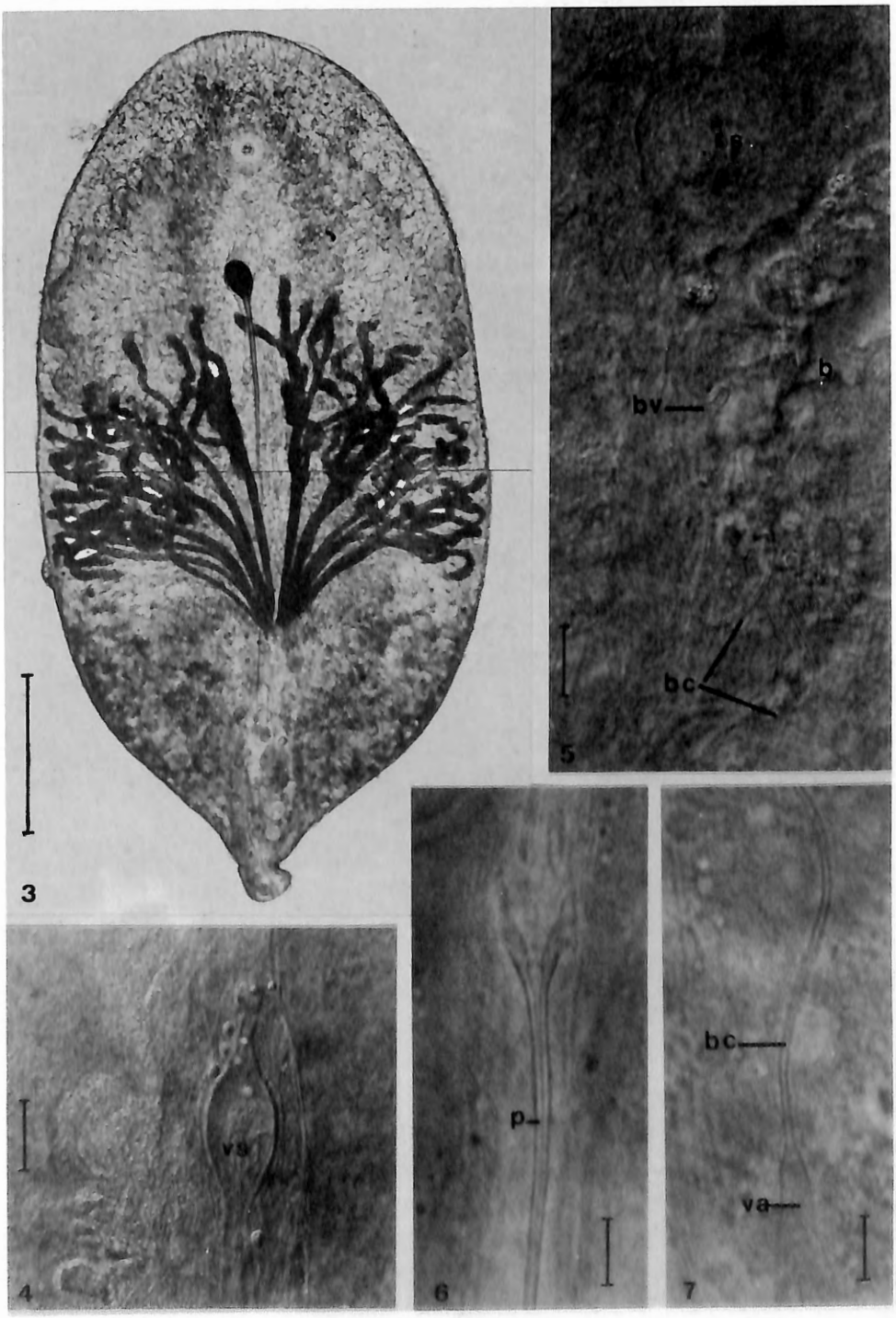
Figs 1-2. — *Syndesmis longicanalis* sp. nov. — 1. Semi diagrammatic medial sagittal reconstruction of the posterior third of the body, seen from the right — 2. Bursal canal, bursal valve, insemination duct and penis stylet (from a whole mount).

Etymology : the distinctive characteristic of the new species is the long bursal canal, hence the species name *longicanalis*.

Living specimens are markedly red to red-orange. The anterior end is rounded while the posterior end tapers to a nipple-like tip. The width is greatest in the middle portion of the body. Body length and width in the living animal are : gliding : 2246 µm ± 174 (1875-2416) and 579 µm ± 91 (458-708)(n = 10) ; rest : 2193 µm ± 259 (1875-2916) and 1262 µm ± 96 (1041-1500) (n = 20). Various measurements in the whole mounts can be found in Table I.

The whole body is ciliated. Three poorly developed glandular papillae are present in the midventral region. The anteriormost one is at the level of the anterior edge of the bursa or receptacle, the second one just posteriorly to the confluence of the vitellaries and ovaries and the third one just anteriorly to the pharynx.

The subterminal mouth is at 229 µm ± 32.7 (102-279, n = 43) from the anterior edge of the body in the living animal ; ratio to bodylength is 1:6.8 (1:8.8-1:5, n = 43). Pharynx diameter is 96 µm ±10 (115-75, n = 45). The blind saccate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intestine extends posteriorly (dorsal to the vitellaries and ovaries) to the anterior edge of the genital atrium which is nearly at the posterior end of the worm. Laterally, the intestine extends to one third of the lateral aspect of the vitellaries.

The paired lobular testes are in the anterior third of the body from the posterior edge of the pharynx and extend backwards to overlap the anteriormost branches of the vitellaries. The medial portions are close to the intestine, the lateral portions of the posterior half come close to the lateral margins of the body. The sperm ducts arise from the posterolateral part of the testis and run towards the middle of the body. They then turn anteriorly and run close and parallel to each other and to the uterus. Just behind the pharynx they become very narrow, turn posteriorly and unite to form a bulb-shaped seminal vesicle from which the ejaculatory duct originates. Both ejaculatory duct and seminal vesicle have two muscle layers: well developed outher circular muscles and inner longitudinal muscles. The narrowed anterior end of the seminal vesicle is surrounded by glands. Seminal vesicle as well as the glands are enveloped by a thin sheath, which in turn is connected to the basement membrane of the body wall just posteriorly to the pharynx. The ejaculatory duct leads posteriorly to the stylet. When the stylet is retracted, the ejaculatory duct has one loop just before the junction with the stylet of which the base is then situated anteriorly to the junction of vitellaries and ovaries. The basis of the stylet is funnel shaped and the total mean length of the stylet is 478 µm ± 139 (296-838, n = 14). The ratio to the body length is 1:4.1 (1:2.3-1:6, n = 10), the diameter 1.5 to 2.5 µm. The penis stylet is enclosed in the elongated male antrum that opens in the common genital atrium the distal part of the stylet protruding into the common genital antrum and in living specimens even out of the genital pore when the animal is slightly compressed.

The vitellaries are posterior to the testes. The anteriormost branches overlap the posterior third of the testes. The 20 to 25 branches converge in five to eight main trunks, which open into the ootype. The lateral branches come very close to the lateral margins of the body. The paired ovaries, just posterior to the vitellaries, have two or three lobes. The uterus extends from the atrium to near the posterior edge of the pharynx where it is connected to the body wall by a thin ligament. In most specimens the uterus contains a fully developed amber egg capsule. The distal part of the long whip-like egg filament is tightly coiled and is to be found in the posterior part of the uterus where the egg filament glands open. These glands are ventrally in the posterior third of the body.

From the anterior wall of the common genital atrium the short female antrum or vagina originates, narrowing to a thin canal. This sclerotic bursal canal (diameter 2 to 3 µm) is very long and coiled. It ends in an obvious bursal valve in the middle

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Figs 3-7. — *Syndesmis longicanalis* sp. nov., micrographs — 3. Living specimen, slightly squeezed (scale bar : 500 µm) — 4. Seminal vesicle (scale bar : 32 µm) — 5. Bursal valve, bursal canal, bursa and seminal receptacle (scale bar : 35 µm). — 6 . Stylet (scale bar : 12 µm) — 7. Vagina and bursal canal (scale bar : 20 µm) ; (4, 5 in whole mount, Nomarski ; 6, 7 in living animal).

and at the ventral side of the bursa. This valve consists of a sclerotic flange that rises in a nipple like structure (13 µm long, 5 µm high) projecting into one of the cavities in the bursa. The seminal receptacle is oval and is close and anterior to the bursa. The posterior end of the seminal receptacle is connected to the bursal valve by a short sclerotic insemination duct. The anterior part of the seminal receptacle is filled with large secretory cells and is connected to the ootype which in turn is connected to the uterus by the thin walled female duct. The latter ends in the uterus just posteriorly to where the egg filament glands open.

The common genital atrium in which the male antrum, vagina and uterus end, opens to the exterior at the posterior tip of the body. The epithelial lining of the atrium constists of cells with apical villosities.

Statistical analysis

Measurements were taken from 52 whole mounts, 28 of specimens from *Toxopneustes pileolus* and 24 of specimens from *Tripneustes gratilla* (Table I). Not all structures could however be measured in all specimens.

Four methods of multivariate analysis of variance (Wilk's Lambda, Pillai's Trace, Hotelling-Lawley Trace, Roy's Graetest Root) indicate a significant difference between the populations from the two hosts (P = 0,0022). The univariate analysis indicates that the differences are to be found in the body width (P = 0,0021), width of the egg capsule (P = 0,0038) and the length of the bursal canal (P = 0,00491). In our opinion the populations in the two hosts can not be distinguished on a morphological basis and are hence considered as populations of one and the same species for the time being.

In order to check whether there is a correlation between the different measures, Pearson correlation coefficients were calculated (Table II). Most measures (26/36 = 75 %) are positively correlated, 9/36 (= 25 %) are negatively correlated. Only two of the correlation coefficients are slightly significant.

DISCUSSION

The comparision between the specimens from the two different species of hosts indicates that they most probably belong to the same species, though there is a statistically significant difference for three of the nine measures (body width and width of the egg capsule and the lenght of the bursal canal). Differences between populations can be caused by ecological factors, in this case the different hosts. Slight morphological differences between individuals from different hosts are also reported for *S. echinorum* (KOZLOFF and WESTERVELT, 1987). Unless infection experiments prove the contrary, we prefer to consider individuals in both hosts as belonging to the same species.

The anatomy of *Syndesmis longicanalis* n. sp. clearly indicates that it belongs to the genus *Syndesmis* SILLIMAN, 1881 or *Syndisyrinx* LEHMAN, 1946. We compared it with the 20 species known in both these genera. The presence of the long coiled

TABLE I

Syndesmis longicanalis sp. nov. — Comparision of parameters of specimens of different hosts.

		ALL					in *Toxopneustes*					in *Tripneustes*				
		$\bar{x}$	SD	max	min	n	x	SD	max	min	n	$\bar{x}$	SD	max	min	n
1	body length	1547	304	2444	908	43	1565	240	1931	908	26	1520	390	2444	1080	17
2	body width	861	159	1322	500	43	810	130	1008	500	26	939	171	1322	748	17
3	1/2	1.83	0.38	3.98	1.35	43	1.97	0.41	2.98	1.42	26	1.61	0.19	1.88	1.35	17
4	diameter pharynx	95.9	10.3	115	75	45	96.2	8.4	114	83	25	95.5	12.4	115	75	20
5	anterior-mouth	229	32.7	279	137	44	229	29.6	279	137	25	229	37.3	279	156	19
6	1/5	6.79	0.91	8.76	4.97	42	6.85	0.69	8.66	4.97	25	6.74	1.19	8.66	5.07	17
7	length egg c.	121	8.6	138	102	38	123	9.5	138	102	24	118	5.7	129	105	14
8	width egg c.	103	11	125	85	38	106	9.6	121	85	24	98	11	125	88	14
9	bursal canal	357	71.5	548	219	46	385	65	548	253	26	320	65	445	219	20
10	1/9	4.55	1.44	9.26	2.7	37	4.15	0.82	5.92	2.7	24	5.29	2.01	9.26	3.22	13
11	length stylet	478	139	838	296	14	546	217	838	317	4	451	97	585	296	10
12	1/11	4.11	1.23	5.98	0.17	10	3.94	0.7	3.34	4.71	3	4.19	1.45	5.98	2.31	7
13	insem. duct	74	19	102	33	17	83	17.2	102	57	7	67	17.3	87	33	10

TABLE II

Syndesmis longicanalis sp. nov. — Correlation between measurements (Pearson correlation coefficients ; figures between brackets is the number of observations).

	body lenght	body width	diameter pharynx	anterior-mouth	length egg	width egg	bursal canal	length stylet	insem. duct
body length	1 (43)								
body width	0.57 (43)	1 (43)							
diameter pharynx	0.39 (42)	0.42 (42)	1 (45)						
anterior-mouth	0.62 (42)	0.31 (42)	0.40 (44)	1 (44)					
length egg	−0.14 (36)	−0.37 (36)	−0.05 (38)	−0.11 (37)	1 (38)				
width egg	0.14 (36)	0.09 (36)	0.35 (38)	0.23 (37)	−0.01 (38)	1 (38)			
bursal canal	0.07 (37)	−0.14 (37)	0.08 (39)	0.03 (38)	0.19 (34)	0.20 (34)	1 (46)		
length stylet	0.17 (10)	0.25 (10)	0.43 (13)	−0.02 (12)	−0.15 (10)	0.09 (10)	0.15 (14)	1 (14)	
insem. duct.	0.05 (11)	0.05 (11)	0.57 (12)	−0.27 (11)	−0.09 (11)	0.05 (11)	0.15 (17)	0.72 (6))	1 (17)

sclerotic bursal canal together with the poorly developed midventral glandular papillae led us to the conclusion that the species we described is new.

Syndesmis philippinensis KOMSCHLIES and VANDE VUSSE, 1980, found in *Echinometra oblonga* de BLAINVILLE, 1825 has a long bursal canal of approximately the same length but the mean length is different (280 µm, 120-560 mm), and most of all it is not sclerotic nor does this species have a bursal valve ; it does not posses glandular papillae. Glandular papillae have as yet only been found in *Syndesmis glandulosa* HYMAN, 1960, found in *Diadema setosum* LESKE, 1778 and *Echinotrix calamaris* PALLAS, 1774 (HYMAN, 1960 ; KOMSCHLIES and VANDE VUSSE, 1980b).

The validity of the genus *Syndisyrinx* and the possible synonymy of both genera is since long a matter of debate. A more detailed historical review has been given by CANNON (1982), KOZLOFF and WESTERVELT (1987, 1990) and HERTEL *et al.* (1990).

MARCUS (1949) synonimized both genera, supported by STUNKARD and CORLISS (1951). The sclerotized bursal valve was not considered a valid distinctive character.

In 1982 Cannon proposed to reinstall the genus *Syndisyrinx* considering the sclerotized bursal valve as a valid apomorphy. He did not consider the inadequate descriptions of the four new species by KOMSCHLIES and VANDE VUSSE (1980a, 1980b). Later on KOZLOFF and WESTERVELT (1987) describe a sclerotized bursal valve in *Syndesmis echinorum* FRANÇOIS 1886 the type species of the genus that should not have a valve ! They nevertheless propose to conserve the genus *Syndisyrinx* LEHMAN 1946 now based on other distinctive features : form and proportions of the parts of the ejaculatory duct, the male antrum and the stylet.

In further analyses of several species of both genera these same authors (WESTERVELT and KOZLOFF, 1990, 1992 ; KOZLOFF and WESTERVELT, 1990) come to the conclusion that only one decisive character remains : in *Syndisyrinx* the male antrum is slender and narrow and the stylet slips freely back and forth in it, whereas in *Syndesmis* the male antrum is broad and the stylet seems to be bound tightly to the wall. However, in their study of four new species of *Syndesmis* (*S. albida* and *S. rubida* KOZLOFF and WESTERVELT, 1990, and of *S. inconspicua* and *S. neglecta* WESTERVELT and KOZLOFF, 1992) we think the description of the male antrum — penis stylet complex is incomplete. Indeed, there is no mention of any connection between the ending of the ejaculatory duct, bearing the basis of the penis stylet, and the male antrum in which the tip of the penis stylet protrudes. In our opinion it is very unlikely that there is no sheath around this thin stylet. In the species we described this sheath is the elongated male antrum. It is clear that in earlier descriptions this character has not been considered. Without a new thorough revision and re-assessment of several characteristics (including ultrastructure) of the *Syndesmis-Syndisyrinx* species complex no final decision can be made on the validity of the genus *Syndisyrinx*. We therefore prefer to provisonally include the new species in the oldest genus.

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Abbreviations to the figures

b : bursa
bc. : bursal canal
bv. : bursal valve
ga. : common genital atrium
de. : ejaculatory duct
ef : egg filament
fd : female duct
fg. : filament glands
gp : glandular papilla
id : insemination duct

in. : intestine
ma : male genital antrum
o. : ovaries
s. : penis stylet
rs. : seminal receptacle
ut. : uterus
va. : vagina
vi. : vitellaria
vs. : seminal vesicle.

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ÉVOLUTION JOURNALIÈRE DE LA DÉRIVE DES EXUVIES NYMPHALES DE CHIRONOMIDAE (DIPTERA) DANS UNE RIVIÈRE SALMONICOLE (LE SAMSON, BELGIQUE)

par

MARC EVRARD
Unité d'Écologie des Eaux Douces (UNECED)
Facultés Universitaires Notre-Dame de la Paix
rue de Bruxelles 61, B-5000 Namur, Belgique

Daily evolution of the drift of pupal exuviae of Chironomidae (Diptera) in a chalk trout stream (the Samson, Belgium)

RÉSUMÉ

Des récoltes d'exuvies nymphales de Chironomidés effectuées dans le Samson obtenues Par dérive au cours d'un cycle de 24 heures, en septembre 1993, ont permis de dénombrer 50 espèces. Il s'agit, pour 14 espèces, de premières citations pour la faune belge.

La diversité spécifique dans les échantillons horaires varie au cours de la journée : 33 espèces sont récoltées au crépuscule, 14 espèces en début d'après-midi. Neuf cycles d'émergence d'espèces abondantes sont étudiées au moyen d'exuvies nymphales.

Mots clés : Diptera, Chironomidae, exuvies nymphales, dérive, rythme circadien, rivière.

SUMMARY

Pupal exuviae of chironomids were collected in the river Samson by means of a drift net, over a period of 24 hours in September 1993. 50 species were identified, 14 of which are new to Belgium.

The incidence of the exuviae of different species changed during the course of the 24 hours : exuviae of 33 species were caught at sunset, 14 at the beginning of the afternoon. The diel periodicity of emergence of 9 abundant species was studied by collecting their pupal exuviae.

Keywords : Diptera, Chironomidae, pupal exuviae, drift, diel periodicity, river.

INTRODUCTION

Récemment, de nombreux auteurs ont utilisé la technique des exuvies nymphales de Chironomidae, aussi bien pour des études taxonomiques (LAVILLE, 1981 ; SERRA-TOSIO et LAVILLE, 1991) que pour des études de qualité des eaux (WILSON et MCGILL, 1982 ; CASAS et VILCHEZ-QUERO, 1989, FRANTZEN, 1992). La faune belge compte actuellement près de 300 espèces de Chironomidae (GODDEERIS et BEHEN, 1991). Des études récentes ont montré que la liste taxonomique était loin d'être terminée, puisque près de 30 espèces sont venues compléter la liste des espèces belges (EVRARD, 1994).

Lors du passage du stade nymphal aquatique au stade adulte aérien, la pupe remonte à la surface de l'eau pour permettre à l'adulte d'émerger (BERG et HELLENTHAL, 1992 ; OLIVER, 1971). A ce moment, l'adulte libère à la surface de l'eau une enveloppe chitinisée, caractéristique de l'espèce, qui est l'exuvie nymphale (PINDER, 1986 ; COFFMAN, 1973). Cette exuvie dérive ensuite à la surface du cours d'eau. L'exuvie peut flotter 2 à 3 jours et se laisser emporter par le vent et les courants jusqu'à ce qu'elle soit retenue le long de la berge par des plantes ou des obstacles divers (WILSON et BRIGHT, 1973 ; HAYES et MURRAY, 1988).

Des échantillons de dérives exuviales sur une période de 24 heures ont permis de suivre la dérive exuviale de cette petite rivière salmonicole avec précision en intégrant le facteur temps (PINDER, 1974 ; WARTINBEE, 1979 ; ROSSARO, 1987). L'évolution des abondances relatives des différentes espèces en fonction de leur distribution temporelle a été approchée (RIERADEVALL et PRAT, 1986).

Dans ce travail, nous étudions les exuvies nymphales de Chironomidae récoltées par dérive au cours d'un cycle de 24 heures dans le cours supérieur du Samson dans le but :

— de dresser un inventaire faunistique des Chironomidae de ce cours d'eau;
— de comparer la valeur faunistique des dérives de courte durée effectuées à des heures différentes;
— de préciser le rythme nycthéméral d'émergence des espèces abondantes (> 10 %) à partir de l'évolution numérique des exuvies nymphales;
— de comparer différentes situations de prélèvements dans le temps en termes d'abondance relative.

MATÉRIEL ET MÉTHODES

Le Samson, rivière salmonicole, prend sa source dans la commune de Gesves à une altitude de 280 m, après un parcours de 20 km, rejoint la Meuse à Namêche à une altitude de 80 m. La pente moyenne est de 0,1 % et la superficie totale du bassin versant est d'environ 120 km^2. Le site étudié, choisi pour sa bonne qualité physico-chimique et biologique, se situe à 10 km de la source (UTM : FR 43S867) et le bassin versant à cet endroit est de 50 km^2, la largeur de la rivière varie de 4 à 10 m et la profondeur de 10 à 30 cm. Une description détaillée de ce site a été réalisée (MAQUET, 1983).

Les prélèvements de dérive ont été réalisés du 07.09.93, 10 h 00 au 08.09.93, 10 h 00 (coucher du soleil 20 h 20 ; lever du soleil 07 h 20). Le filet de dérive (ouverture circulaire de 30 cm de diamètre — vide de maille de 300 microns) reposait sur le fond et filtrait toute la colonne d'eau dirigée artificiellement vers l'entrée du filet au moyen de planches. Il était relevé toutes les heures. Afin d'éviter les interférences avec la dérive exuviale en amont, le tronçon étudié a été isolé 48 heures auparavant, au moyen d'un autre filet (vide de maille de 300 microns) disposé sur toute la largeur du cours d'eau. Au cours de ce cycle de 24 heures, le ciel est resté dégagé et le débit constant avec une vitesse de courant d'environ 50 cm/s à l'entrée du filet. Le matériel obtenu a été trié sous loupe binoculaire et conservé en alcool à 95 %. Une partie du matériel récolté a été montée dans de l'Euparal en préparation permanente. Les clés de détermination utilisées sont celles de WILSON et MCGILL (1982) et LANGTON (1991).

RÉSULTATS

Ce cycle de 24 heures ne reflète en aucune façon les cycles correspondants en période printanière, ni même en période estivale, il reste ponctuel et automnal. 11653 exuvies nymphales ont été récoltées et identifiées. Elles appartiennent à 50 espèces dont 15 sont citées pour la première fois en Belgique (Tableau 1). Les Orthocladiinae et les Tanytarsini sont plus diversifiés (respectivement 27 et 10 espèces) que les Chironomini (5 espèces), les Tanypodinae (6 espèces) et les Prodiamesinae (2 espèces).

TABLEAU 1

Liste des Diptères Chironomidae récoltés dans le Samson.
Les nouvelles espèces pour la faune belge sont notées (*).

Tanypodinae

Apsectrotanypus trifascipennis (Zetterstedt)
Conchapelopia pallidula (Meigen)
Macropelopia nebulosa (Meigen)
Nilotanypus dubius (Meigen)
Thienemannimyia carnea (Fabricius)
Zavrelimyia barbatipes (K)

Diamesinae

Potthastia longimanus Kieffer

Prodiamesinae

Prodiamesa olivacea (Meigen)

Orthocladiinae

* *Brillia flavifrons* Johannsen

Brillia modesta (Meigen)
Corvnoneura lobata Edwards
Cricotopus (Cricotopus) annulator Goetghebuer
Cricotopus (Cricotopus) tremulus (Linnaeus)
Cricotopus (Isocladius) intersectus (Staeger)
* *Eukiefferiella brevicalcar* (Kieffer)
Eukiefferiella claripennis (Lundbeck)
* *Eukiefferiella coerulescens* (Kieffer)
* *Heleniella ornaticollis* (Edwards)
* *Nanocladius rectinervis* (Kieffer)
Orthocladius (Eudactylocladius) fuscimanus (Kieffer)
* *Orthocladius (Orthocladius) oblidens* (Walker)
Orthocladius (Orthocladius) rubicundus (Meigen)
Paracladius conversus (Walker)
Paracricotopus niger (Kieffer)
* *Parakiefferiella bathophila* (Kieffer)
* *Parametriocnemus stylatus* (Kieffer)
Paratrichocladius rufiventris (Meigen)
Paratrissocladius excerptus (Walker)
Rheocricotopus (Psilocricotopus) chalvbeatus (Edwards)
Rheocricotopus (Rheocricotopus) fuscipes (Kieffer)
* *Rheorthocladius* sp. A Thienemann
* *Synorthocladius semivirens* (Kieffer)
Thienemanniella clavicornis (Kieffer)
Tvetenia calvescens (Edwards)
Tvetenia verralli (Edwards)

Chironominae - Chironomini

Microtendipes diffinis (Edwards)
Paratendipes albimanus (Meigen)
Polypedilum (Pentapedilum) uncinatum (Goetghebuer)
Polypedilum (Polvpedilum) convictum (Walker)
Polvpedilum (Tripodura) pullum (Zetterstedt)

Chironominae - Tanytarsini

Cladotanvtarsus mancus (Walker)
Micropsectra atrofasciata (Kieffer)
Micropsectra notescens (Walker)
Paracladopelma camptolabis (Kieffer)
* *Rheotanvtarsus pentapoda* (Kieffer)
* *Stempellinella flavidula* (Edwards)
* *Tanvtarsus brundini* (Lindeberg)
Tanytarsus ejuncidus (Walker)
Tanvtarsus eminulus (Walker)
* *Tanvtarsus palletaris* (Verneaux)

Du point de vue numérique, les Orthocladiinae représentent 47,8 % des récoltes d'exuvies avec 6 espèces principales *Corynoneura lobata* (13 %), *Nanocladius rectinervis* (2 %), *Parakiefferiella bathophila* (9 %), *Parametriocnemus stylatus* (3 %),

Paratrichocladius rufiventris (8 %), *Paratrissocladius excerptus* (6 %). Les Chironominae représentent 45,5 % des récoltes réparties entre les Chironomini (5,3 %) et les Tanytarsini (40,2 %). Deux espèces dominent nettement cette communauté : *Tanytarsus ejuncidus* (26 %) et *Tanytarsus eminulus* (6 %). Les Prodiamesinae sont représentés par *Prodiamesa olivacea* (4 %). Plus de la moitié des espèces présentent une abondance relative inférieure à 0,1 % de l'effectif total capturé.

Le nombre d'espèces et le nombre d'individus suivent la même évolution générale (Fig. 1), caractérisée par la prépondérance des valeurs nocturnes et par l'apparition d'un pic d'émergence (plus de 2500 exuvies) après le coucher du soleil, entre 21 h et 22 h.

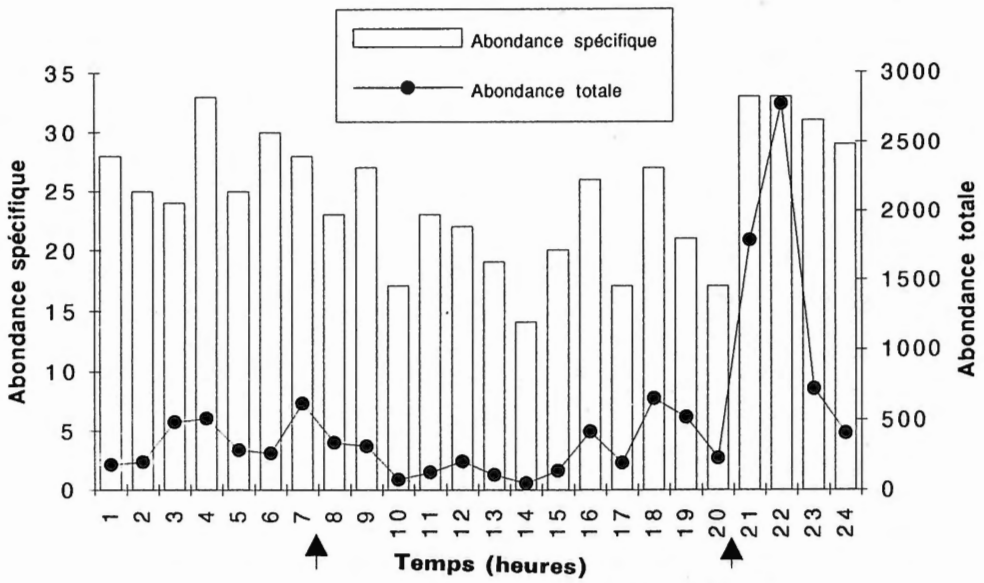
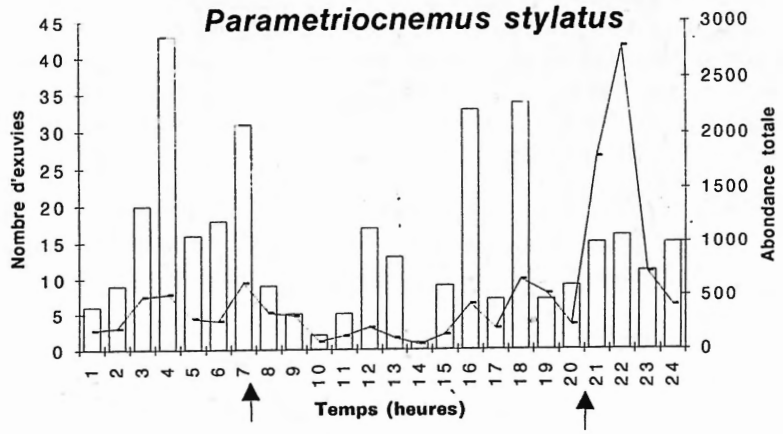
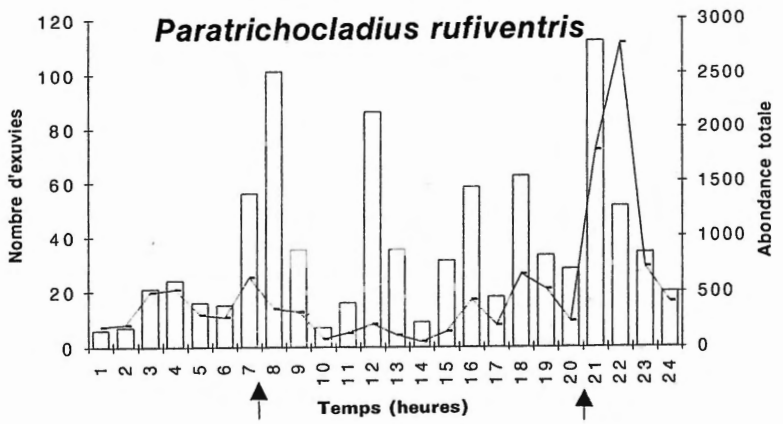


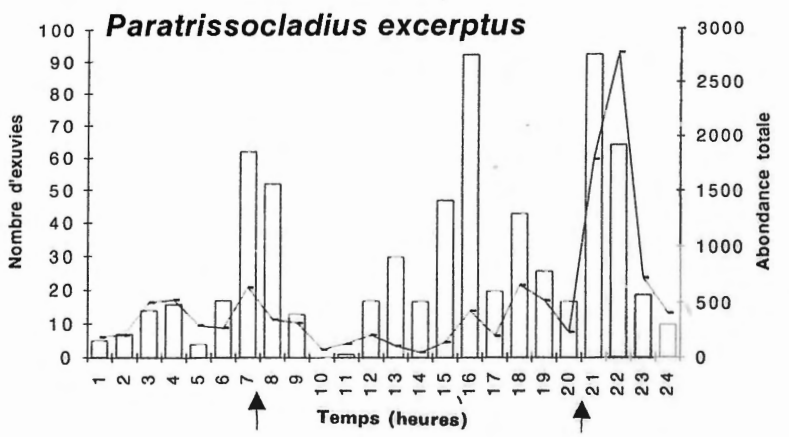
Fig. 1. — Evolution circadienne du rythme d'émergence des Diptères Chironomidae dans le Samson (Bois Gesves, septembre 1993).

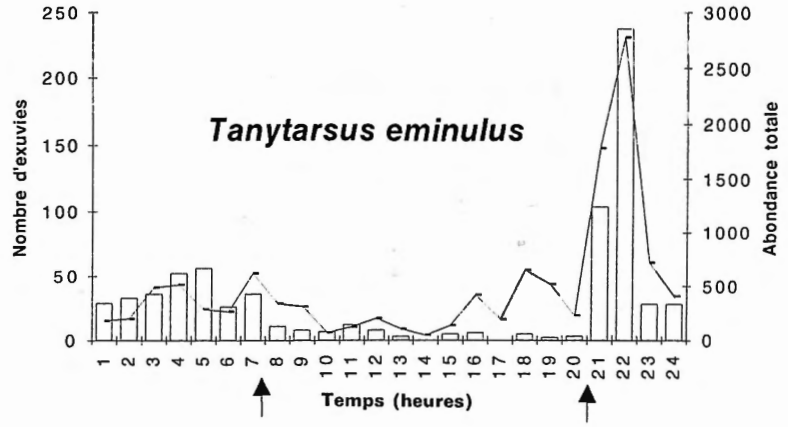
Les récoltes les plus diversifiées sont faites au crépuscule et à l'aube : 33 espèces capturées entre 21 et 22 h, ainsi qu'à 4 h, soit 65 % du nombre total d'espèces obtenues au cours du cycle de 24 heures. Les relevés nocturnes, avee en moyenne 29 espèces différentes récoltées entre 21 h et 7 h, sont nettement plus riches que les relevés diurnes qui renferment en moyenne 21 espèces.

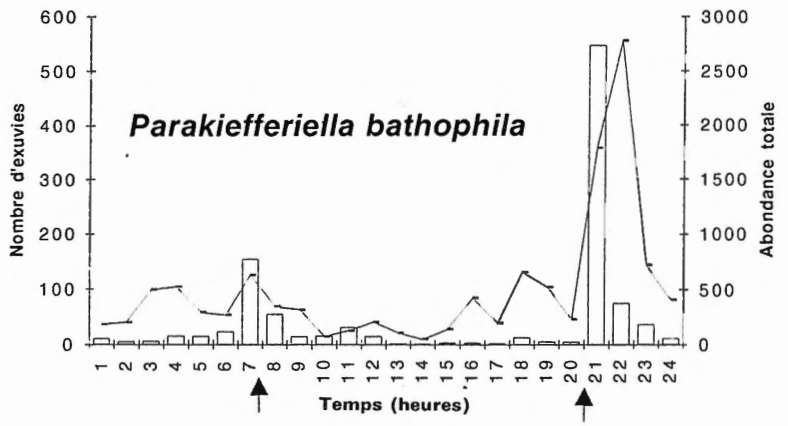
Le minimum — 14 espèces, soit 27 % du total — est observé en début d'après-midi entre 13 h et 14 h, les 9 espèces les plus abondantes, c'est-à-dire représentées au moins une fois par plus de 10 % en abondance relative dans un des 24 relevés horaires, sont toutefois présentes. Sur un total de 50 espèces, 26 sont absentes dans plus de la moitié des relevés ; 18 espèces sont représentées par plus de 5 % dans au

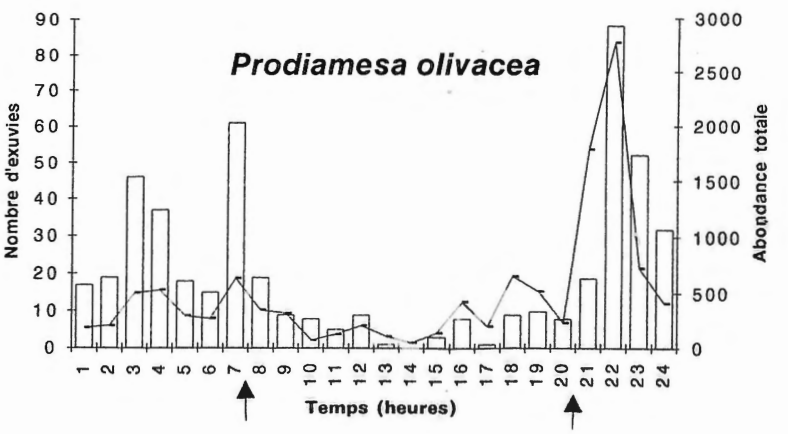

Parametriocnemus stylatus
Nombre d'exuvies
Abondance totale
Temps (heures)


Paratrichocladius rufiventris
Nombre d'exuvies
Abondance totale
Temps (heures)


Paratrissocladius excerptus
Nombre d'exuvies
Abondance totale
Temps (heures)


Tanytarsus eminulus
Nombre d'exuvies
Abondance totale
Temps (heures)


Parakiefferiella bathophila
Nombre d'exuvies
Abondance totale
Temps (heures)


Prodiamesa olivacea
Nombre d'exuvies
Abondance totale
Temps (heures)

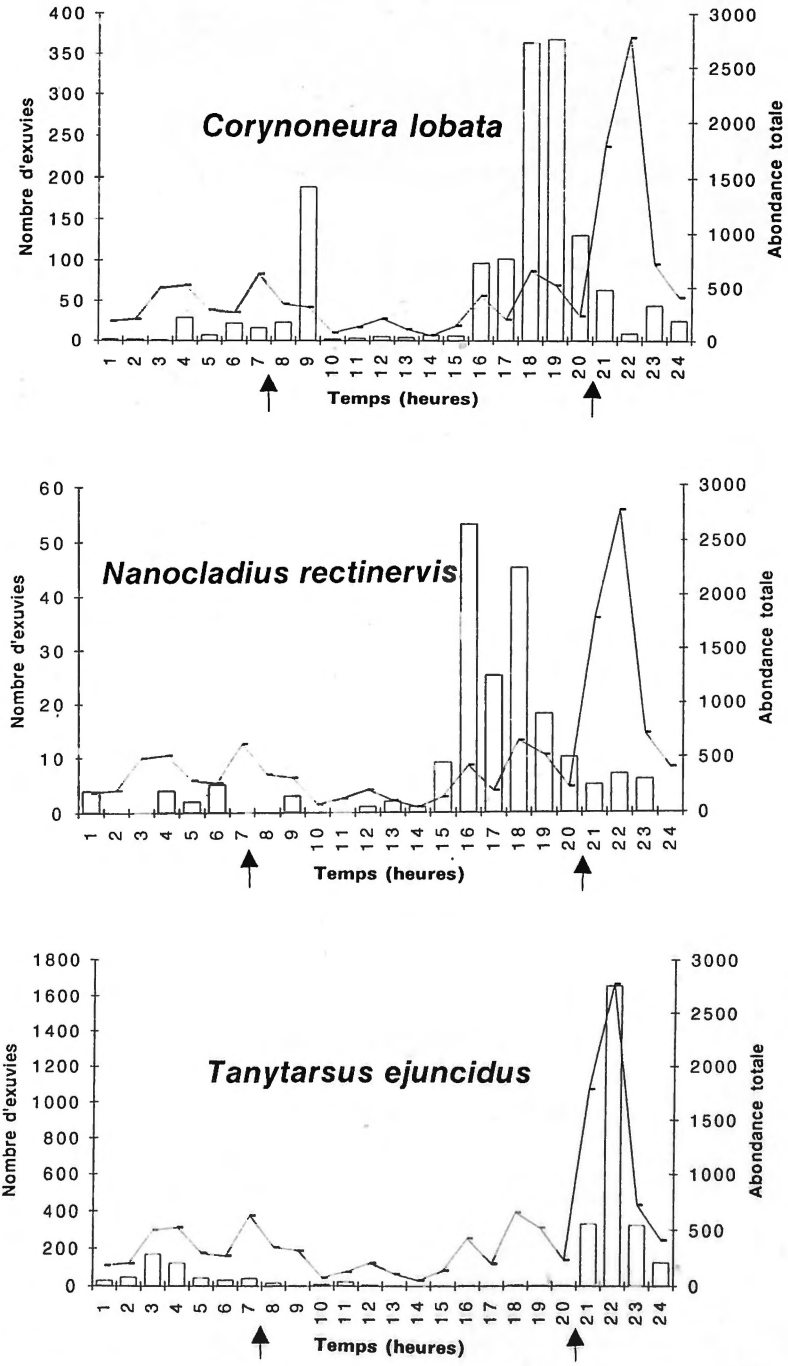


Fig. 2. — Rythme d'émergence de neuf espèces abondantes dans le Samson au niveau du Bois Gesves, septembre 1993 (le trait continu représente l'abondance totale; les flèches représentent le lever et le coucher du soleil respectivement).

moins un des relevés horaires ; 9 espèces sont représentées par plus de 10 % dans au moins un des relevés horaires.

L'évolution numérique des exuvies qui reflète le cycle nycthéméral d'émergence des espèces dépend essentiellement des formes principales. Cinq types de dérives peuvent être reconnus parmi les 9 espèces dominantes (Fig. 2).

— La dérive est essentiellement diurne avec deux maxima le matin et en fin d'après-midi (*Corynoneura lobata*) ;
— la dérive est essentiellement diurne avec un maximum (*Nanocladius rectinervis*) ;
— la dérive présente un maximum au crépuscule et dans les premières heures de la nuit (*Tanytarsus ejuncidus, Tanytarsus eminulus*) ;
— la dérive présente deux maxima en début et en fin de nuit (*Parakiefferiella bathophila, Prodiamesa olivacea*) ;
— la dérive est surtout nocturne sans maximum net (*Parametriocnemus stylatus, Paratrichocladius rufiventris, Paratrissocladius excerptus*).

Les autres espèces, moins abondantes, dérivent préférentiellement la nuit.

L'évolution des proportions relatives par tranche horaire renseigne également sur l'évolution des différentes sous-familles et tribus.

Fig. 3 représente l'évolution globale des sous-familles et tribus ; elle concerne les 50 espèces répertoriées au cours du cycle de 24 heures. La prédominance des Orthocladiinae en période diurne est nettement visible, alors qu'en période nocturne, les Tanytarsini montrent un rythme d'émergence plus soutenu au crépuscule et durant la nuit où ils dominent. Les Chironomini évoluent de manière plus sporadique, ce

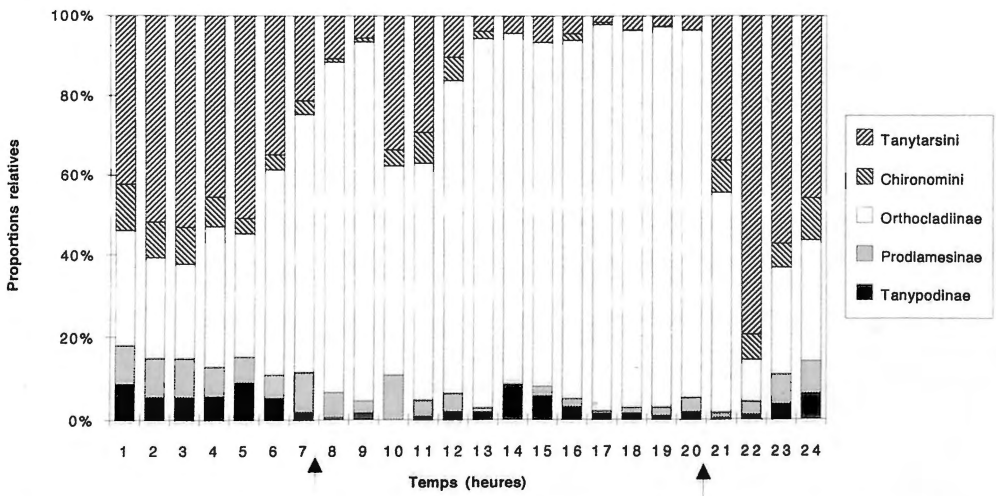


Fig. 3. — Evolution des proportions relatives des différentes sous-familles et tribus de Diptères Chironomidae dans le Samson (Bois Gesves, septembre 1993) au cours d'un cycle de 24 heures.

qui est également le cas des Prodiamesinae et Tanypodinae avec toutefois une légère tendance nocturne.

DISCUSSION

Parmi les 50 espèces recensées, 14 sont citées pour la première fois en Belgique : *Brillia flavifrons, Eukiefferiella brevicalcar, Eukiefferiella coerulescens, Heleniella ornaticolis, Nanocladius rectinervis, Orthocladius oblidens, Parakiefferiella bathophila, Parametriocnemus stylatus, Rheorthocladius* sp.A Thienemann, *Synorthocladius semivirens, Rheotanytarsus pentapoda, Stempellinella flavidula, Tanytarsus brundini, Tanytarsus palletaris.*

Les relevés horaires n'apportent pas tous la même information, chacun d'eux sousestimant, en outre, assez largement le nombre total d'espèces présentes dans le milieu. Dans le Samson, les relevés les plus diversifiés, réalisés au crépuscule et à l'aube, regroupent seulement 2/3 des espèces capturées au cours du cycle de 24 h ; le relevé le moins diversifié, fait en début d'après-midi en recueille moins du tiers — toutes les espèces principales sont néanmoins présentes.

Ces proportions rendent compte des dérives de courte durée, où 1 heure de dérive (selon la période durant les 24 h) apporte entre 27 et 67 % des espèces récoltées en 24 h. Si on allonge la durée des prélèvements de dérive, le nombre d'espèces présentes dans chacun d'eux augmente sensiblement. Ainsi, selon les périodes considérées, un relevé de 2 heures de dérive consécutives apporte 51 à 78 % des espèces; un relevé de 3 heures de dérive consécutives en recueille 53 à 82 %. En pratique toutefois, il est difficile d'allonger la durée des dérives (colmatage du filet, temps nécessaire au dépouillement des données) et il est préférable de cumuler plusieurs prélèvements de courte durée répartis au cours de la journée. La nuit constitue toujours une période privilégiée mais le protocole d'échantillonnage doit être adapté à chaque situation. D'autre part, il est vraisemblable que dans les rivières importantes (potamon profond), des relevés de courte durée donnent des résultats relativement homogènes compte tenu de la durée de flottaison des exuvies et des conditions d'écoulement. Le facteur responsable du schéma d'émergence de la plupart des espèces semble corrélé au lever et au coucher du soleil. toutefois la complexité du mécanisme d'émergence ne permet pas d'attribuer la production de ce phénomène au seul facteur lumière. Dans les régions tempérées, l'émergence des Orthocladiinae domine pendant la journée, alors que les tanytarsini et les Chironomini émergent plutôt après le crépuscule. Les résultats observés dans le Samson confirment cette tendance. Dans certains cas, l'émergence des insectes aquatiques (adultes, nymphes et exuvies) montre nettement un schéma d'émergence avec un pic dans l'après-midi et un autre tôt le matin (WATERS, 1972), dans d'autres cas, l'émergence a lieu pendant la nuit (MÜLLER, 1974). Ceci traduit l'existence d'un rythme circadien endogène qui aurait pour déclencheur de l'émergence, le changement lumière-obscurité (MÜLLER, 1974). Des études en laboratoire sur Chironomus riparius ont montré l'importance de la lumière comme déclencheur (FISCHER et ROSIN, 1968, KURECK, 1980). Cependant, de basses températures ou des chutes brutales de température

peuvent également influencer le rythme et l'intensité des émergences, la température agissant alors comme déclencheur. Généralement, la photopériode reste le plus important déclencheur du rythme circadien. D'autre part, la température fluctue en fonction des conditions locales. Pour les adultes en phase d'émergence, la température de l'air atmosphérique est plus importante que la température de l'eau, spécialement les jours froids. La préférence pour la photopériode comme déclencheur, permet aux Chironomidae de pressentir le plus chaud moment de la journée pour émerger, même si la température de l'eau est basse.

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SCALING OF SKELETAL ELEMENT MASS IN BIRDS

by

JORGE CUBO and ADRIÀ CASINOS
Department of Animal Biology (Vertebrates)
University of Barcelona
08028 Barcelona (Spain)

SUMMARY

The dry mass from different skeletal elements of 63 specimens belonging to 49 species of birds was measured. The body mass range was 5.7 g-98 kg. Correlations of the mass of the skeletal elements to body mass were established by means of Model II of regression. Positive allometry was found in the case of the femur, tibiotarsus-fibula, tarsometatarsus, synsacrum and thoracic vertebrae, while the skull and sternum showed negative allometry. For a given body mass, a larger mass of avian humerus, ulna-radius and tibiotarsus-fibula can be expected, in comparison with the corresponding bones in mammals. Finally, some species displayed special values for some of their skeletal elements. For example, two orders (Galliformes and Columbiformes) displayed a tendency to lighter skeletal structures.

Keywords : Allometry, adaptation, birds, locomotion.

INTRODUCTION

In recent years several papers dealing with the problems of the scaling of the skeletal mass to the body mass of animals, mainly vertebrates, have been published ; for example, REYNOLDS and KARLOTSKI (1977) and CASADEVALL *et al.* (1990) on teleosteans, LECLAIR *et al.* (1993) on amphibians, PRANGE *et al.* (1976) on reptiles, BOU and CASINOS (1985) on insectivores and rodents, ROBINEAU and DE BRUFFRÉNIL (1993) on cetaceans, POTTER (1986) on primates, PRANGE *et al.* (1979) comparing birds and mammals, REYNOLDS (1977) on vertebrates in general, and ANDERSON *et al.* (1979) on animal skeletons in general. With the exception of BOU and CASINOS (1985) and CASADEVALL *et al.* (1990) all the papers cited refer to the whole skeleton. Nevertheless, some of the results for the masses of separate skeletal elements seem to indicate that some particular characteristics may be a response to environmental pressures.

The only paper referring to birds (PRANGE *et al.*, 1979) shows that similar allometries of skeletal mass exist in birds and mammals when entire skeletons are considered. Consequently, the present research had two main aims. First, to study the scaling of the different skeletal elements of birds to body mass, comparing

results for long bones and the skull with those previously found by BOU and CASINOS (1985) for the same structures in insectivores and rodents. Second, to discuss possible adaptative reasons for particular values of some skeletal structures.

MATERIAL AND METHODS

Some 63 specimens from 49 different species were studied, although the size of the sample varies according to the structure studied. The maximum corresponds to the skull and the minimum (30 specimens and 20 species) to the cervical and thoracic vertebrae. The species were namely :

Order Gaviiformes

Family Podicipedidae
Rollandia rolland (Quoy and Gaimard, 1824) (1)

Order Palaeognathiformes

Family Struthionidae
Struthio camelus Linnaeus, 1758 (1)

Order Ciconiformes

Family Ardeidae
Ardea cinerea Linnaeus, 1758 (1)
Bubulcus ibis (Linnaeus, 1758) (1)
Egretta garzetta (Linnaeus, 1766) (1)

Family Threskiornithidae
Plegadis chihi (Vieillot, 1817) (1)

Order Falconiformes

Family Strigidae
Tyto alba (Scopoli, 1769) (2)

Family Accipitridae
Buteo buteo (Linnaeus, 1758) (2)
Circus cinereus Vieillot, 1816 (1)
Milvago chimachima (Vieillot, 1816) (1)
Milvus migrans (Boddaert, 1783) (1)

Order Anseriformes

Family Anatidae
Aix sponsa (Linnaeus, 1758) (1)
Cairina mostacha Fleming, 1822 (1)
Coscoroba coscoroba (Molina, 1782) (1)
Cygnus olor (Gmelin, 1789) (1)
Netta rufina (Pallas, 1773) (1)

Order Galliformes

Family Opisthocomidae
Guira guira (Gmelin, 1788) (1)

Family Megapodiidae
Gallus sonnerati Temminck, 1813 (1)

Family Numididae
Numida meleagris (Linnaeus, 1758) (1)

Family Phasianidae
Alectoris rufa (Linnaeus, 1758) (2)
Phasianus colchicus Linnaeus, 1758 (2)

Order Gruiformes

Family Rallidae
Fulica leucoptera Vieillot, 1817 (1)

Order Charadriiformes

Family Sternidae
Sterna albifrons Pallas, 1764 (3)

Family Laridae
Larus argentatus Pontoppidan, 1763 (1)
Larus ridibundus Linnaeus, 1766 (1)

Family Recurvirostridae
Himantopus himantopus (Linnaeus, 1758) (1)
Recurvirostra avosetta Linnaeus, 1758 (1)

Family Charadriidae
Charadrius alexandrinus Linnaeus, 1758 (2)
Vanellus chilensis (Molina, 1782) (1)

Family Scolopacidae
Calidris alpina (Linnaeus, 1758) (2)
Calidris ferruginea (Pontoppidan, 1763) (2)
Calidris minuta Leisler, 1812 (1)
Tringa erythropus (Pallas, 1764) (1)

Order Columbiformes

Family Columbidae
Columba livia Gmelin, 1789 (2)
Columba palumbus Linnaeus, 1758 (1)

Order Psittaciformes

Family Psittacidae
Amazona aestiva (Linnaeus, 1758) (1)
Myopsitta monachus (Boddaert, 1783) (1)
Poicephalus senegalus (Linnaeus, 1766) (1)

Order Piciformes

Family Picidae
Melanerpes candidus (Otto, 1796) (1)

Order Passeriformes

Family Prunellidae
Prunella modularis (Linnaeus, 1758) (1)

Family Muscicapidae
Erithacus rubecula (Linnaeus, 1758) (2)
Turdus philomelos Brehm, 1831 (3)
Sylvia atricapilla (Linnaeus, 1758) (1)

Family Certhiidae
Certhia brachydactyla Brehm, 1870 (1)
Family Corvidae
Corvus corone Linnaeus, 1758 (1)
Cyanocorax caeruleus (Vieillot, 1818) (1)
Family Fringillidae
Carduelis carduelis (Linnaeus, 1758) (1)
Fringilla coelebs Linnaeus, 1758 (2)
Serinus serinus (Linnaeus, 1766) (1)

The systematic scheme is that of CRACRAFT (1981). The number of specimens studied is given in brackets. From some species not all the the skeletal elements were available. This is the origin of the variability in the samples (Table 1).

The sample was obtained from the Barcelona Zoological Garden and several Spanish natural parks. Some of the skulls, belonging to neotropical species, correspond to material studied by one of us (A.C.) some years ago in the museum of Mar del Plata (Argentina). For preparation, hot water and a drying-chamber were used (BOU and CASINOS, 1985). Regression of the individual skeletal elements against body mass were calculated by means of Model II. The calculation of confidence intervals enabled comparison with the corresponding values for insectivores and rodents to be made (BOU and CASINOS, 1985).

RESULTS

In Table 1 the different equations calculated, the size of the samples, the correlation coefficients and the confidence intervals are shown.

In two cases (skull and sternum) a clear negative allometry appears, since the confidence intervals of b (the exponent) exclude the isometric value (slope 1). In the case of the skull, this is not very surprising, because brain mass also scales with negative allometry. Inversely, the femur, tibiotarsus and fibula, tarsometatarsus, synsacrum and thoracic vertebrae scale with positive allometry, the confidence intervals also excluding the isometric value for b.

It is known that wing length scales with positive allometry. Therefore it can be expected that wing bone mass does likewise. When comparisons with long bones of insectivores and rodents are established, the humerus and ulna-radius scale with exponents significantly different from those of mammals and in all cases, except femur, the y-interceptions (Table 1, a) are higher than the corresponding values for insectivores and rodents and the confidence intervals calculated for birds exclude mammalian values. The femur is the only long bone for which a similar mass can be expected in both birds and mammals. Finally, the avian skull scales slower than the mammalian skull and the confidence intervals of exponent (Table 1, b) in the case of birds exclude those calculated for insectivores and rodents (BOU and CASINOS, 1985) whether the calculation is made with the least-square system (as was originally the case) or model II.

TABLE 1

Equations calculated for the regressions of the different skeletal elements to body mass. Confidence intervals for both the y-interception (a) and the slope (b) are shown. Abbreviations : n, size of the sample ; r, correlation coefficient.

Skeletal element	Equation	n	r	a Confidence interval	b Confidence interval
Skull	$y = 0.0194 * x^{0.805}$	61	0.941	0.0286-0.0131	0.876-0.734
Humerus	$y = 0.0034 * x^{1.007}$	53	0.979	0.0046-0.0025	1.064-0.949
Ulna-radius	$y = 0.0034 * x^{0.990}$	52	0.955	0.0053-0.0022	1.073-0.907
Femur	$y = 0.0008 * x^{1.151}$	53	0.993	0.0009-0.0006	1.188-1.113
Tibiotarsus + fibula	$y = 0.0015 * x^{1.126}$	51	0.984	0.0021-0.0011	1.183-1.068
Tarsometatarsus	$y = 0.0007 * x^{1.159}$	52	0.971	0.0011-0.0005	1.238-1.080
Clavicle	$y = 0.0007 * x^{1.024}$	31	0.945	0.0013-0.0003	1.151-0.897
Scapula + coracoid	$y = 0.0018 * x^{1.008}$	32	0.992	0.0023-0.0014	1.056-0.960
Sternum	$y = 0.0046 * x^{0.950}$	33	0.992	0.0059-0.0036	0.993-0.907
Synsacrum	$y = 0.0021 * x^{1.114}$	33	0.995	0.0027-0.0016	1.156-1.072
Cervical vertebrae	$y = 0.0026 * x^{1.047}$	30	0.975	0.0044-0.0015	1.137-0.957
Thoracic vertebrae	$y = 0.0010 * x^{1.077}$	30	0.991	0.0014-0.0008	1.131-1.023
Caudal vertebrae	$y = 0.0005 * x^{1.008}$	31	0.959	0.0011-0.0003	1.117-0.899

DISCUSSION

According to the results found in this research, it seems very clear that for a given body mass, larger masses in avian humerus, ulna-radius and tibiotarsus and fibula than for the corresponding bones of insectivores and rodents (tibia and fibula instead of tibiotarsus and fibula) can always be expected. The femur is the exception. As noted above, a similar femur mass can be expected for birds and mammals. In fact, the femur is the most constant bone within mammals (BOU *et al.*, 1991 ; CASINOS *et al.*, 1993) both from a mechanical and a biometrical point of view. At the same time the variation in the mechanical behaviour of the avian and mammalian femur, both as regards bending and twisting, seems to be minimal (BOU *et al.*, 1991). Since the avian femur is at the same time shorter and thicker (ALEXANDER *et al.*, 1979, MALOIY *et al.*, 1979, and unpublished data from OLMOS, 1988), possibly there exists a compensation, in which case the similarity of mass between bird and mammal femur would not be surprising.

We can wonder about the reason for the greater mass in most avian long bones compared with the same bones in mammals. One reason could be biometrical : in general long bones scale faster in birds than in mammals, according to the equations of ALEXANDER *et al.* (1979) and unpublished data from OLMOS (1988). For example, the slope of the avian humerus length against body mass is 0.43, while it is only 0.36 in the case of the mammalian humerus. But the y-interceptions are very

TABLE 2

Theoretical masses (in grams), calculated by means of the predictive value of the equations obtained in this study, for birds of 100 g, 1,000 g and 10,000 g of body mass, respectively.

	100 g	1,000 g	10,000 g
Humerus mass	0.351	3.568	36.264
Ulna-radius mass	0.325	3.173	31.008
Femur mass	0.160	2.270	32.143
Tibiotarsus + fibula mass	0.268	3.582	47.873
Tarsometatarsus mass	0.146	2.099	30.276

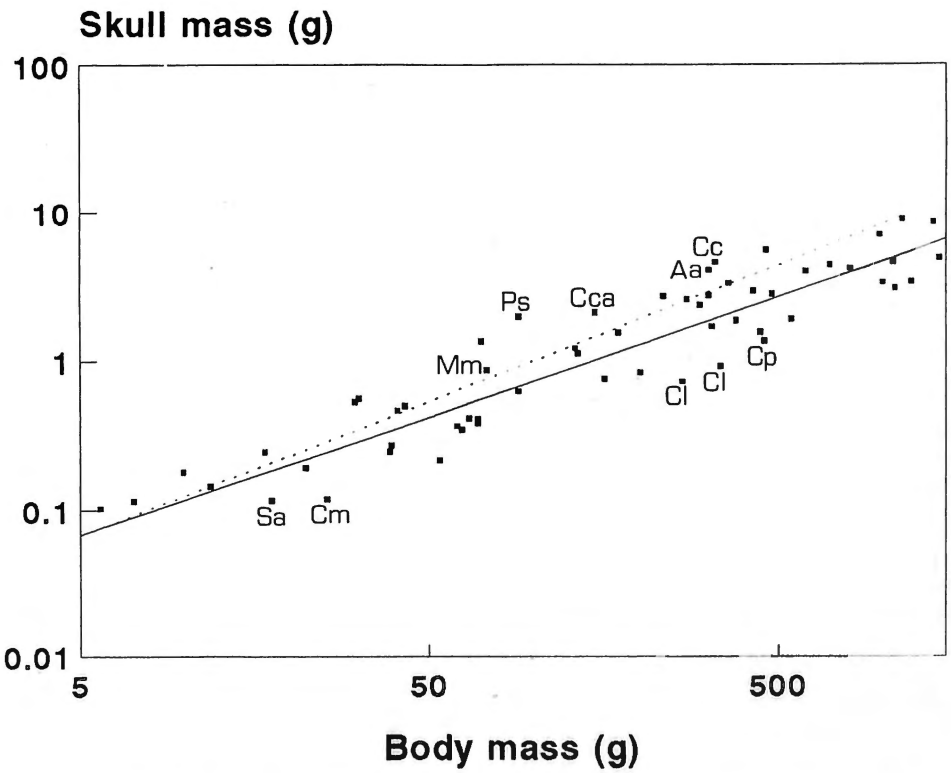

Fig. 1. — Graph on logarithmic coordinates of the skull mass to body mass, both in grammes. Dotted and solid line correspond to mammal and bird regressions, respectively. The points corresponding to *Cygnus olor* and *Struthio camelus* were excluded in all the plotters. Abbreviations : Aa, *Amazona aestiva* ; Cc, *Corvus corone* ; Cca, *Cyanocorax caeruleus* ; Cl, *Columba livia* ; Cm, *Calidris minuta* ; Cp, *Columba palumbus* ; g, grams ; Mm, *Myopsitta monachus* ; Ps, *Poicephalus senegalus* ; Sa, *Sylvia atricapilla*.

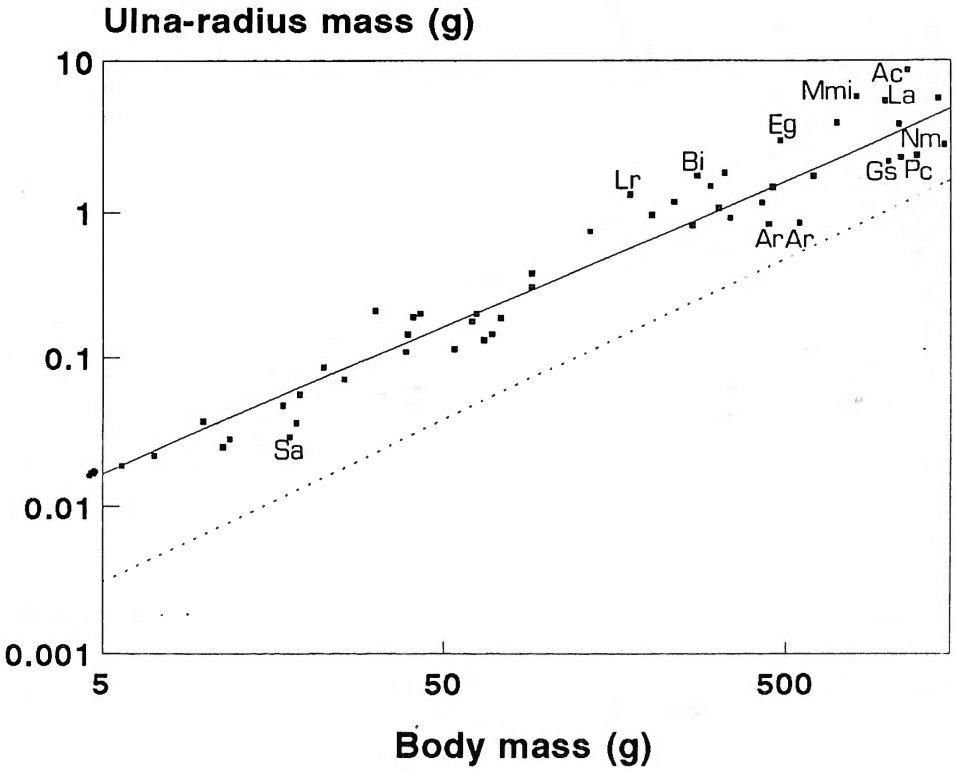

Fig. 2. — Graph on logarithmic coordinates of the ulna-radius mass to body mass, both in grammes. Abbreviations : Ac, *Ardea cinerea*; Ar, *Alectoris rufa*; Bi, *Bubulcus ibis*; Eg, *Egretta garzetta*; Gs, *Gallus sonnerati*; La, *Larus argentatus*; Lr, *Larus ridibundus*; Mmi, *Milvus migrans*, Nm, *Numida meleagris*; Pc, *Phasianus colchicus*. For other abbreviations and details, see figure 1.

close (0.46 and 0.51, respectively). This means that lengths are likely to be very similar for small body masses, but they become far larger in birds than in mammals when the body mass increases. This is not the case for skeletal masses : the slopes for birds and small mammals are practically parallel in such a way that the ratio is constant. In fact, the present results are completely opposed to the generalized assumption that avian skeletal structures are lighter than the corresponding mammalian structures. However, since PRANGE *et al.* (1979) found that the scaling of the mass of the whole skeleton to body mass is not significantly different in birds and mammals, some bony structures other than the skull must be heavier in mammals than in birds. At the same time, the prediction of PRANGE *et al.* (1979) « ...the structural material that is saved in the long pneumatized wing bones has had to be added to the more robust leg bones » would seem to be unjustified. In Table 2 the masses of the different long bones of three hypothetical birds of 100 g, 1,000 g and 10,000 g of body mass, respectively, are shown. These figures have been calculated using the predictive value of the equations obtained in this research (Table 1). It

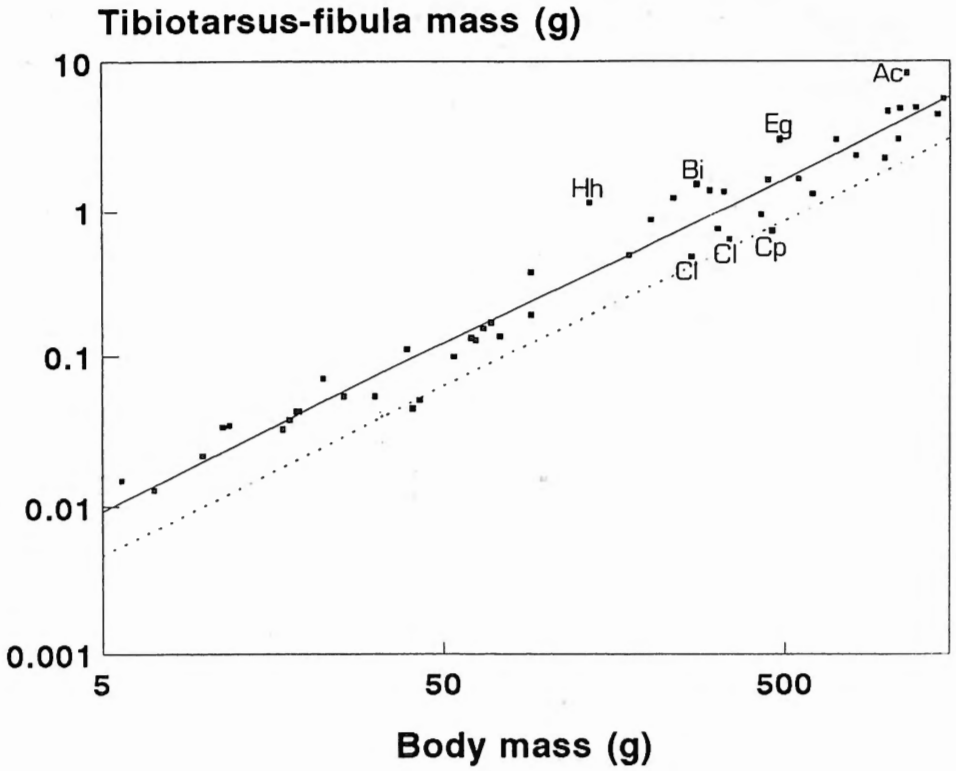

Fig. 3. — Graph on logarithmic coordinates of tibiotarsus-fibula mass to body mass, both in grammes. Abbreviations : Hh, *Himantopus himantopus*. For the other abbreviations and symbols, see figures 1 and 2.

can be seen that in the case of a bird of 100 g, the humerus and ulna-radius are heavier than any hindlimb bone (femur, tibiotarsus and fibula, tarsometatarsus). For a body mass of 1,000 g only the tibiotarsus and fibula reach a value comparable to those of the fore limb long bones. Only in the extreme case of 10,000 g are the tibiotarsus and fibula together the heaviest skeletal structures and is the femur a little heavier than the ulna-radius, but still lighter than the humerus. In fact, 10 kg is not a normal body mass for a flying bird. As far as we know, only bustards arrive at this range of body mass (CRAMP, 1980).

In Fig. 1 skull mass values are plotted against body masses. Psittaciformes display particularly heavy skulls (Aa, *Amazona aestiva* ; Ps, *Poicephalus senegalus* ; Mm, *Myopsitta monachus*) and the Corvidae studied are also placed above the regression line (Cc, *Corvus corone* ; Cca, *Cyanocorax caeruleus*). Clearly below the regression line are found the Columbiformes (Cp, *Columba palumbus* ; Cl, *Columba livia*) and one species of Charadriiformes (Cm, *Calidris minuta*) and one species of Passeriformes (Sa, *Sylvia atricapilla*).

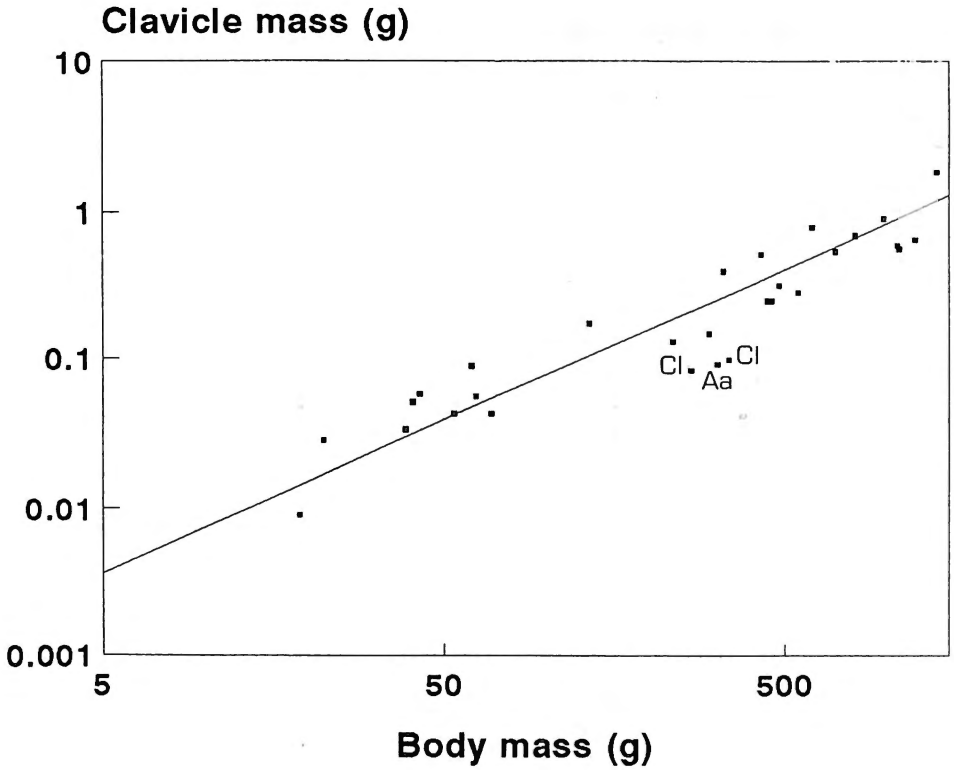

Fig. 4. — Graph on logarithmic coordinates of clavicle mass to body mass, both in grammes. For abbreviations, see figure 1.

Fig. 2 shows the plotting of the ulna-radius masses. In particular, above the regression line we can recognize the Ciconiiformes that were studied (Ac, *Ardea cinerea* ; Eg, *Egretta garzetta* ; Bi, *Bubulcus ibis*) the Laridae (La, *Larus argentatus* ; Lr, *Larus ridibundus*) and *Milvus migrans* (Mmi). Inversely, all the Galliformes studied are clearly below the regression line (Nm, *Numida mealeagris* ; Pc, *Phasianus colchicus* ; Gs, *Gallus sonnerati* ; Ar, *Alectoris rufa*). The distribution of the humerus values is very similar to that discussed for the ulna-radius.

Whilst the dispersion of femur points is very small, some of the tibiotarsus-fibula values are clearly separated from the regression line (Fig. 3). For example, the Ciconiiformes species studied (Ac, *Ardea cinerea* ; Eg, *Egretta garzetta* ; Bi, *Bubulcus ibis*) and *Himantopus himantopus* (Hh) are above the regression line. The Columbiformes studied (Cp, *Columba palumbus* ; Cl, *Columba livia*) are situated below the regression line. The tarsometatarsus points shows a distribution pattern very similar to that of the tibiotarsus.

The skeletal elements of both girdles, with the single exception of the clavicle, show practically no dipersion, as might be expected from the sample sizes and the

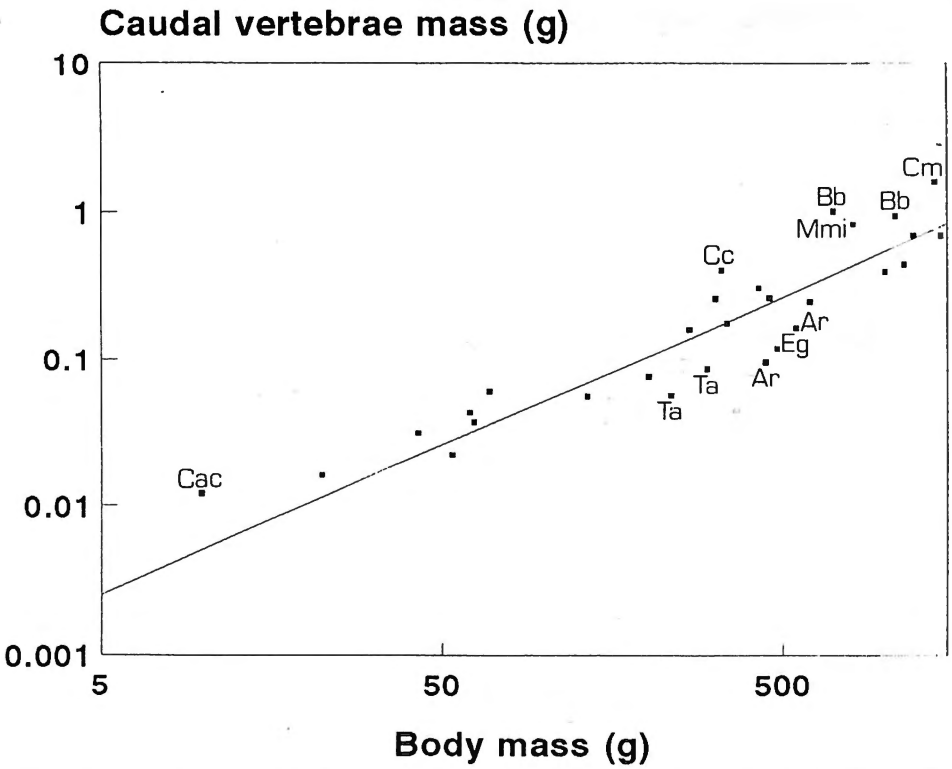

Fig. 5. — Graph on logarithmic coordinates of caudal vertebrae mass to body mass, both in grammes. Abbreviations : Bb, *Buteo buteo*; Cac, *Carduelis carduelis*; Cm, *Cairina mostacha*; Ta, *Tyto alba*. For the other abbreviations, see figures 1 and 2.

correlation coefficients. Even the dispersion of clavicle values is less marked than those found for long bones (Fig. 4).

Within the vertebral elements, the thoracic region is that with the minimum dispersion, whilst the caudal vertebrae show the maximum dispersion (Fig. 5).

In general it seems that two orders (Galliformes and Columbiformes) show a tendency to display lighter skeletal structures, at least in the cases illustrated by the figures.

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ON THE FUNCTIONAL SIGNIFICANCE OF THE LOSS OF THE INTERHYAL DURING ONTOGENY IN *CLARIAS GARIEPINUS* BURCHELL, 1822 (TELEOSTEI : SILUROIDEI)

by

DOMINIQUE ADRIAENS and WALTER VERRAES
University of Ghent, Institute of Zoology
K.L. Ledeganckstraat 35, B-9000 Gent (Belgium)

SUMMARY

In larval *Clarias gariepinus* the cartilaginous interhyal is continuous with the dorsal and ventral part of the hyoid arch. During later ontogeny the interhyal becomes reduced and is completely lost in the adult specimens. The connection between the suspensorium and the hyoid is replaced by a stout ligament, the ligamentum hyomandibulo-ceratohyale. It is hypothesised that this will reduce the mobility of the hyoid bar. Some specific lifestyle adaptations of *C. gariepinus* overrule the necessity of highly mobile hyoid bars. Large hyoid bar depressions would destabilise the dorso-ventrally flattened skull when resting on the bottom. As the Clariidae are able to perform aerial respiration, no large hyoid depression is needed for an extensive aquatic respiration. As *C. gariepinus* is not a suction feeding species, no sudden volume increase of the orobranchial cavity is required through a large hyoid depression. Morphological evidence indicating a restricted possibility of the depression of these bars consists of a small skin fold between the hyoid and the lower jaw, allowing a restrained ventral excursion of the rostral tip of the hyoid. Due to the strongly dorso-ventrally flattened skull the suspensorium is relatively small, in its dorso-ventral direction, which restricts the lateral displacement of the caudal tip of the hyoids during depression. A short sternohyoideus muscle connects the hyoid bar to the pectoral girdle, thus enabling a restricted movement of the bar during contraction. The branchiostegal membrane is rather firm and can be little folded and unfolded.

Keywords : interhyal, hyoid, *Clarias*, ontogeny, functional morphology

INTRODUCTION

The interhyal, also referred to as the stylohyal (DAGET, 1964), forms in most teleosts the connection between the dorsal and ventral part of the hyoid arch, respectively the hyosymplecticum and the ceratohyal. In a generalised teleost this interhyal initially consists of a cartilaginous bar-like structure which is already or becomes isolated from the cartilaginous hyoid arch early during ontogeny. In

C. gariepinus, and in most Siluroidei, the interhyal remains continuous with both the hyosymplecticum and the ceratohyal (HOEDEMAN, 1960 ; HOWES and TEUGELS, 1989 ; ARRATIA, 1990). In a generalised teleost the cartilaginous interhyal becomes ossified during ontogeny, except at its two articulating ends which come in contact with the hyomandibular and the posterior ceratohyal bones. In catfish the interhyal, if present, becomes ossified or remains cartilaginous. An ossified interhyal is present in *Callichthys*. A rudimentary interhyal can be observed in some primitive species, such as *Diplomystes*, *Nematogenys* and *Loricaria*, where the dorsal articulation between the interhyal and the hyomandibular bone is lost (ARRATIA, 1990). In *C. gariepinus* a reduction of the interhyal occurs during ontogeny until it is completely lost, already in juvenile specimens. The loss of the interhyal seems to be a feature which is present in several groups of Ostariophysi. In the gonorhynchiform *Phractolaemus* (Phractolaemidae) (DAGET, 1964) and the cypriniform *Gobio gobio* (Ostariophysi : Cyprinidae) (VANDEWALLE, 1975) the interhyal is lacking. In the Siluroidei the absence of the interhyal seems to be general, except for some, already mentioned, species (ARRATIA, 1990).

Commonly, in the adult teleostean situation, the interhyal forms two articulation facets, with the posterior ceratohyal bone and the hyomandibular bone, respectively. In general these articulations are of the ball and socket type, although variation is present in some teleosts. In several cases the interhyal-ceratohyal connection becomes ligamentous (KARRER, 1967 ; OSSE, 1969 ; ANKER, 1974 ;1989 ; BIRDSONG, 1975 ; VANDEWALLE *et al.*, 1982). In *Blennius pholis* (Perciformes : Blenniidae) also the dorsal articulation becomes ligamentous (VANDEWALLE *et al.*, 1982). In some cases some additional ligaments are present, connecting the interhyal to surrounding structures other than the posterior ceratohyal bone. In *Gasterosteus* (Gasterosteiformes : Gasterosteidae) a ligamentum interhyalo-suspensoriale is present connecting the interhyal to the preopercular bone (ANKER, 1974), as is the case in *Microgobius* (Perciformes : Gobiidae) (BIRDSONG, 1975) and in *Haplochromis* (Perciformes : Cichlidae) (ANKER, 1989). In *Ammodytes* and *Embolichthys* (Perciformes : Ammodytidae) a ligament is present between the bony interhyal and the interopercular bone (PIETSCH and ZABETIAN, 1990). In those teleosts where the interhyal seems to be absent, a ligament is present between the suspensorium and the hyoid (VANDEWALLE, 1975 ; ARRATIA, 1990). This is also the case for *C. gariepinus* where a stout ligament runs from the hyomandibular bone to the posterior ceratohyal bone. The absence of the interhyal in adult *C. gariepinus* and the presence of a ligament was already noticed by NAWAR (1954).

The loss of the interhyal and its replacement by a stout ligament in *C. gariepinus* will probably have an influence on the mobility of the hyoid. As stated by ANKER (1989), the interhyal plays an important role in the four bar sytem of the hyoid, the interopercular bone, the lower jaw and the suspensorium. In this system the length of the interhyal is related to the movement range of the hyoid, and thus of the lower jaw. Apart from their role in the opening of the mouth, the hyoid bars play an important role in the depression of the mouth floor and the lateral expansion of the branchial cavity (AERTS, 1991) which is necessary for generating a negative pressure in the mouth cavity.

ARRATIA (1990) stated that the loss of the interhyal and its replacement by a ligament is a result of the strongly dorso-ventral flattening of the skulls. This paper deals with the functional significance of the loss of the interhyal in *C. gariepinus* and its possible effect on the movements of the hyoid. The interhyal and surrounding structures are studied in three ontogenetic stages of *C. gariepinus*.

MATERIAL AND METHODS

Specimens of *Clarias gariepinus* BURCHELL, 1822 of three ontogenetic stages were used to describe the morphology of the interhyal element and surrounding structures. Fertilised eggs were obtained from the Laboratory of Ecology and Aquaculture (Catholic University of Leuven, Belgium) and were raised at a temperature of 25° C. At different moments (8 days and 120 days after fertilization) specimens where sedated in MS 222. An 8 days old specimen (TL = 7.77 mm, SL = 7.19 mm, PAL = 3.76 mm) (PAL = PreAnal Length) was fixated in a paraformaldehyde-glutaraldehyde solution, the 120 days old fish (TL = 50.15 mm, SL = 46.75 mm, PAL = 23.90 mm) in a buffered 4% formaldehyde solution. Both were used for serial sectioning. The former was embedded in EPON. The sections of 2 µm were stained with toluidine. The 120 days old fish were embedded in Paraplast. The 5 µm thick serial sections were stained with an improved trichrome staining (MANGAKIS *et al.*, 1964).

Other juvenile specimens were used for clearing and staining *in toto*, according to HANKEN and WASSERSUG (1981). These where commercially raised specimens with an age of approximately 100 days, obtained from Mr. FLEURE (Someren, the Netherlands). One specimen was used for drawing (TL = 144.90 mm, SL = 125.45 mm, PAL = 67.10 mm), another was used for further observations (TL = 149.90 mm, SL = 132.50 mm, PAL = 68.20 mm). Still another specimen was used for dissection and drawing (TL = 154.05 mm, SL = 136.20 mm, PAL = 71.30 mm).

The serial sections were studied and drawn using a WILD M12 light microscope, equiped with a camera lucida. Three-dimensional reconstructions were made using a commercial software package. A WILD M5 stereo-microscope with camera lucida was used for studying the cleared and stained specimens.

RESULTS

In the examined specimens it is hypothesised that the morphological state of development is more likely to be related to the body length of the fish instead of to the age. It was observed in the specimen of *C. gariepinus* of 120 days (SL = 46.75 mm) that the interhyal is still present, although in a reduced form. In the younger, but larger specimen (age of 100 days, SL = 125.45 mm) the interhyal is already absent. The difference in length of the two specimens is due to the fact that the 100 days old specimen was raised under commercial conditions, thus obtaining perhaps maximal growth. In this paper the ontogenetic development of

the interhyal and surrounding structures will be discussed in a non-chronological order, but in relation to increasing standard length.

1. Standard length 7.19 mm (8 days) :

In early ontogeny one continuous cartilaginous plate is formed, containing both the mandibular and hyoid arch, except for the pars palatina of the palatoquadratum, as was observed in 5.2 mm specimens by SURLEMONT *et al.* (1989). This part has become isolated from the mandibular arch, which is a typical feature of siluroid fishes (ALEXANDER, 1965 ; GOSLINE, 1975). In the examined specimen of 8 days, the Meckelian cartilage had already become separated from the pars quadrata of the palatoquadratum (Fig. 1). The interhyal, on the contrary, is still a continuous cartilaginous bar between the ventral and dorsal parts of the hyoid arch. Muscles related to the depression and elevation of the hyoid can already be observed. The sternohyoideus muscle, which enables the depression, inserts on a ventral process of the anterior copula. In the 5.2 mm fry, no such an insertion was observed

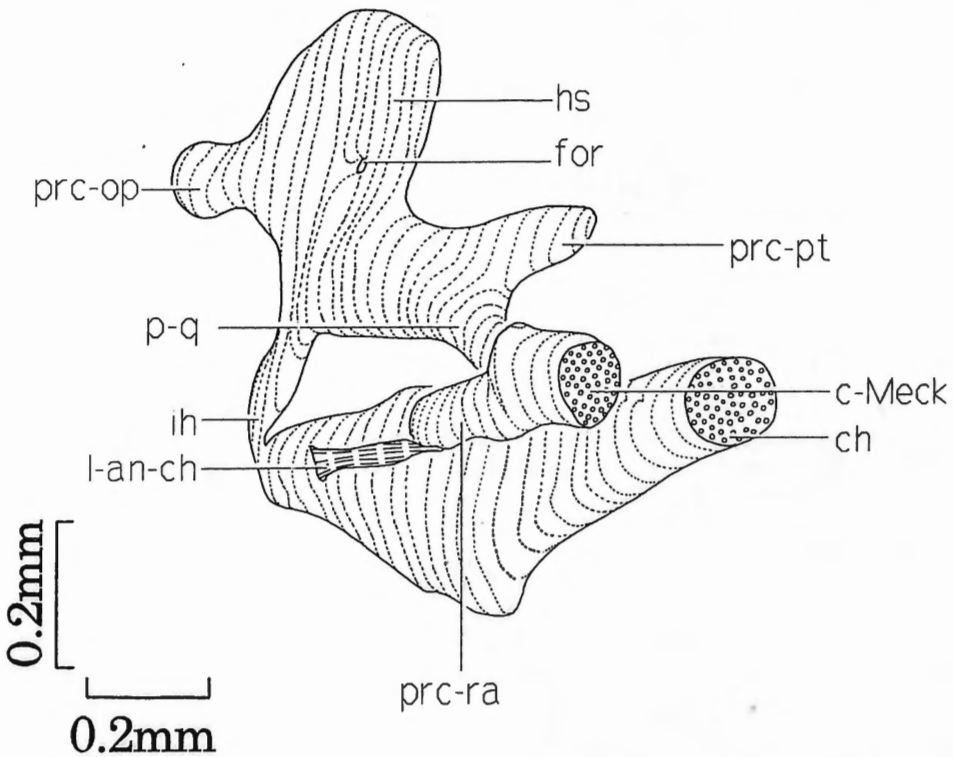

Fig. 1. — Graphical 3D-reconstruction : oblique, anterio-lateral view (right side) of cartilaginous suspensorium, lower jaw (partim) and ceratohyal (partim) of *C. gariepinus* (SL = 7.19 mm) (small circles indicate cartilage) (palatinum not drawn) (Abbreviations see page 152).

yet (SURLEMONT *et al.*, 1989). The elevation muscle, the hyoid protractor muscle, did reach the lower jaw.

No ligament could yet be found between the ceratohyal and the suspensorium but a ligamentum angulo-ceratohyale was already present.

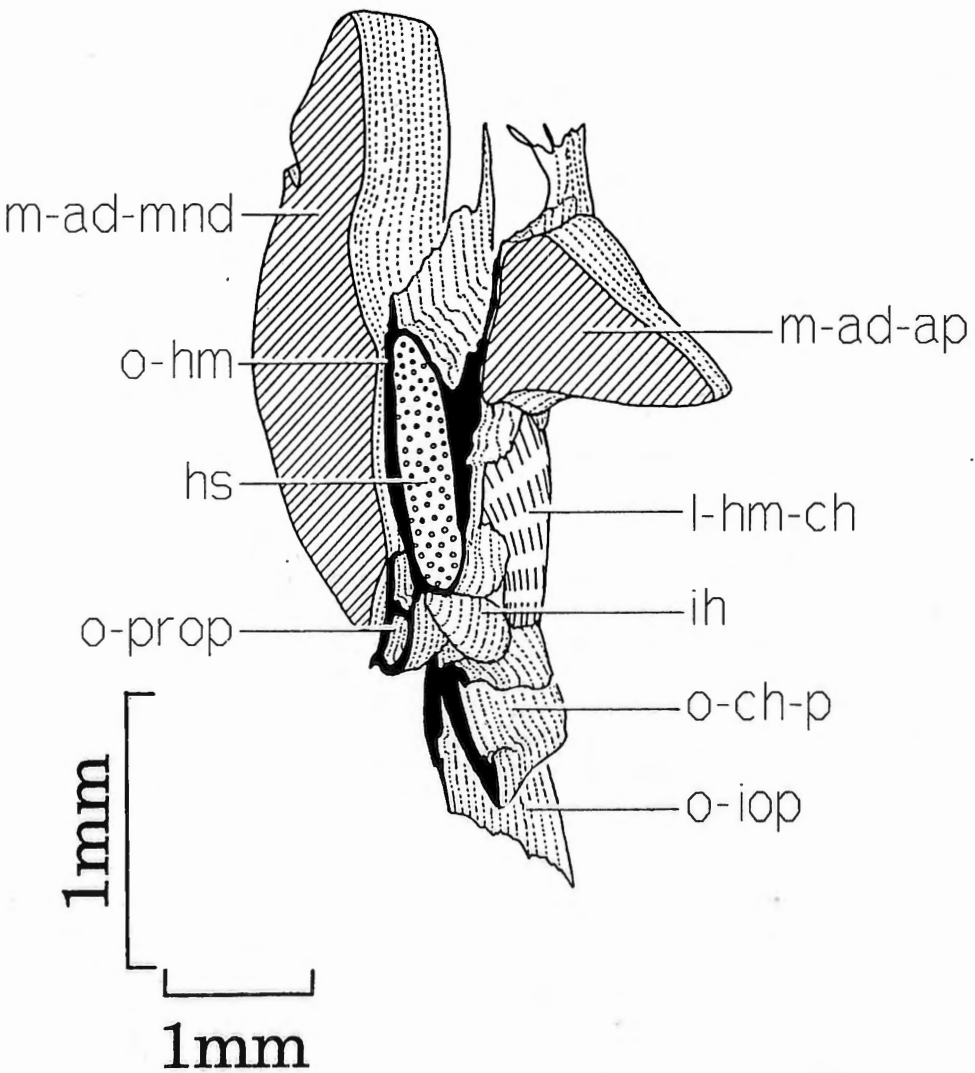

Fig. 2. — Graphical 3D-reconstruction : oblique, posterio-medial view of the suspensorium (right side) at the level of the interhyal and the ligamentum hyomandibulo-ceratohyale of *C. gariepinus* (SL = 46.75 mm) (small circles indicate cartilage, black areas indicate bone, hatched areas indicate muscles).

2. Standard length 46.75 mm (120 days) :

At this stage all the suspensorial ossifications are present : the quadrate bone, the metapterygoid bone, a sesamoid bone refered to as the 'entopterygoid' type 4 according to ARRATIA (1992), the hyomandibular bone and the preopercular bone. The symplectic bone is not present, which is a general feature of most siluroid teleosts (ALEXANDER, 1965 ; ARRATIA, 1990). The interhyal has become separated from the ceratohyal (Fig. 2), but seems to be still continuous with the hyosymplecticum. The non-ossified interhyal is situated at the ventro-medial side of the hyomandibular bone, medial to the connection between the latter and the preopercular bone. Ventrally the interhyal articulates with the posterior part of the posterior ceratohyal bone. The histological aspect of the interhyal differs from that of the ceratohyal and the hyosymplecticum. In the latter a lot of extracellullar matrix, surrounding small chondrocytes is present, whereas the interhyal has a small amount of matrix, separating large cells.

Medial to the interhyal a stout ligament is present, connecting the hyomandibular bone to the posterior ceratohyal bone (Fig. 2). This ligamentum hyomandibulo-ceratohyale is attached to the medial face of the hyomandibular bone, ventrally to the posterior insertion of the arcus palatini adductor muscle, and to the dorsal face of the posterior ceratohyal bone, right in front of the articulation with the interhyal (Fig. 2).

The muscles involved in the movements of the hyoids are completely developed and their presence is comparable with the situation in the 125.45 mm specimens. The sternohyoideus muscle is a relative short but broad muscle connecting the shoulder girdle to the hyoid, through the urohyal bone (WINTERBOTTOM, 1974). The muscle is attached to the rostral margin of the cleithral bone, along the whole length of the ventral part (Fig. 3B). Rostrally, the muscle inserts onto the forked urohyal bone. This bone is attached to the rostral tips of the two ventral hypohyal bones through two ligaments, *i.e.* the ligamenta urohyalo-hypohyalia. The hyoid protractor muscle inserts on the ventral face of the posterior part of the anterior ceratohyal bone, and the anterior part of the posterior ceratohyal bone (Fig. 3A). Rostrally the insertion of the muscle is spread out. The superficial fibers insert on the bases of the mandibular barbels, whereas the deeper ones insert on the ventral face of the lower jaws.

The lower jaw is connected to the ceratohyal bone in a direct and an indirect way. The direct connection occurs through the ligamentum angulo-ceratohyale, which has become a stout ligament. It runs from the caudalmost tip of the lower jaw to the lateral face of the posterior ceratohyal bone (Fig. 3B). Indirectly, the lower jaw is connected to the posterior ceratohyal bone through the interopercular bone : a ligamentous connection is present (1) between the angular bone and the interopercular bone and (2) between the interopercular bone and the posterior ceratohyal bone. The ligamentum angulo-interopercularе inserts on the caudalmost tip of the lower jaw, lateral to the ligamentum angulo-ceratohyale (Fig. 3A-B).

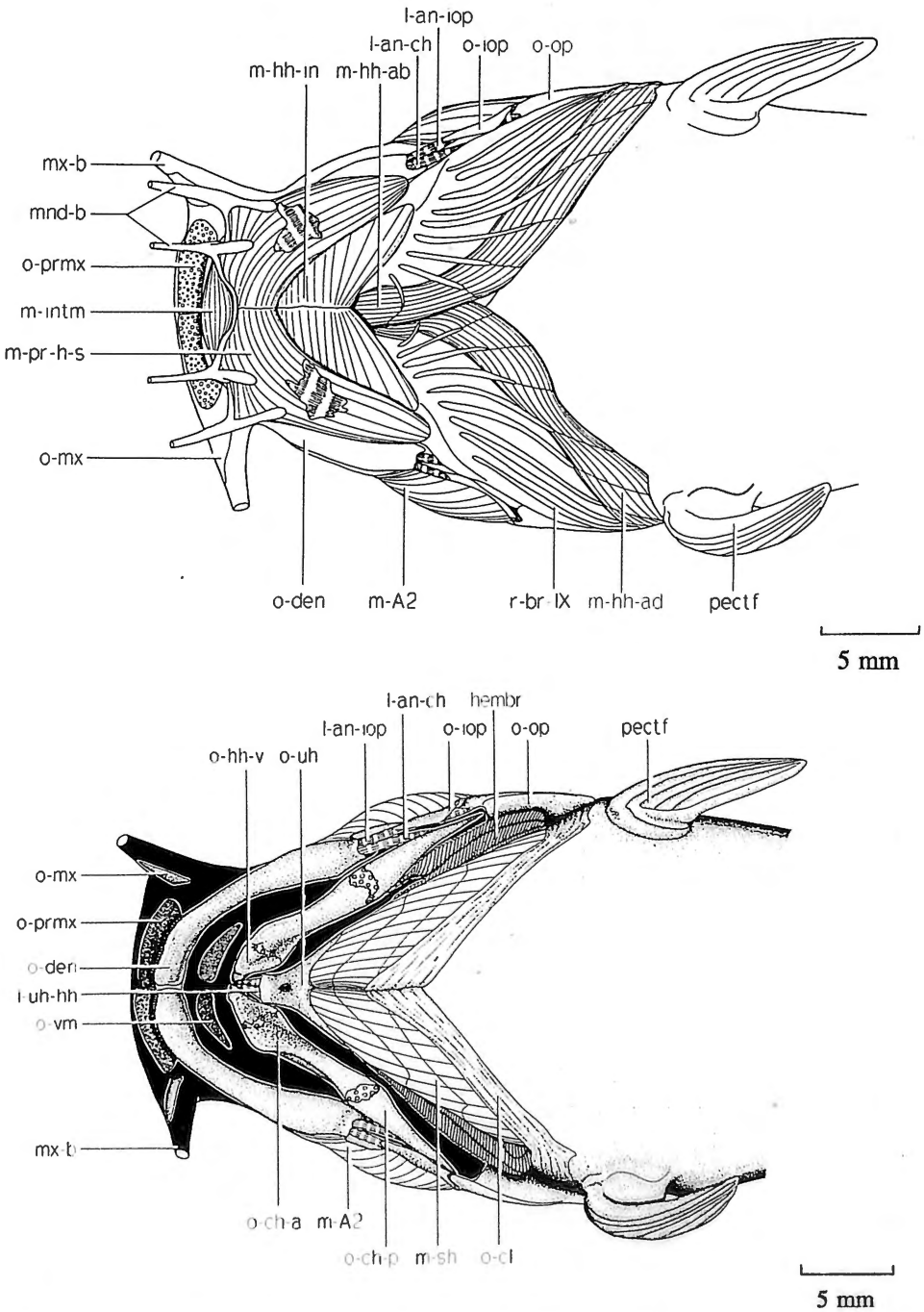

Fig. 3. — Ventral view of a juvenile *C.gariepinus* (SL = 136.20 mm) : A. skin removed ; B. superficial muscles and branchiostegal membrane removed (small circles indicate cartilage).

3. Standard length 125.45 mm (100 days) :

At this stage the interhyal has become completely reduced. The only firm connection between the posterior ceratohyal bone and the suspensorium is the strongly developed ligamentum hyomandibulo-ceratohyale (Fig. 4). It is attached to a ridge on the medial face of the hyomandibular bone, and runs up to the dorsal face of the posterior part of the hyoid.
The description of the muscles involved in the depression and elevation of the hyoid is comparable to that given for the 46.75 mm specimens.

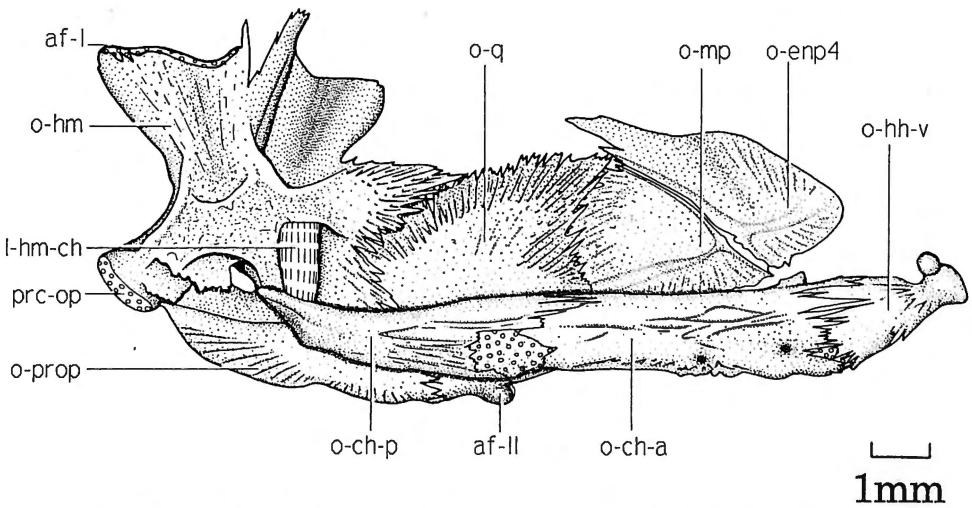

Fig. 4. — Medial view (left side) of suspensorium and hyoid of a juvenile *C. gariepinus* (SL = 136.20 mm) (small circles indicate cartilage).

DISCUSSION

In juvenile specimens of *C. gariepinus* the ceratohyal is ligamentously connected to the lower jaw and to the interopercular bone. However in larval specimens (7.19 mm) only the former, the ligamentum angulo-ceratohyale, could be distinguished. The latter was not present yet, as well as the interopercular bone itself. The ligamentum angulo-ceratohyale plays an important role in the mouth opening mechanism, partially generated through the retraction of the ceratohyal (MULLER, 1987). This mechanism could eliminate the need for a passive recovery depression of the lower jaw through the cartilaginous connection between the lower jaw and the suspensorium, of its adduction by contraction of the mandibular adductor muscle as was observed in the 5.2 mm fry (SURLEMONT *et al.*, 1989). The ligament was found in most other siluroid fishes as well (SCHAEFER and LAUDER, 1986). In the 46.75 mm specimens the ligament between the ceratohyal and the interopercular bone could be distinguished, as well as the ligament between the interopercular

bone and the lower jaw, the latter inserting laterally to the ligamentum angulo-ceratohyale on the lower jaw (Fig. 3A-B). As is the case for the latter, the ligamentum angulo-interoperculare as well plays an important role in the opening of the mouth. The ligament takes part in the four bar mechanism, consisting of the interopercular bone, the opercular bone, the suspensorium and the lower jaw (AERTS and VERRAES, 1984).

A shift can thus be observed in mouth opening mechanisms during ontogeny in *C. gariepinus*, going from a passive recovery depression of the cartilaginous connection between the lower jaw and the suspensorium, to a bar system which depresses the lower jaw by the depression of the hyoid bars, mediated by the sternohyoideus muscle and the ligamentum angulo-ceratohyale. Later in ontogeny a second bar system, the opercular four bar system (opercular bone, interopercular bone, suspensorium and lower jaw), may play a role in the mouth opening which is then coupled to the above mentioned hyoid bar system.

ANKER (1989) stated that the range of the movement of the hyoid increases with a longer interhyal. The loss of the interhyal and its functional replacement through a ligament must have an effect on the movements of the hyoid. Moreover, the rotation of an interhyal can be related to the abduction of the lower jaws and the abduction and the rotation of the hyoids (ANKER, 1974). The replacement of a skeletal element through a ligament can be functionally interesting when only tensile forces are applied on the ligament. When compressed, the ligament would of course crumple. In the case of *C. gariepinus* this implicates that the ventral excursion of the posterior part of the hyoid, during its forward and backward swinging, could be reduced, so that mainly an anterior-posterior translation is performed (Fig. 5).

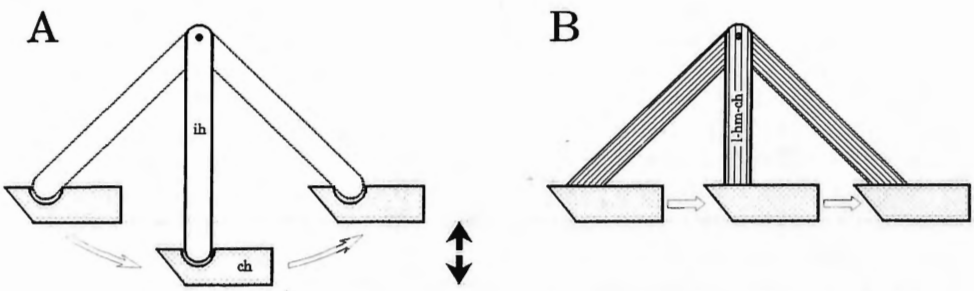

Fig. 5. — Scheme : A. rotation of the interhyal with a ventral excursion of the hyoid ; B. ligament replacing the interhyal with an anterior-posterior translation of the hyoid.

According to SURLEMONT *et al.* (1989) the functional significance of a cartilaginous interhyal, which is continuous with the dorsal and ventral part of the hyoid arch, is related to the mechanical properties of cartilage. Such a connection assists a passive recovery displacement of the depressed hyoid. The depression of the hyoid can be accomplished by the contraction of the sternohyoideus muscle. In the 7.19 mm fry this muscle was already functional, which was not the case in the

5.2 mm fry (SURLEMONT *et al.*, 1989). The hyoids can normally be elevated by the contraction of the hyoid protractor muscle. In the 7.19 mm fry this muscle although the inserts on the lower jaw, as well elevation can then be generated by the elasticity of the cartilage of the interhyal. Once the connection between the interhyal and the ceratohyal is lost, the muscle takes over.

As the interhyal is lacking in adult *C. gariepinus* it could be expected that this would affect the rotation possibilities, more specifically a depression, of the hyoid. Some morphological features supporting this hypothesis where observed :

1. The rostralmost tip of the hyoid is connected to the lower jaw through skin and connective tissue. The degree of depression of the hyoids partially depends on the length of that skin and connective tissue. Cross sections (Fig. 6A) show that the fold between the jaw and the hyoid is rather small, allowing only a small ventral excursion of the hyoid tip. As the depression of the lower jaw itself is restricted by a kind of lateral skin valve between the maxillary barbel and the lower jaw, this will not increase the depression possibility of the hyoid.

2. During depression of the hyoids their posterior tips are abducted. This results in the lateral rotation of the suspensorium (AERTS, 1991). A strong abduction of the suspensoria would require a strongly developed articulation with the skull. In most fish species, where the abduction of the suspensorium, related to the depression of the hyoid, is important, the suspensorium articulates rostrally with the skull through the palatine and the ethmoid part of the neurocranium and caudally through two consecutive ball and socket articulations between the hyomandibular bone and the skull (*e.g.* in Badidae (BARLOW *et al.*, 1968), in Percidae (OSSE, 1969), in Gasterosteidae (ANKER, 1974), in Serranidae (BENMOUNA *et al.*, 1984), in Gobiidae (MESTERMANN and ZANDER, 1984), in Pleuronectiformes (BRILL, 1988), in Cyprinidae (ARRATIA, 1992)). In *C. gariepinus*, and catfish in general, the suspensorium has lost its rostral articulation between the palatine and the skull. As already mentioned, the palatine has become an isolated structure which plays an important role in the movements of the maxillary barbel (ALEXANDER, 1965 ; GOSLINE, 1975). Also the ball-like articulations are lacking on the hyomandibular bone (Fig. 4). Instead, a hardly distinguishable cartilaginous articulation ridge can be observed. This morphological feature suggests that the rotation possibilities of the suspensorium are reduced. Another fact is that the height of the skull, which is dorso-ventrally flattened, is reflected in the height of the suspensorium. As a decrease in the height of the suspensorium will result in a decrease of the lateral displacement of the posterior tip of the hyoids, this displacement will be restricted in *C. gariepinus*. ALEXANDER (1970) stated that in fish with dorso-ventrally flattened heads the depression of the hyoids plays a relatively more important role for increasing the volume of the orobranchial cavity than in fish with lateral depressed heads, where the abduction of the suspensorium is far more important. Due to the dorso-ventrally flattened skull, a small depression of the hyoids will generate a relatively large increase in volume.

3. Muscular evidence for a reduced depression of the hyoids is present as well. The sternohyoideus muscle is responsible for the depression of the hyoid. In those teleosts where a large depression is needed, the sternohyoideus muscle is rather long

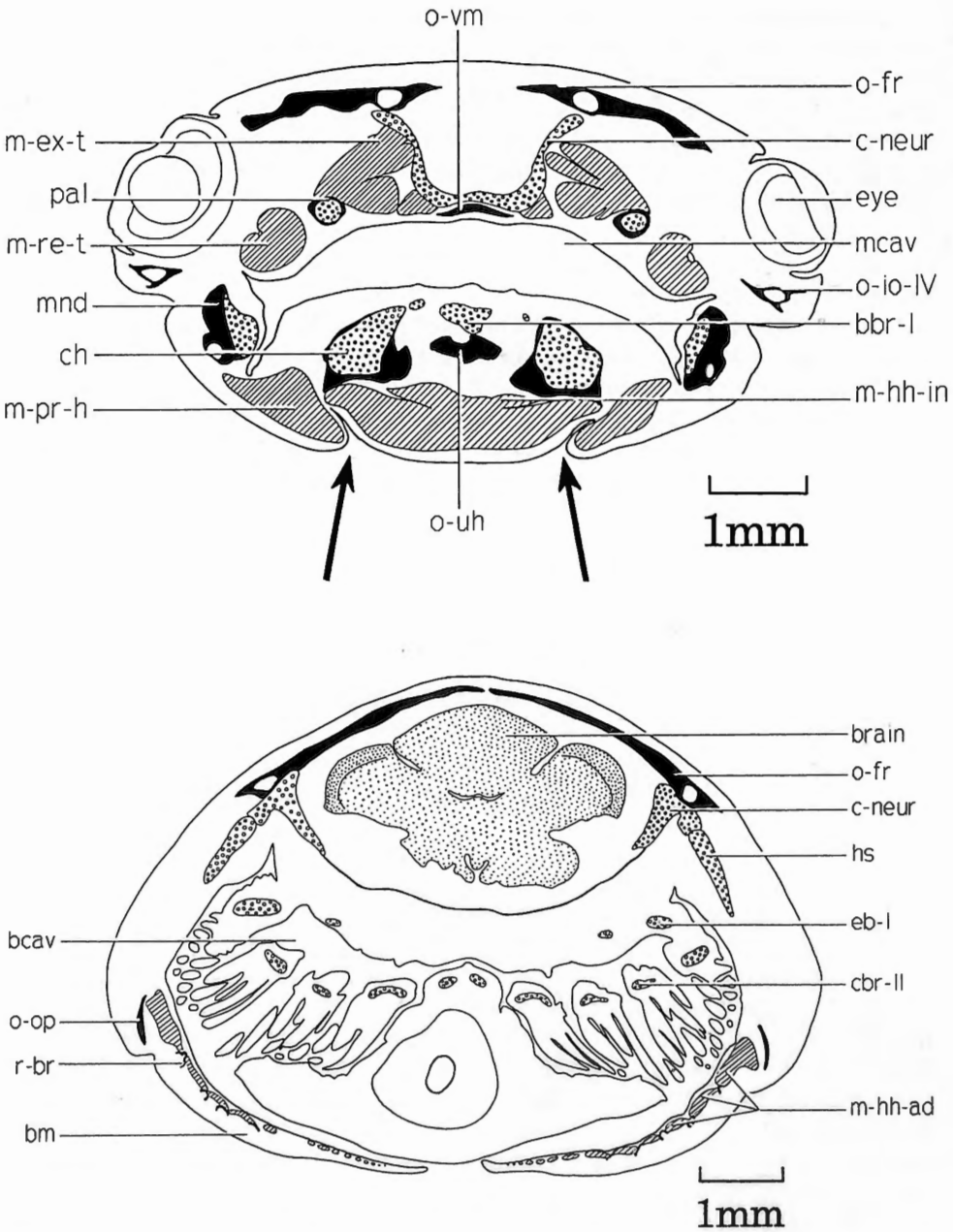

Fig. 6. — Cross section of juvenile *C. gariepinus* (SL = 46.75 mm) : A. at the level of the eyes showing the small fold between the hyoid and the lower jaw (arrows) ; B. at the level of the anterior part of the opercular bone showing the firm, unfolded branchiostegal membrane (small circles indicate cartilage, black areas indicate bone, hatched areas indicate muscles).

and slender (ANKER, 1974; 1989) (*e.g.* in gobies (ADRIAENS, *et al.*, 1993)). In *C. gariepinus* the muscle consists of three myomeres, separated by myocommata. The muscle is enlarged laterally, but is rather short in the anterior-posterior direction (Fig. 3B), which results in a larger contraction force but a reduced displacement of the rostral tip of the hyoid during contraction. What has to be taken in account is the cooperative function of the inferior obliquus muscle, which is a hypaxial body muscle inserting on the posterior border of the cleithral bone. The muscle plays an important role in the retraction of the pectoral girdle, and thus in the retraction of the hyoid through the sternohyoideus muscle (MULLER, 1987). However, cross sections show that in *C. gariepinus* the ventral part of the inferior obliquus muscle is rather small.

4. A large expansion of the orobranchial cavity would require an expanding branchiostegal membrane. This membrane can be extended from the folded situation because the skin is supported by a series of branchiostegal rays. In *C. gariepinus* this membrane is well developed and is rather firm (Fig. 3A). However, cross sections show that the thick branchiostegal membrane is not folded (Fig. 6B), which implicates a restricted expansion possibility of the membrane, and thus of the orobranchial cavity.

5. Aquarium observations of live material show that *C. gariepinus* exert a restricted depression of the hyoid during respiration phases. Also manipulation of fixed material suggests that little depression of the hyoid is possible.

Some additional arguments, related to specific lifestyle adaptations of *C. gariepinus*, contribute to the need of a restricted depression of the hyoid :

1. Like several benthic fishes, *C. gariepinus* has a strongly, dorso-ventrally flattened head. If, when resting on the bottom, the mouth floor should be depressed to a far extent during repiration, the stabilisation by the flattened head would be overridden.

2. A large depression of the hyoid for respiration is probably not required. Clariidae are able to perform aerial respiration by means of a suprabranchial organ, which is a modified, posterior part of the branchial arches (ALEXANDER, 1965; HELLIN et CHARDON, 1981). This structural adaptation enables the species to survive in tropical swamps and other ponds with a low level of oxygen. *Clarias* is also known to make rather important terrestrial excursions between two ponds, which is facilitated by aerial respiration (BABIKER, 1984). The hyoids do play an important role in the transport of the swallowed air. During aerial inspiration at the water surface, the elevated hyoids are depressed, resulting in the suction of the air. Then they are elevated through muscle contraction in order to press the air bubble from the orobranchial cavity into the suprabranchial cavity. A second elevation of the bars is noted during expiration when the bubble is transported from the suprabranchial cavity to the outside through the opercular slits (HELLIN et CHARDON, 1981 ; VANDEWALLE and CHARDON, 1991). In abnormal *C. gariepinus*, where the hyoid bars were immobilised, VANDEWALLE and CHARDON (1991) noted that these fish were still able to perform aquatic respiration due to only opercular

movements. So neither for terrestrial nor for aquatic ventilation large hyoid depression seems to be needed in *C. gariepinus*.

3. A sudden volume increase of the orobranchial cavity is necessary for suction feeding fishes. Movement of the hyoids is one of the mechanisms responsible for the production of a large negative pressure in the orobranchial cavity. Three possible movements are important : depression, retraction and elevation. The backward rotation in the plane of the suspensorium is also of great importance for a rapid jaw depression (AERTS, 1991). In generalised suction feeding teleosts, powerful suction is associated with a protrusion of the anterior parts of the mouth, *i.e.* the premaxillary and the maxillary bones (WESTNEAT and WAINWRIGHT, 1989). The premaxillary bone of such teleosts bears a notable ascending process where in biting species the arm is relatively shorter than in suction feeding species (WITTE, 1984). In *C. gariepinus* however, no ascending process can be observed, as the premaxillary bone is a plate-like bone bearing small conical teeth. The maxillary bone has completely lost its function as part of the feeding apparatus, as it has become part of the palatine-maxillary mechanism. This enables the extension and the retraction of the maxillary barbel, with the maxillary bone as a supporting base for the barbel (Fig. 3B) (GOSLINE, 1975). Additionally the vomeral bone also bears many small teeth (Fig. 3B). The lower jaw is equiped with a large battery of both narrow and broad conical teeth wich are usefull for grasping and holding prey. Aquarium observations show that *C. gariepinus* does not exert a powerful suction feeding but is more likely to swim to the given food.

CONCLUSIONS

Early in ontogeny (SL = 7.19 mm) the interhyal is present in *C. gariepinus* as a cartilaginous structure, continuous with the hyosymplecticum and the hyoid. The depressor muscle of the hyoid, the sternohyoideus muscle, is already developed and functional, but its antagonist, the hyoid protractor muscle, is yet only partially developed. It does insert on the lower jaws but is partially functional. Its function is faciliated by the elastic properties of the cartilaginous interhyal. Later in ontogeny (SL = 46.75 mm), the interhyal becomes separated from the hyoid and is present in a reduced form. The hyoid protractor muscle is completely formed and functional here. The connection between the suspensorium and the hyoid is replaced by a stout ligamentous strap. In the adult situation (SL = 125.45 mm) the interhyal has been lost completely, where the only connection between the suspensorium and the hyoid is the ligamentum hyomandibulo-ceratohyale.

In this paper it is hypothesised that a reduction and loss of the interhyal will have effect on the mobility of the hyoid. Evidence is provided that the loss of the interhyal can result in a restricted depression of the hyoids. Morphological evidence supporting the hypothesis of a restricted depression is : (1) the presence of a small fold between the hyoid and the lower jaw, (2) a restricted abduction of the suspensorium, (3) a relatively short (but broad) sternohyoideus muscle and (4) a branchiostegal membrane which is only capable of a restricted expansion. The

reduced depression of the hyoid probably has no important negative effect on gill ventilation because *C. gariepinus* is able to perform aerial respiration. No powerful suction feeding is performed either, as *C. gariepinus* has few protrusible mouth parts and many, small teeth on the lower jaw, the premaxillary and the vomeral bone.

ABBREVIATIONS

af-I	=	articulation facet of the hyomandibular bone with the neurocranium
af-II	=	articulation facet of the quadrate bone with the mandibula
bbr-I	=	basibranchial I
bcav	=	branchial cavity
bm	=	branchiostegal membrane
cbr-II	=	ceratobranchial II
ch	=	ceratohyal
c-Meck	=	cartilago Meckeli
c-neur	=	cartilaginous neurocranium
eb-I	=	epibranchiale I
for	=	foramen truncus hyomandibularis
hembr	=	hemibranchia
hs	=	hyosymplecticum
ih	=	interhyal
l-an-ch	=	ligamentum angulo-ceratohyale
l-an-iop	=	ligamentum angulo-interoperculare
l-hm-ch	=	ligamentum hyomandibulo-ceratohyale
l-uh-hh	=	ligamentum urohyalo-hypohyale
m-A2	=	A2 part of the mandibular adductor muscle
m-ad-ap	=	arcus palatini adductor muscle
m-ad-mnd	=	mandibular adductor muscle
mcav	=	mouth cavity
m-ex-t	=	tentacular extensor muscle
m-hh-ab	=	hyohyoid abductor muscles
m-hh-ad	=	hyohyoid adductor muscles
m-hh-in	=	inferior hyohyoid muscle
m-intm	=	intermandibular muscle
mnd	=	mandibula
mnd-b	=	mandibular barbel
m-pr-h	=	hyoid protractor muscle
m-pr-h-s	=	superficial part of the hyoid protractor muscle
m-re-t	=	tentacular retractor muscle
m-sh	=	sternohyoideus muscle
mx-b	=	maxillary barbel
o-ch-a	=	anterior ceratohyal bone
o-ch-p	=	posterior ceratohyal bone
o-cl	=	cleithral bone
o-den	=	dental bone
o-enp4	=	sesamoid bone 'entopterygoid' type 4
o-fr	=	frontal bone

o-hh-v = ventral hypohyal bone
o-hm = hyomandibular bone
o-io-IV = infraorbital bone IV
o-iop = interopercular bone
o-mp = metapterygoid bone
o-mx = maxillary bone
o-op = opercular bone
o-prmx = premaxillary bone
o-prop = preopercular bone
o-q = quadrate bone
o-uh = urohyal bone
o-vm = vomeral bone
pal = palatinum
pectf = pectoral fin
p-q = pars quadrata of the palatoquadratum
prc-op = processus opercularis
prc-pt = processus pterygoideus of the palatoquadratum
prc-ra = processus retroarticularis
r-br = radii branchiostegii

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THE *GYRATRIX HERMAPHRODITUS* SPECIES-COMPLEX (PLATYHELMINTHES KALYPTORHYNCHIA) IN MARINE TROPICAL AREAS : FIRST DATA FROM THE CARIBBEAN

by

MARCO CURINI-GALLETTI * and ILEANA PUCCINELLI **

* Istituto di Zoologia, Università di Sassari,
via Muroni 25, 07100 Sassari, Italy.

** Dipartimento di Biomedicina Sperimentale,
Infettiva e Pubblica, Università di Pisa,
via Volta 4, 56126 Pisa, Italy.

SUMMARY

The finding of specimens belonging to the *Gyratrix hermaphroditus* species-complex (Platyhelminthes Kalyptorhynchia) in marine habitats of Puerto Rico and Bermuda is reported. They differ for karyotype and for details of the sclerotized organs, and are tentatively attributed to four sibling species.

INTRODUCTION

The *Gyratrix hermaphroditus* EHRENBERG, 1831 species-complex is represented in Western Europe by several sibling species, karyologically and ecologically distinct : species with n = 3 are marine, whereas species with n = 2 are found in fresh water. On the basis of outgroup comparisons, the haploid set formed by three isobrachial metacentric chromosomes and the marine habitat have been assumed to be plesiomorphic. Sets with n = 2 have been interpreted as derived from a Robertsonian mechanism of fusion (CURINI-GALLETTI and PUCCINELLI, 1989 ; PUCCINELLI and CURINI-GALLETTI, 1987 ; PUCCINELLI *et al.*, 1990).

While the few data available from fresh water habitats in areas other than W. Europe (Russia (BIRSTEIN, 1991) ; N. Australia (CURINI-GALLETTI and PUCCINELLI, 1990)) confirm the above picture, this clear cut scenario has been challenged by results on the composition of the species-complex in a tropical marine area (Darwin, Northern Territory, Australia) (CURINI-GALLETTI and PUCCINELLI, 1990). There, both species groups with n = 2 and n = 3 have been found in intertidal habitats. However, the area around Darwin presents wide fluctuations of salinity (from 6 to 41 ‰), with coastal habitats being brackish for part of the year. Adaptations to local ecological conditions could result in the coexistence of the two species

groups, as the high diversity of Platyhelminthes found in brackish waters has been shown to be the result of overlapping of marine and fresh-water species (ARMONIES, 1988a). More data from strictly marine tropical areas are therefore needed before any generalisation on the evolutionary biology of the group can be formulated.

Research on Platyhelminthes in Puerto Rico and Bermuda revealed few specimens of the *G. hermaphroditus* species-group ; although very limited, data are interesting, being the first contribution from tropical habitats without wide fluctuations of salinity.

MATERIAL AND METHODS

Samplings were performed in marine habitats off SW Puerto Rico (in the proximity of the Magueyes Marine Biological Station) in December 1988 and in Bermuda in August 1992. Specimens of the *Gyratrix hermaphroditus* species-group were found in two stations off Magueyes :

i) Corona de Pietra, $-4/-6$ m, poorly sorted silty medium sand (one specimen, Port 1),

ii) Turrumote Cay, exposed beach, intertidal, poorly sorted granule (two specimens, Port 2 ; Port 3).

In Bermuda, four stations yielded specimens of the group :

i) Flatts Inlet, intertidal, fine silty sand with vegetal debris (one specimen, Berm1) ;

ii) Flatts Inlet, lower intertidal, very poorly sorted medium sand (one specimen, Berm 2) ;

iii) off Non-Such Island, -10 m, fine sand (one specimen, Berm 3) ;

iv) Spanish Point, $-0.5/1$ m, poorly sorted medium sand with shell debris (one specimen, Berm 4).

Samples were collected by scooping the upper sediment layers ; extraction was done in laboratory using the $MgCl_2$ technique (MARTENS, 1984).

Measurements were taken for each specimen from camera lucida drawings of the two sclerotized pieces of the male copulatory apparatus (stylet and sheath) from semi-squashed mountings. For karyological purposes, specimens were placed in 0.2 % colchicine solution in sea water for 6-8 h, transferred into a 2 % acetic acid solution for about 1 min, stained with lactic acetic orcein for 3-5 min, and squashed. Relative lengths (r.l. = length of chromosome × 100/total length of haploid genome) and centromeric indices (c.i. = length of the short arm × 100/ length of entire chromosome) were obtained from measurements of camera lucida drawings of 5-10 spermatogonial mitoses for each specimen. Idiograms (Fig. 1) are based on mean values given in Table 1. Chromosome nomenclature is that of LEVAN *et al.*, 1964.

Data were subjected to a cluster analysis using NTSYS-pc, version 1.60 (ROHLF, 1990) (coeff. : average taxonomic distance ; method : UPGMA), based on the

following parameters for each specimen : absolute length and centromeric index of each chromosome, length of stylet, and length of sheath.

TABLE 1

Karyometric and morphological data (means ± standard deviation) of the specimens of the *Gyratrix hemaphroditus* species-complex found in Puerto Rico and Bermuda. Nomenclature : m = metacentric ; st = subtelocentric.

Specimen		Chromosome			Haploid genome length (µm)	Stylet length (µm)	Sheath length (µm)
		1	2	3			
PORT 1	r.l.	37.69 ± 1.72	33.35 ± 1.64	28.96 ± 0.67	56.1 ± 3.5	186	179.5
	c.i.	46.70 ± 1.30	45.07 ± 2.41	44.29 ± 2.90			
	nom.	m	m	m			
PORT 2	r.l.	37.19 ± 1.30	33.17 ± 1.11	29.64 ± 1.82	15.4 ± 4.6	90	75.5
	c.i.	47.05 ± 1.21	43.54 ± 3.58	42.12 ± 2.33			
	nom.	m	m	m			
PORT 3	r.l.	58.73 ± 2.32	41.27 ± 2.32		16 ± 6.2	111.1	90
	c.i.	46.31 ± 1.56	22.78 ± 2.73				
	nom.	m	st				
BERM (4 specimens)	r.l.	37.51 ± 2.06	33.91 ± 2.35	28.57 ± 1.98	15.5 ± 3.9	121.5 ± 4.1	100.6 ± 4.5
	c.i.	46.37 ± 1.88	47.37 ± 2.64	46.85 ± 3.01			
	nom.	m	m	m			

RESULTS

Samples from both islands yielded few specimens of the *Gyratrix hermaphroditus* species-group (three in Puerto Rico and four in Bermuda). The three specimens from Puerto Rico differed markedly from each other either for chromosome numbers or for genome length and size of the sclerotized organs (Table 1 ; Figs 1, 2 A-F).

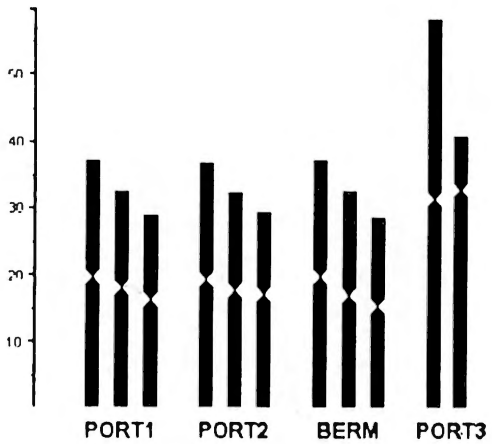

Fig. 1. — Idiograms based on the karyometric data given in Table 1.

Port 1 has three large metacentric pairs and large sclerotized organs.

Port 2, although similar to the former in the relative length and centromeric indices of the three chromosomes, has markedly smaller genome length (nearly one quarter) and sclerotized organs (nearly half the size).

Port 3 has n = 2, with one large metacentric and one smaller subtelocentric ; it has a small genome length and small copulatory organs.

The four specimens from Bermuda (Berm) do not differ appreciably among themselves as to the parameters above, and are grouped together in Table 1. They are similar to Port 2 for size and shape of chromosomes ; the sclerotized organs are, however, larger (Fig. 3 A-B).

In the cluster analysis performed on both cuticular and karyological data (Fig. 4), the specimens from Puerto Rico are markedly separated from each other, while the specimens from Bermuda are grouped together with Port 2 into a loose cluster.

Fig. 5 presents the result of a cluster analysis performed on the cuticular data of the specimens above plus four additional Bermudian specimens (K1-K4), whose biometric data are known (KARLING, 1978). Though some differences are evident (most noticeably in the position of Port 3, isolated in Fig. 4 due to its unique

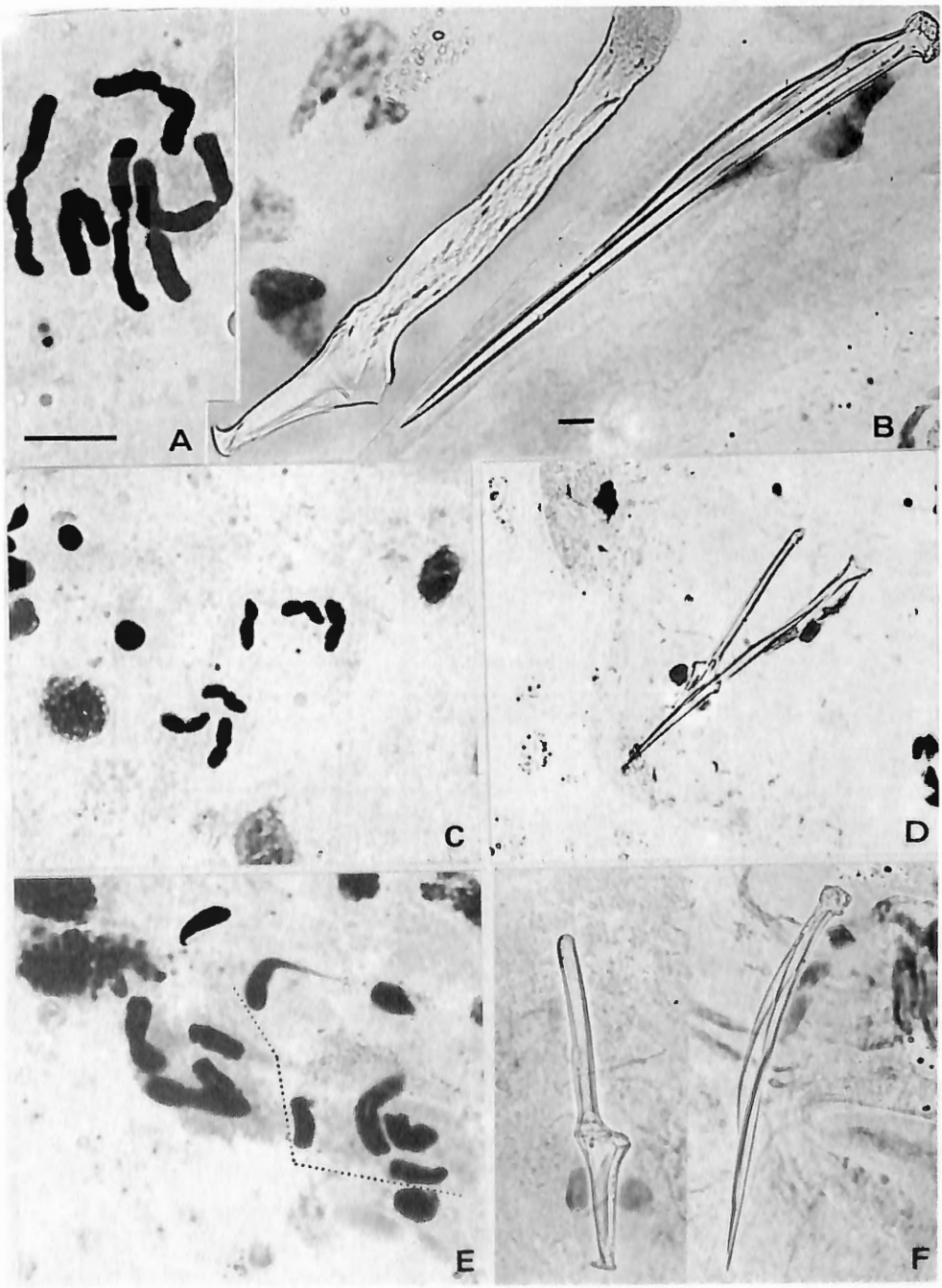

Fig. 2. — A-F, metaphase plates and male sclerotized organs of the three specimens of *Gyratrix hermaphroditus s.l.* from Puerto Rico. A-B, Port 1 ; C-D, Port 2 ; E-F, Port 3. Scale bars = 10 µm

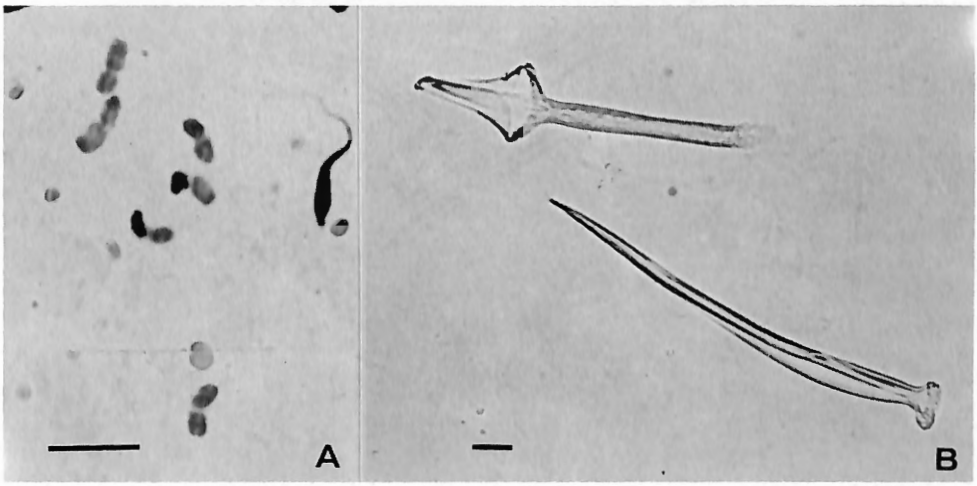

Fig. 3. — A-B, metaphase plate and male sclerotized organs of *G. hermaphroditus s.l.* from Bermuda. Scale bars = 10 μm.

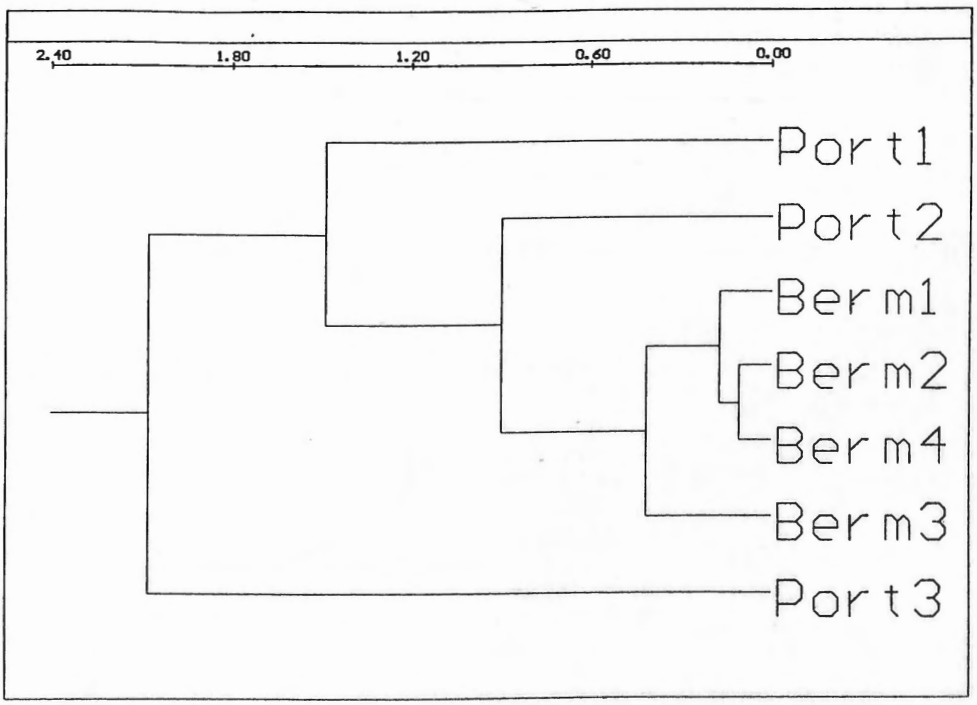

Fig. 4. — Cluster analysis performed on karyometrical and morphological data (see Table 1).

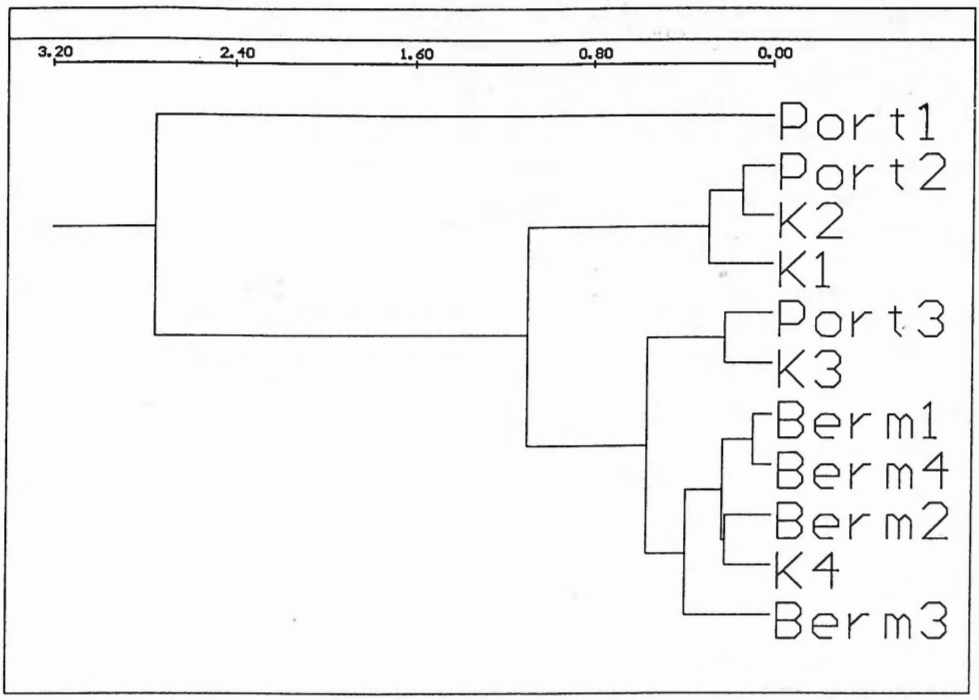

Fig. 5. — Cluster analysis performed on morphological data, including the specimens from Bermuda (K1-K4) described by KARLING (1978).

chromosome number), the number of clusters is comparable to the previous analysis.

DISCUSSION

Albeit the sample of the *Gyratrix hermaphroditus* species-complex from the Caribbean is limited and most certainly under-representative, it nonetheless allows some considerations :

Relationships among the n = 2 and n = 3 species-groups

Both in Puerto Rico and in Bermuda the stations sampled are not expected to withstand anything but negligible variations in salinity. The finding of one species with n = 2 in a truly marine environment in Puerto Rico confirms that in tropical areas the ecological separation between the two species groups observed in Europe is absent. The phenomenon is possibly related to the different level of species diversity in the areas considered. In Europe, in fact, marine species of the complex mostly occur singly, with one record only (Roscoff, Brittany) of two species occurring sympatrically (CURINI-GALLETTI and PUCCINELLI, 1989). On the contrary, sam-

ples from tropical areas have revealed a much higher number of sympatric species : eight in Darwin, at least three in Puerto Rico (where each specimen found belonged to a different species). Our sample from Bermuda is under-representative as well : KARLING (1978), sampling in different stations, possibly found two additional species (Fig. 5). A high number of sympatric species (at least seven) has also been found in the Northern Red Sea (CURINI-GALLETTI and PUCCINELLI, umpubl. data). All the sympatric species of the group known so far differ markedly either in size and shape of the sclerotized organs and/or in their karyotype (possible pre- and post-zygotic isolation mechanisms). Karyotype differentiation in the group usually proceeds through genome size growth and/or chromosome rearrangements, such as pericentric inversions and translocations (PUCCINELLI *et al.*, 1990). Chromosome fusion might be a further karyological evolution mechanism, evolved in areas of high selection for differentiated karyotype, *i.e.* areas with high species number, and thus a possibly homoplasous character. One or more lines in the group with n=2 eventually managed to colonise fresh waters, spreading world-wide.

Relationships among the Caribbean species

Port 1 and Port 2 represent a striking example of differentiation between sibling species of the group. Port 1 has been found in mixed silty substrate, where most of the meiofauna was of the burrowing kind, thus comparatively large and stocky ; Port 2 occurred in clean coarse sediments, and is a typical small interstitial organism. Their difference in body size is reflected by karyology : relative karyometric data are nearly identical, but the genome length is nearly four times larger in Port 1. Since these organisms are basically eutelic, an increase of genome and cell size is an effective means for attaining larger dimensions, and thus exploit different habitats. The sclerotized organs, whose definitive length — at least as far as the stylet is concerned — is attained within the cocoon, and is not related to the age of the animals (KARLING, 1963 ; CURINI-GALLETTI and PUCCINELLI, pers. obs.), are accordingly smaller in Port 2.

On the basis of data available, it is rather unclear whether or not Berm is a species distinct from Port 2 (see Fig. 4). They are karyologically nearly identical, though the difference in size of the sclerotized organ is remarkable. KARLING's (1978) finding in Bermuda of specimens with sclerotized organs nearly identical to Port 2 (see Fig. 5) seems to suggest that Berm and Port 2 are indeed distinct and that the two species occur sympatrically in Bermuda. Furthermore, one of KARLING's specimens is nearly identical to Port 3 — though the lack of karyological data does not allow further speculations.

As a rule, Bermuda is poorer in number of marine species than the rest of the Caribbean. This is reflected in the specific composition of another group of mesopsammic Platyhelminthes, the Proseriata (CURINI-GALLETTI, 1991), as well as by the marine fauna as a whole(STERRER, 1986), and is reasonably connected with the problems of colonisation of a relatively distant, minute oceanic island, enhanced, in the case of interstitial organisms, by dispersal limitation caused by direct development and low adult vagility. In the *G. hermaphroditus* species group,

however, the number of species found in Bermuda and in Puerto Rico seems comparable. Since the sample of Bermuda is larger, results might be biased. However, *G. hermaphroditus* specimens are often found in the periphyton and are known to actively emerge into the water column (ARMONIES, 1988b). This can effectively result into larger distributions than strictly mesopsammic species.

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VARIATION IN SINGING ACTIVITY DURING THE BREEDING CYCLE OF THE EUROPEAN STARLING *STURNUS VULGARIS*

by

MARCEL EENS, RIANNE PINXTEN and RUDOLF-FRANS VERHEYEN
Department of Biology, University of Antwerp, U.I.A.
Universiteitsplein 1, B-2610 Wilrijk, Belgium

SUMMARY

We examined the pattern of song output of male European starlings during different stages of the breeding cycle. Song activity dropped dramatically at pairing, suggesting that the song has an important mate-attraction function. Singing in the nest box occurred almost only when males were unpaired and when prospecting females were in the vicinity of the nest box. Pairing in starlings had several other effects on male behaviour : the occurrence of wing-waving (a visual display sometimes associated with singing) and of carrying green nest materials dropped significantly after pairing. Unpaired males sang significantly more close (≤ 1 m) to the nest box than paired males. After pair formation, an increase in singing activity was observed in the period coinciding with the presumed fertile period of the female. Evidence is presented that by singing males try to stimulate their females to solicit copulations during this period. Monogamous males almost completely stop singing after the egg laying period, whereas males attempting to become polygynous start/continue singing at another nest box at a level comparable to that of unpaired males.

Keywords : starling, *Sturnus vulgaris*, song, sexual selection, extra-pair copulations, mate guarding.

INTRODUCTION

Although the function of the song of the European starling *Sturnus vulgaris* has recently received much attention (EENS *et al.*, 1990, 1993 ; MOUNTJOY and LEMON, 1991 ; BÖHNER, 1993), the variation in male singing activity during the breeding season has so far not been quantified. Nevertheless, studying the pattern of song output during different stages of the breeding cycle may provide important information on the function(s) of song (CATCHPOLE, 1982 ; JOHNSON and KERMOTT, 1991). In a recent review, KROODSMA and BYERS (1991) even stressed that knowing exactly how a male uses his songs in natural situations, for instance during pair formation or during copulation, is a prerequisite for further work.

The aim of this paper is to document the variation in singing activity of male European starlings during the breeding season. As European starlings are facultatively polygynous (PINXTEN *et al.*, 1989 ; PINXTEN and EENS, 1990), we look at both monogamous and polygynous males. In particular, we pay attention to differences in singing activity and behaviour between unpaired and paired male starlings.

STUDY AREA AND METHODS

During the breeding seasons of 1988 and 1989, we obtained information on the pattern of song output during different stages of the breeding cycle from three starling males. Among these three males, two were monogamous and one became polygynous. The three males were watched almost daily during 30 minutes in the morning (between 0700 and 1100 hours) : during this period, we recorded every minute, at the signal from an electronic timer (Casio), whether they were singing or not. From another seven males, the singing activity and behaviour was recorded during similar observation periods of 30 minutes both when they were unpaired and immediately after they had obtained a female (*i.e.* the first day when they were observed with a female). From all 10 males, we also recorded whether they were (1) wing-waving (this is a visual display sometimes associated with singing : see FEARE, 1984 ; Eens *et al.*, 1990 ; BÖHNER and VEIT, 1993) ; (2) carrying green nest materials ; (3) sitting close (≤ 1 m) to the nest box ; (4) singing in the nest box (small electret microphones implanted in the nest boxes and connected to a tape-recorder allowed us to verify this). All ten males were individually marked with colour-coded wing tags and/or colour rings. All observations were done in a nest box colony in Zoersel, near Antwerp, Belgium. Detailed information on the study area, the study population and the general methods employed in this study can be found elsewhere (PINXTEN *et al.*, 1989 ; PINXTEN and EENS, 1990 ; EENS *et al.*, 1991).

RESULTS

In Fig. 1 the percentage of time that male starlings spent singing in relation to the onset of egg-laying of their female, is shown for two monogamous males and one polygynous male. It can be seen that the singing activity decreased markedly at pairing. Considering all 10 males whose song activity was recorded before and immediately after pairing, a highly significant decrease in singing activity was observed (Table 1). Singing occurred significantly more close to the nest box when males were unpaired than when they had attracted a female (Table 1). Singing in the nest box also occurred significantly more when males were unpaired (Table 1). Unpaired males only sang in the nest box when a prospecting female was in the vicinity of their nest box. Finally, both wing-waving and carrying of green nest materials occurred significantly more in unpaired males (Table 1).

TABLE 1

A comparison of behavioural variables between unpaired and paired males (N = 10 males). Values given are means ± SE. Differences between unpaired and paired males were tested using Wilcoxon matched pairs signed ranks tests.

Behavioural variable	Unpaired	Paired	Wilcoxon test
% of time singing	58.3 ± 4.4	19.6 ± 2.8	$P < 0.01$
% of song produced close to the nest box	68.0 ± 4.0	9.0 ± 3.0	$P < 0.01$
% of time singing in the nest box	6.7 ± 1.7	0.7 ± 0.4	$P < 0.05$
% of time wing-waving	14.3 ± 3.5	2.7 ± 1.1	$P < 0.05$
% time carrying green nest materials	7.3 ± 2.5	0.7 ± 0.4	$P < 0.05$

In both monogamous males, an increase in singing activity after pair formation could be observed from about 2 to 4 days prior to laying; before the end of the laying period (which lasted 7 and 6 days, respectively), however, the singing activity decreased to zero or almost zero (Fig. 1a). After the egg-laying period, both monogamous males (almost) completely stopped singing.

When looking at the polygynous male (Fig. 1b), a similar increase in singing activity could be observed 2 to 3 days before the start of laying. At day 4 of the laying period of his female, however, this male temporarily deserted his female and he started singing at another nest box about 35 meters away from his first (between his first and second nest box there were 4 nest boxes occupied by another male). From this moment, he spent most of the time he was present in the colony singing in front of this nest box and he completely neglected his (first) female. The amount of time he spent singing from that moment, increased to a level that is comparable to that of unpaired males (Fig. 1b). Eight days later, the male succeeded in attracting a second female and again a dramatical decline in the singing activity was observed. The second female of this male never started laying and left the colony at day 20 (Fig. 1b) after which the male returned to his first female and started helping this female with the feeding of the nestlings. Later we never observed this male singing again.

DISCUSSION

Pairing in starlings had several major effects on the males' singing and general behaviour. First of all, the song activity of males decreased markedly at pairing. A similar decrease at pairing has been observed in other species (*e.g.* sedge warbler *Acrocephalus schoenobaenus* (CATCHPOLE, 1973), white-throated sparrow *Zonotrichia albicollis* (WASSERMAN, 1977); wood warbler *Phylloscopus sibilatrix* (TEMRIN, 1986), great tit *Parus major* (BJÖRKLUND *et al.*, 1989) and pied flycatcher *Ficedula hypoleuca* (ESPMARK and LAMPE, 1993)) and has been interpreted as

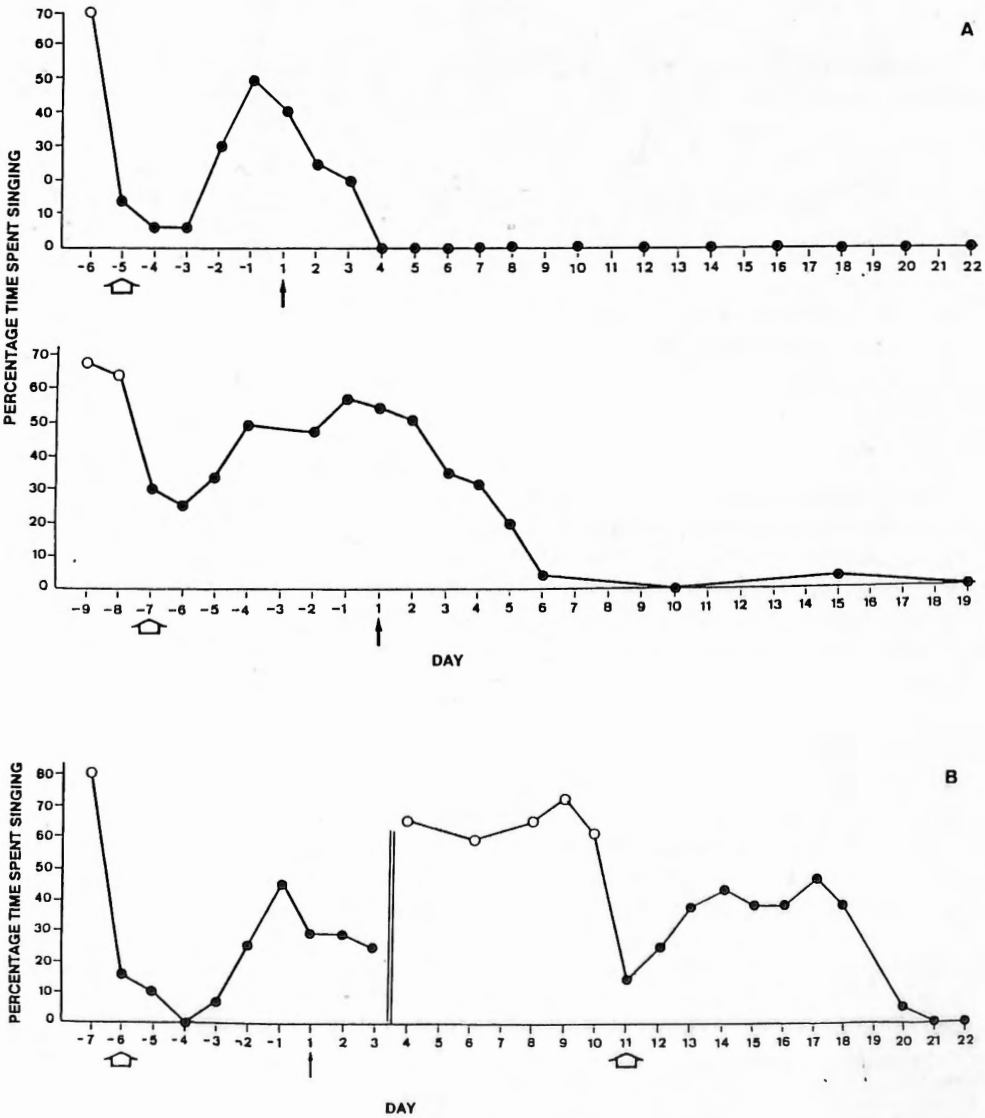

Fig. 1. — Percentage of time (based on the percentage of intervals) that males spent singing in relation to the onset of egg-laying by their female for (A) two monogamous males and (B) a polygynous male breeding in the nest box colony of Zoersel. Large arrows indicate the date of pair formation; small arrows indicate the onset of egg-laying of the females. Egg laying dates were 13 April 1988 (upper) and 9 April 1989 (lower) for the monogamous females, respectively, and 12 April 1988 for the primary female of the polygynous male. Open circles accentuate that the males were still unmated at that time. The vertical double line in Figure B indicates that this male started singing at a second nest box from this moment.

evidence that an important function of song is female attraction (SEARCY and ANDERSSON, 1986). The observed decrease in singing activity of male starlings after pairing is in agreement with earlier experimental work demonstrating that the starling song functions primarily in intersexual communication. CUTHILL and HINDMARSH (1985) showed that experimental removal of the female from pairs of starlings led to a dramatical increase in male singing activity. Accordingly, EENS *et al.* (1990, 1993) showed experimentally that unpaired captive male starlings strongly increased their singing activity when presented with a female.

The observation that unpaired male starlings sing in the nest box when a prospecting female comes in the neighbourhood of the nest box (or even in the nest box) indicates that males do not only sing to be rapidly detected by any potential female passing by (*i.e.* passive attraction : see SEARCY and ANDERSSON, 1986 and SLAGSVOLD *et al.*, 1988), but also suggests that females may actually use song as a cue for their mate choice. In agreement with this, it has been shown both in field and aviary conditions that female starlings prefer males singing more 'complex' songs (EENS *et al.*, 1991).

According to HINDMARSH (1984), male starlings almost completely stop singing as they get paired (see also CUTHILL and HINDMARSH, 1985). This is in strong contrast with our data which suggest that from two to four days prior to laying, the song activity of paired starlings increases again and stays at a similar (high) level until the end of the laying period when it decreases to zero or almost zero (at least in monogamous males). This was partly also noted by KLUYVER (1933 : p. 49) who mentioned that male starlings sing the most during the period of egg laying. The period of increased song activity after pair formation coincides with the 'presumed fertile period' of the females (see MØLLER, 1985 ; BIRKHEAD, 1987 ; BIRKHEAD *et al.*, 1987 for information on the fertile period). Previously, it was observed that most of the within-pair copulations occur between four days before egg-laying till the fourth day of the egg-laying period (EENS, 1992). This combined with the fact that all copulations are preceded by singing in the starling (EENS and PINXTEN, 1990 ; EENS, 1992) strongly suggests that an important function of the song after pairing might be to invite and stimulate the female to solicit copulations, as was also noted by HARTBY (1969). Indeed, it is interesting to mention that male starlings, in contrast to many other male songbirds (*e.g.* bunting species : BAKER and BAKER, 1988 ; redwinged blackbird *Agelaius phoeniceus* : SEARCY, 1989), do not have a copulation call or precopulatory vocalization. We suggest that by singing during the fertile period, male starlings try to stimulate their females to solicit copulations. We feel that it is not unlikely that female starlings at this moment assess the quality of their mate on the basis of his song (*e.g.* song rate and/or complexity) and adjust their copulation behaviour (both within- and extra-pair) accordingly. An alternative explanation for the high song activity during the fertile period might be that males sing at a high level during the fertile period of their mate in order to deter (neighbouring or other) males that want to obtain extra-pair copulations (MØLLER, 1988, 1991). We think, however, that in a (semi)-colonially breeding songbird that defends only a few meters around its nesthole, the presence of the male close to his female is more important to deter other males than his song. In agreement with

this, we never observed extra-pair courtship behaviour when the female's partner was nearby (EENS and PINXTEN, 1990 ; EENS, 1992).

The difference in the occurrence of wing-waving and the carrying of green nest materials before and after pairing confirms that both behaviours probably serve mainly a mate-attraction function (see EENS *et al.*, 1990, 1993). A final difference between unpaired and paired starlings concerned the position where males were singing : unpaired males sing most of their song close to the nest box, while paired males sing mostly from high in the tree (to which their nest box is attached). Unpaired males probably sing very close to their nest box to show it to prospecting females : in a hole-nesting species like the starling males can probably not obtain a pairbond with a female without having a nest box. A possible explanation why mated males sing high in the tree may be that in this way they can better mate guard their female. PINXTEN *et al.* (1987) showed that male starlings guard their females intensively during their fertile periods to avoid extra-pair copulations (EENS and PINXTEN, 1990 ; PINXTEN *et al.*, 1993). Another possibility might be that high in the tree, males can better observe eventual predators or that the distance over which the song is an effective signal is higher.

ACKNOWLEDGEMENTS

We thank Jörg BÖHNER and Bart KEMPENAERS for comments on the manuscript. This study was supported by a IWONL-grant to Marcel EENS and by Postdoctoral Research Assistantships from the Belgian National Fund for Scientific Research to Rianne PINXTEN and Marcel EENS.

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MORPHOMETRIC EVIDENCE OF THE MONOTYPIC STATUS OF THE AFRICAN LONG-NOSED MONGOOSE *XENOGALE NASO* (CARNIVORA, HERPESTIDAE)

by

MARC COLYN and HARRY VAN ROMPAEY
CNRS URA 373, Laboratoire de Primatologie-Biologie Evolutive,
Université de Rennes I, Station Biologique de Paimpont,
F-35380 Paimpont, France
Royal Museum for Central Africa, B-3080 Tervuren, Belgium

SUMMARY

Xenogale naso has a discontinuous distribution between three nominal subspecies : *X. n. naso, X. n. almodovari* and *X. n. microdon*. Examination of extant specimens shows that *X. naso* occurs throughout forested areas of Central Africa, including the « South Central » faunal region. A morphometric analysis of 122 skulls, indicates that the three nominal subspecies cannot be distinguished cranially, nor any specimens originating from the « South Central » region. *X. naso* should be regarded as a monotypic species and evolved in an area close to the three faunal regions, « West Central » (WC), « South Central » (SC), and « East Central » (EC). We believe it dispersed in a centrifugal manner. Indeed, if *X. naso* had originated from isolated peripheral refuges in mountain areas, centripetal dispersal would have favoured subspeciation in other faunal regions. These data support the theory that, during the dry climatic period of the Late Pleistocene, the lowland forests of the Central Zaire Basin constituted areas of refuge.

Keywords : morphometrics, refuges, dispersion, Zaire, Herpestidae, *Xenogale*.

INTRODUCTION

The rare long-nosed mongoose, *Xenogale naso* (DE WINTON, 1901) is known from only about 40 museum specimens, originating primarily from the rain forests of Central Africa (ALLEN, 1919 ; CABRERA, 1902 ; COETZEE, 1977 ; HALTENORTH and DILLER, 1980 ; ORTS, 1970 ; ROSEVEAR, 1974 ; SCHOUTEDEN, 1947 ; Fig. 1). In the northwest part of the region, *X. n. naso* inhabits the forests between the Cross River (Nigeria) and the north bank of the Sanaga River in Cameroon. South of this river, *X. n. almodovari* is limited to the coastal regions of Cameroon, Equatorial Guinea, and Gabon. In the east, *X. n. microdon* is distributed over a large area on the right bank of the Zaire River, including the gallery forests of the upper reaches of the

Fig. 1. — Long-nosed mongoose (*Xenogale naso*) from the Niger Delta, Nigeria. *Photo : A. P. Leventis.*

Zaire/Lualaba River and the Bas-Zaire region, as well as of areas south of the Zaire River (area around Lake Tumba and Lake Mai-Ndombe areas, and the upper reaches of the Sankuru River). According to these data, *X. naso* has a discontinuous distribution, and the three « subspecies » are separated either by a fluvial barrier (Sanaga River), or by a gap of several hundred kilometers (Fig. 2).

Recently a specimen was caught near Yenagoa in the Niger Delta, Nigeria, approximately 200 km west of the Cross River, thus extending the species' range of distribution to the Niger River (C. B. Powell, in litt.).

The distribution described above could result from a scarcity of specimens, taxonomic confusion, or both. Confusion exists at the generic and specific levels and is based on similarities of morphological characters.

Long nosed mongooses, first described as *Herpestes naso* (De Winton, 1901), were alternately named *Mungos* (Cabrera, 1912 ; Thomas, 1912) for specimens from Equatorial Guinea and Cameroon, respectively and *Xenogale* (J. A. Allen, 1919) for specimens from NE Zaire. Later these three genera were considered to be synonyms and regrouped into the genus *Atilax* (Allen, 1939). Monard (1951) pointed out that the specimen of *Herpestes galera*, described by Jeannin (1936) from South Cameroon, was actually *Xenogale naso*. *X. naso* has 40 teeth, while *H. galera* (= *Atilax paludinosus*) has only 36 teeth. The genus *Xenogale* has also been considered a subgenus of *Herpestes* (Petter, 1969).

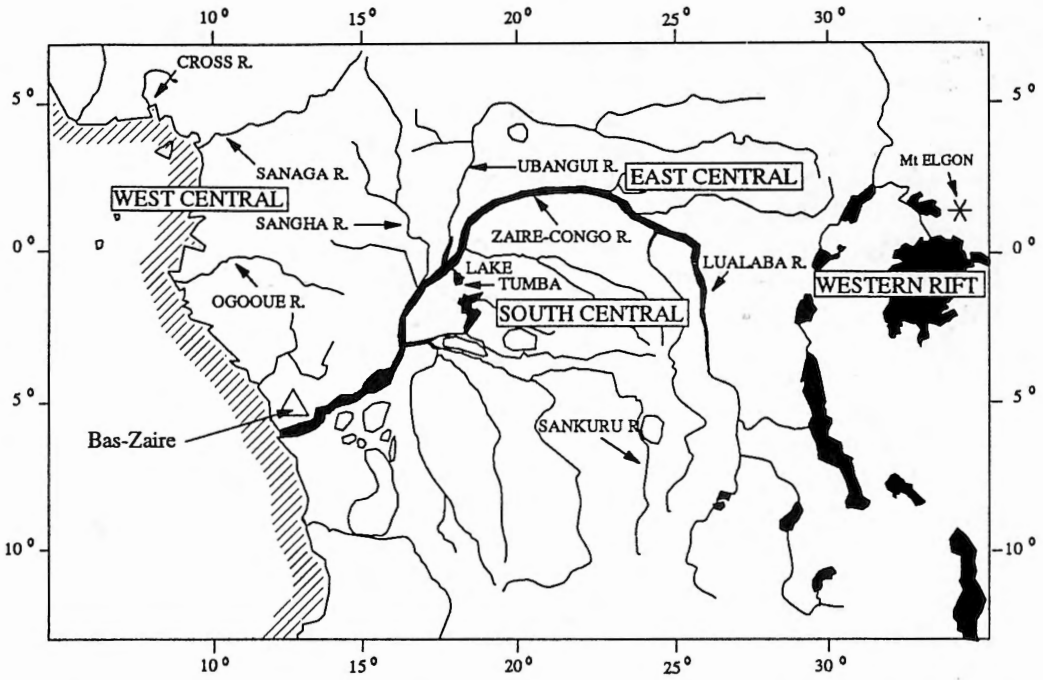

Fig. 2. — Principal faunal regions and rivers of Central Africa : West Central (WC), East Central (EC), South Central (SC); after MISONNE (1963), KINGDON (1980), GRUBB (1978, 1982), and COLYN (1988, 1991).

ORTS (1970) underlined the difficulty in distinguishing between *Xenogale, Atilax*, and the black-tailed variety of *Ichneumia*, all of which are almost identical in coat color. These similarities in external characters had been previously noted by many authors (J. A. ALLEN, 1919, 1924 ; CABRERA, 1903 ; DE WINTON, 1901 ; LÖNNBERG, 1917 ; SANDERSON, 1940 ; THOMAS, 1915) and ORTS (1970) pointed out that having similar external markings has led to incorrect identifications. For example, he found that ten specimens were misidentified as either *Atilax* or *Ichneumia*, and three specimens were mislabelled as *Xenogale* in SCHOUTÊDEN's (1947) list. On the basis of cranial analyses of *Xenogale* from Zaire and *Herpestes ichneumon* from Central Africa, ORTS (1970) retained the two genera. ROSEVEAR (1974) confirmed this distinction. In summary, while many authors agree with the name *Herpestes naso* (COETZEE, 1977 ; CORBET and HILL, 1991 ; HAPPOLD, 1987 ; HINTON and DUNN, 1967 ; PERRET and AELLEN, 1956 ; KINGDON, 1977 ; WILSON and REEDER, 1993 ; WOZENCRAFT, 1989), others use the name *Xenogale naso* (ANSELL, 1960, 1978 ; DEKEYSER, 1955 ; EISENTRAUT, 1963 ; GREGORY and HELLMAN, 1939 ; MALBRANT and MACLATCHY, 1949 ; MONARD, 1951 ; SIMPSON, 1945).

Confusion has been greater at the specific and subspecific levels. The best example is given by CABRERA (1902, 1903, 1908, 1912) who describes a new long-nosed mongoose from Equatorial Guinea that he named successively *Herpestes*

almodovari (1902), *H. albicauda* var. *almodovari* (1903), *Mungos albicaudus almodovari* (1908, 1912b), and *H. almodovari* (1912a). Each original description of a 'subspecies' (*naso, almodovari*, and *microdon*) was done without any knowledge of the existence of the other(s). Each author thought he was describing a new species, that is, *Herpestes naso, Herpestes almodovari*, and *Xenogale microdon*. So no comparisons were made, only ROSEVEAR (1974) remarked that *almodovari* skulls are in general larger than *naso* skulls.

In this study, we retain the classification of ORTS (1970) at the generic level, based on cranial differences, and discuss only the validity of the subspecies classification.

genus
Xenogale J. A. ALLEN, 1919
species
X. naso (DE WINTON, 1901)
subspecies
X. n. naso (DE WINTON, 1901)
= *Mungos naso nigerianus* THOMAS, 1912
X. n. almodovari (CABRERA, 1902)
X. n. microdon J. A. ALLEN, 1919

This study is based on a re-examination of all extant museum material, as well as an analysis of newly-collected material. It examines the taxonomic relationships of long-nosed mongooses based on cranial differences and their patterns of distribution. Biogeographic considerations arising from these results allow us to hypothesize how evolution of these taxa occurred.

MATERIAL AND METHODS

Material. All known specimens of *Xenogale, Atilax*, and *Ichneumia* in museums and 46 newly-collected specimens from Zaire (COLYN *et al.*, 1988) were examined. From this sample, a total of 122 adult specimens showing permanent dentition and fusion of the basioccipital and basisphenoid were considered to belong to the genus *Xenogale*. Because there exists no external morphological character that allows the differentiation of specimens of *Xenogale* at the subspecific level and, because skins of all three described subspecies exhibit marked color polymorphism, only cranial material was used (Appendices 1, 2). Institutions housing the specimens examined are listed in Appendix 3.

Skull measurements. Measurements were taken with calipers and recorded to the nearest 0.1 mm (Appendix 4). Seventeen cranial measurements as defined by GOLDMAN (1984) were used : GSL : greatest skull length, from the anterior edge of I^1 to posterior edge of occipital bone ; CBL : condylobasal length of the skull, from anterior edge of of I^1 alveolus to posterior edge of occipital condyle ; ROL : length of rostrum, from lateral base of hamular process of lacrimal to anterior most edge of premaxillae ; PAL : length of palate, from posterior edge of alveolus of I^1 to posterior edge of palatine ; MAX : greatest crown length of maxillary toothrow ; TYM :

greatest length of tympanic bulla, not along longitudinal axis of skull ; CAN : breadth of canines, distance between labial crown edges of C^1-C^1 ; ROB : breadth of rostrum, distance between lateral base of hamular process of lacrimals ; IOB : least interorbital breadth ; PAB : breadth of palate, distance between labial crown edges of M^1-M^1 ; ZYG : greatest zygomatic breadth ; BRB : greatest breadth of braincase at the right angle to longitudinal axis of skull ; MAS : mastoid breadth ; BRH : height of braincase, distance from occipital bone between bullae to parietal, excluding sagittal crest ; MAL : mandible length from anterior edge of I_1 alveolus to posterior surface of mandibular condyle ; MAN : greatest crown length of mandibular toothrow ; CMH : mandible height, perpendicular distance from dorsal edge of coronoid process to line from angular process to ramus.

Data analysis. Of the 122 skulls examined, only the 103 intact skulls were used for multivariate analyses to reduce missing data (Appendices 1, 4). On the basis of taxonomic and biogeographic criteria, four operational taxonomic units (OTU's) were made (Fig. 3). These include the four principal populations comprising the three nominal subspecies, and also the specimens originating from the left bank of the Zaire River.

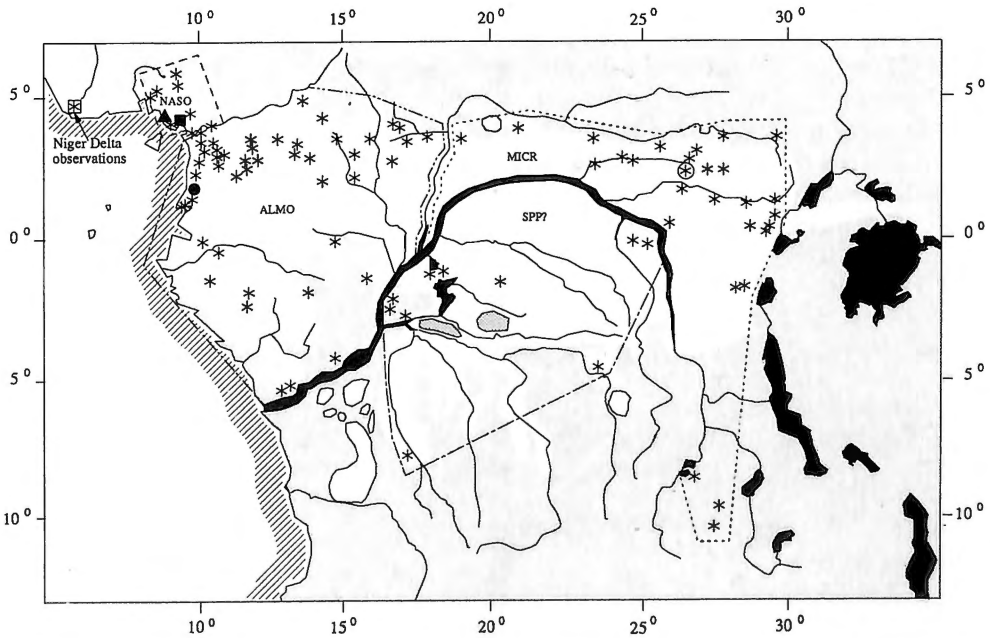

Fig. 3. — Distribution of *Xenogale naso* in Central Africa based on data from museum material (stars). Holotypes: triangle, *X. n. naso*; square, *Mungos naso nigerianus*; full circle, *X. n. almodovari*; star in circle, *X. n. microdon*. The unshaded areas represent rain forest areas.

OTU « NASO » : *X. n. naso* from the « West Central » region : 21 specimens from Nigeria and North Cameroon.

OTU « ALMO » : *X. n. almodovari* from the « West Central » region : 51 specimens from South Cameroon, Equatorial Guinea, Gabon, Central African Republic, Congo, and Zaire (coastal region).

OTU « MICR » : *X. n. microdon* from the « East Central » region : 21 specimens from the right bank of the Zaire River (Zaire).

OTU « SSP ? » : *X. naso* ssp. from the « South Central » region : 29 specimens from the left bank of the Zaire River (Zaire).

We conducted several multivariate analyses to differentiate these populations. Principal component analysis was undertaken on the basis of the nine most significant skull measurements (ROL, PAL, MAX, CAN, ROB, BRB, MAL, MAN, and CMH) chosen by the CASEL program from the 17 cranial measurements. Results were then tested by canonical dispersal analysis, using the method of SEAL (1964) further adapted by HERBRANT (1974). This analysis maximizes the variation between groups in relation to the variation within groups. The original variables (skull measurements) are transformed into a new set of canonical variables. Each original variable is multiplied by its corresponding coefficient of the calculated eigenvector and the resulting values are added up. Each specimen can be plotted in a diagram of canonical variates represented as an abscissa or an ordinate. The OTUs are represented by the contour of the most extreme values and by the canonical means (= centroids).

In order to identify phenetic affinities between the four populations on the basis of the same cranial variables, discriminant analyses were conducted and phenograms drawn from the matrices of generalized Mahalanobis distances using the UPGMA method (SNEATH and SOKAL, 1973 ; Table 2).

TABLE 1

Eigenvectors of the nine variables for the first two Canonic Variables (CVs).

Variable	CV I	CV II
ROL	1.9276	−2.8297
PAL	−4.0460	−4.4084
MAX	0.8531	−1.9804
CAN	−3.3020	−4.9126
ROB	0.2845	0.8985
BRB	4.2293	0.5718
MAL	2.4999	1.0345
MAN	5.3790	2.4980
CMB	1.4564	6.8908

TABLE 2

Matrices of the generalized Mahalanobis distances (D^2m ; lower triangle) and possibility of a faulty determination (% ; upper triangle). OTU's = NASO, ALMO, MICR and SSP ?

	NASO	ALMO	MICR	SSP ?
NASO		29.62	14.82	1.42
ALMO	1.15		16.83	3.84
MICR	4.35	3.66		7.82
SSP ?	19.22	12.52	8.51	

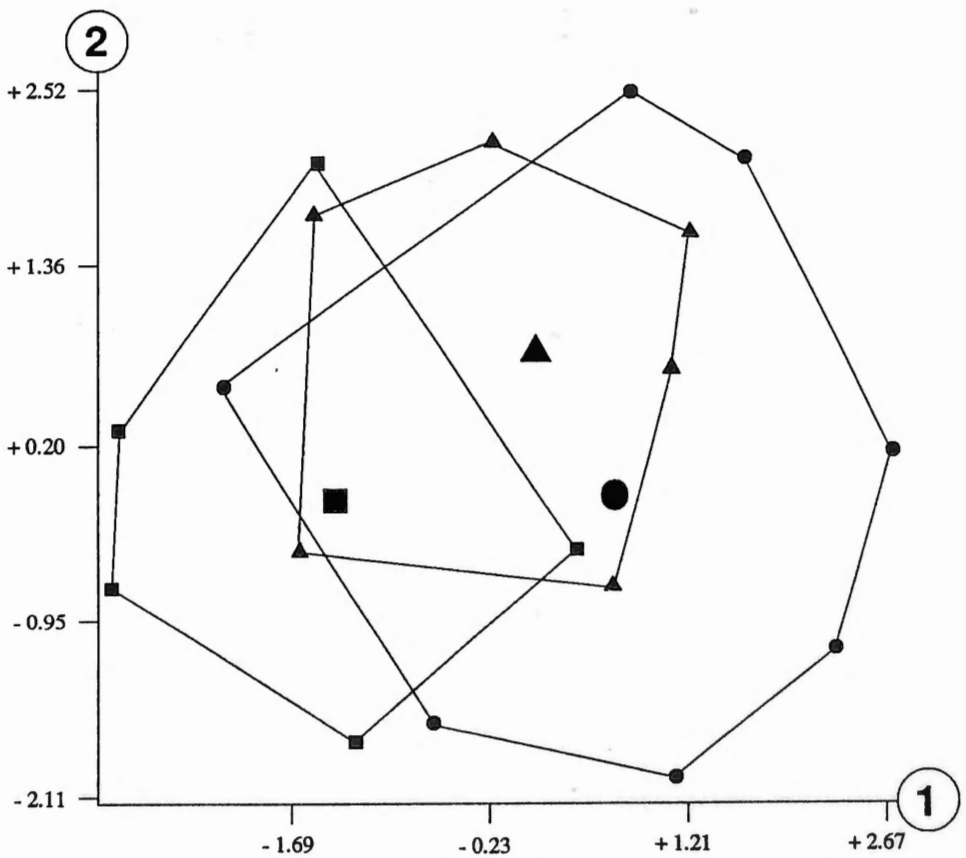

Fig. 4. — Results of the Canonical Variate Analysis of nine cranial characters of three OTU's of *Xenogale naso*. Dispersion of the three OTU's: triangles = *X. n. naso* (NASO), circles = *X. n. almodovari* (ALMO), and squares = *X. n. microdon* (MICR).

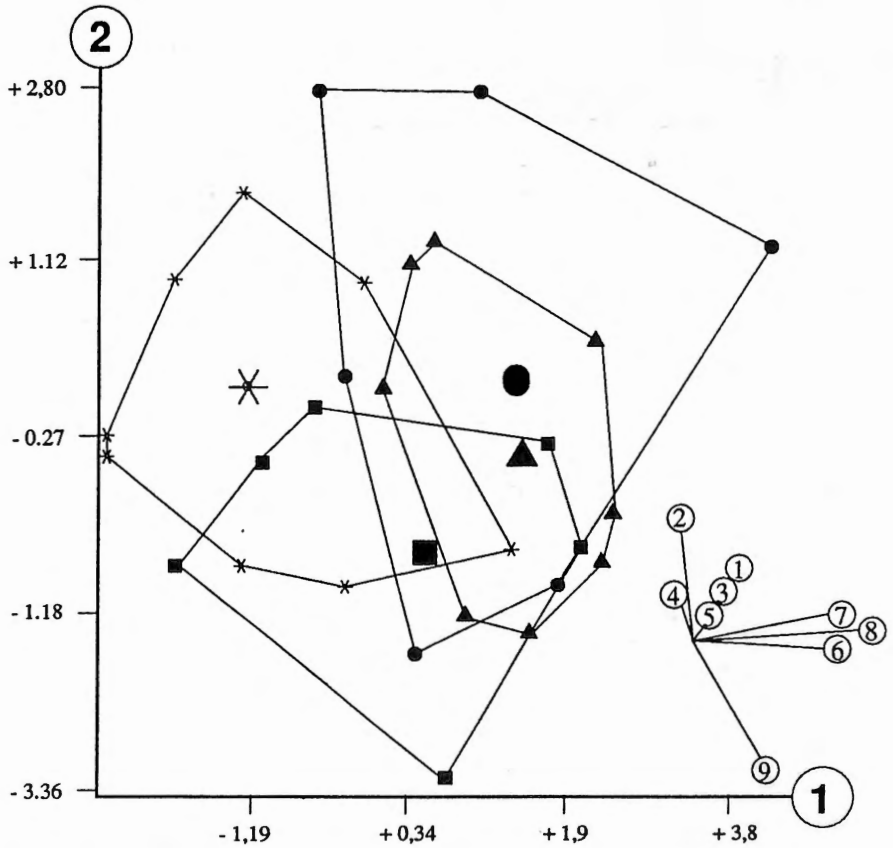

Fig. 5. — Results of the Canonical Variate Analysis of nine cranial characters of four OTU's of *Xenogale naso*. Dispersion of the four OTU's: triangles = *X. n. naso* (NASO); circles = *X. n. almodovari* (ALMO); squares = *X. n. microdon* (MICR), and stars = *X. naso* ssp? (SSP?) specimens from the « South Central » faunal region.

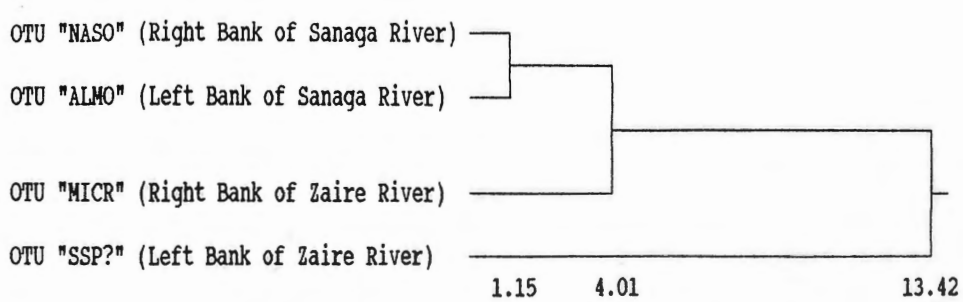

Fig. 6. — Phenogram based on the Discriminant Analysis of nine cranial variables, schematically representing the morphological distances between the four principal population aggregates of *Xenogale naso*.

RESULTS

Patterns of distribution of the genus Xenogale. — The present number of specimens allows a refinement of the distributional data on long-nosed mongooses. Results show that genus *Xenogale* is more evenly distributed than previously thought (Fig. 3). Long-nosed mongooses are present in the entire forested area north of the Zaire River and without any obvious gaps between the western and eastern areas. The species is also present south of the Zaire River to ca. 10°30'S.

Taxonomic relationships. — The first canonical dispersal analysis does not distinguish the three nominal subspecies (P=0.8454), in spite of the large size of the skull in *X. n. almodovari.* The diagram based on the eigenvectors of the nine significant variables shows that the three OTUs overlap considerably and that the centers of dispersion are all located within the contour of points representing *X. naso* (Table 1, Fig. 4).

The second analysis includes the four populations and gives similar results. The first axis of the canonical analysis contains 81.3 % of the total variation, the second axis 15.2 %. On the diagram derived from the eigenvectors (Table 1), the three OTUs, *X. n. naso, X. n. almodovari,* and *X. n. microdon* overlap considerably so that the dispersion centres are nearly all located within the OTU NASO (Fig. 5). The OTU SSP, although slightly distinguished on Axis 1, does overlap considerably with the three other OTUs.

The projection of the nine cranial variables, regrouped near the centroid of the two CVs, does not allow the identification of any cranial character that is specific to populations from the SC region.

Phenetic affinities were searched for by a discriminant analysis. The phenogram (Fig. 6) represents the morphological distances between the four population aggregates. The results show that :

1. — *X. naso* ssp. from the left bank of the Zaire River is the most differentiated of all the populations ; 2. — *X. n. microdon* from eastern Zaire closely resembles *X. n.naso* and *X. n. almodovari* from western Africa ; and 3. — *X. n. naso* and X. n. almodovari are phenetically very close to each other.

DISCUSSION

Although there is a range of variation of skull dimensions in the four populations studied, there is also a large degree of overlap between them, and none of the populations can be characterized by any specific cranial character. The least distinct populations are those from the WC faunal region (*X. n. naso* and *X. n. almodovari*) and which clearly belong to the same subspecies. Differences are more obvious for the EC population, and especially for the SC population. However, without more additional data, the erection of a new subspecies for the SC population does not seem justifiable. We tentatively propose that the long-nosed mongooses of Central Africa belong to the monotypic *Xenogale naso*, however, we cannot exclude the

possibility that the relatively small sample size, which originates from a large geographic area could mask geographical variation.

The distribution pattern of *Xenogale naso* in western Cameroon and northeastern Zaire described previously largely agrees with the long-standing biogeographical theory which recognises only two main faunal regions : the EC and the WC (GRUBB, 1978, 1982 ; KINGDON, 1980 ; MISONNE, 1963 ; MOREAU, 1966 ; PRIGOGINE, 1988 ; RAHM, 1966), and accords a minor role to the SC area (GRUBB, 1978, 1982 ; KINGDON, 1977, 1980 ; MISONNE, 1963 ; RAHM, 1966). According to this scenario, the main Quaternary refugia would have been in the proximity of montane forests at the foot of the Central Rift in eastern Zaire, and at the periphery of Mt Cameroon in the west.
Dispersal would have occurred from these peripheral refugia, and would have been limited by fluvial barriers, thus favouring subspeciation.

The actual distribution of *X. naso* shown by this study suggests that the main fluvial barriers (either the Sanaga River, the Ubangui River, or the huge Zaire River) did not, however, play an important role in the subspeciation of *Xenogale*. The fact that long-nosed mongooses have colonized the whole of Central Africa's forests but without showing any clear differentiation does not support centripetal dispersion from the peripheral montane refugia Mt. Cameroon and the Central Rift. We propose that the species originated from a refugium in the lowland forests, situated at the centre of the three faunal regions, and that dispersal occurred in a centrifugal manner. Such a hypothesis supports the existence of lowland forest refugia within the whole drainage area of the Central Basin and particularly of the Zaire River, as previously suggested by studies on African primates (COLYN, 1987, 1988, 1991, 1993 ; COLYN *et al.*, 1991).

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APPENDIX 1

List of known material : specimens used in the statistical analyses are shown in bold type ; FO : field observation

CAMEROON : Ajos Höhe, 1 (**MNHU-31442**) ; Akak, 1 (**MHNC-37021117**) ; Akonangi, 1 (**MNHU-82942**) ; Balaga, between Dingi and, 1 (MNHU-83134) ; Balingekore, between Balasane and, 1 (**MNHU-82945**) ; Bange Forest, 1 (**SMF-4615**) ; Basho, 4 (**MNHU : 82925, 83035**, 83136, 83137) ; Batouri District, 1 (PCM-no No.) ; Bipindi, 17 (BMNH-1171 ; **MNHU :** 18727, 82909, **82941, 82944,** 82946, 82950, **82963, 82966, 82967,** 83139, 83142, **91380, 92604**, no No., no No., no No.) ; Cameroon River, estuary, 1 (**BMNH-0751**) ; Debundscha, 2 (**NRST : A580173, A582404**) ; Dendeng, 1 (**MNHU-18461**) ; Djaposten, 1 (AMNH-85194) ; Douala, 1 (**MNHU-18392**) ; Edea region, 9 (MNHU : 18541, 18542/43, 18545/44, 18547/46, 18548, 18549, 18550, 18551, 18553) ; Efulen, 2 (**BMNH : 22131, 552320**) ; Ekom, Dja Faunal Reserve, FO ; Idenau, 1 (**BMNH-68335**) ; Koto-Barombi Lake, 1 (**SMNS-6389**) ; Kribi, 1 (**ZSM-1903/1545**) ; Lolodorf, 1, (**MNHU-82959**) ; Lomie District, 1 (P-CM-M552) ; Longji, 2 (MNHU : 83099, 83141) ; Mainju Bridge, Mamfe, 1 (**BMNH-48838**) ; Mamfe, 2 (**BMNH : 48836, 36103011**) ; Metet, 1 (**MCZ-42019**) ; Minkan, near Kiango, 1 (**PCM-ZIV21**) ; Moloundou, 2 (**MNHU-82939, SMF-4614**) ; Muele, 1 (**ZFMK-61396**) ; Mundame, 1 (**MNHU-82957**) ; Niede River, 1 (**PCM-ZII2**) ; Nkalla, between Njong River and, 1 (**MNHU-31319**) ; Obala, 1 (**PCM-M692**) ; Okoiyono, 1 (BMNH-48837) ; Sakbayemé, 7, (FMNH : 25308, 43737, 43738, 43739, **MCZ : 18620, 23199**, MNHU-48393) ; Sanaga River, between Ossa Lake and, 1 (**MNHU-82586**) ; Sanga-Dja, 1 (**ZSM-1913/1169**) ; Sangmelima, 7 (**MNHU : 18355, 18356,** 18363, **19097, 19099, 35209, 35212**) ; South Cameroon, 1 (**MNHU-82954**) ; Victoria, 10 (**MNHU : 82912, 82940, 82943,** 83138, no No., no No., **ZSM :** 1902/3004, 1902/3005, **1902/3006, 1902/30À07**) ; Yaoundé, 8 (AMNH-236489, PCM-CAMI193, **MNHU :** 11429, **82969, 82970, 82980**, no No., no No.) ; Yem, near Efulen, 1 (**MCZ-26836**).

CENTRAL AFRICAN REPUBLIC : Balondo, N'Gotto Forest, FO ; Bambio, N'Gotto Forest, FO ; Bomboko Forest, 1 (**MNHU-17073**) ; Kongana, Dzanga-Sangha Reserve (Ray, 1994) ; La Maboké, 1 (**MNHN-1970/20**) ; Londo, N'Gotto Forest, FO ; Salo2, Dzanga-Sangha Reserve, FO.

CONGO : Etoumbi, 1 (PCM-273) ; Karagoua River, near Souanké, 1 (**AMNH-54339**) ; Kinkala, 1 (AMNH-118823) ; Makoua, 3 (AMNH : 119897, 119941, 119942).

EQUATORIAL GUINEA : Bata, 2 (MNHU : 31443, **31444**) ; Benito River, 3, (**BMNH : 111218, 111219, 112715**).

GABON : Franceville region, FO (Carpaneto, in litt.) ; Ngori, 1 (**NMNH-220398**) ; Kango, 1 (**AMNH-119938**) ; M'bigou, 1 (**FMNH-73796**) ; N'djolé region, 1 (**AMNH-119937**) ; Ngori, 1 (**NMNH-220398**) ; Yombi (FMNH-73797).

NIGERIA : Niaji, 1 (**BMNH-106114**) ; Otuopoti, near Yenagoa (C. B. Powell, in litt.)

ZAIRE : Akenge, 5 (RMCA-12306, **AMNH :** 51617, 51620, **51621, 51625**) ; Amadjabe, 42 (**MC : ZX4312, ZX4313, ZX4315, ZX4339, ZX4517, ZX4654, ZX4655, ZX4734, ZX4881 to ZX4883, ZX4943, ZX4960, RMCA** : 88047M68, 88047M69, **89023M77,** 90042M43, **90042M44,** 90042M45, 90042M46, **90042M48,** 90042M49, **90042M50 to 90042M52, 90042M53,** 90042M54, **90042M55,** 90042M56 to 90042M59, **90042M60**, 90042M61, **90042M62,** 90042M63, **90042M64, 90042M65,** 90042M66, 90042M67, **90042M68, 90042M69**) ; Avakubi, 2 (AMNH-51604, 51605) ; Bambesa, 1 (RMCA-23990) ; Batiakuya, 5 (**MC : Z1093, Z2204, Z2770, RMCA : 90042M40**, 90042M41) ; Beni, 1 (**RMCA-3250**) ; Bokuma, 1 (RMCA-20552) ; Bolobo, 3 (RMCA : 15795, 15796, 15797) ; Buta, 4 (RMCA : **10433bis,** 10434, **11582, 18692**) ; Dali, 1 (**RMCA-1904**) ; Faradje, 1 (AMNH-51093) ; Go, 1

(ZSM-1912/1555); Ibembo, 5 (RMCA : **19600, 19621,** 20235, **20236, 21712**); Inkongo, 1 (**RMCA-7834**); Ituri River, 80 km SW of Irumu, 1 (BMNH : 301111225); Kasongo Lunda Falls, 1 (RMCA-15063); Koteli, 1 (**RMCA-16577**); Kundulungu, 1 (RMCA-4995); Kunungu, 1 (RMCA-8150); Lesse, 1 (RMCA-3249); Lukafu, 1 (RMCA-11097); Mabwe, 2 (IRSNB : 11862, 11864); Makaia, 1 (RMCA-5848); Manguredjipa, 1 (RMCA-18391); Medje, 5 (AMNH-51007, 51088, 51089, 51091, 51609); Molegbe St. Antoine, 1 (RMCA-10345); Mushie, 1 (RMCA-17593); Niangara, 1 (AMNH-51092); Niapu, 3 (**AMNH : 51624, 51637**, 51673); Panga, 1 (**RMCA-3409**); Poko Welle, 1 (**BMNH-195831**); Sambo River, right bank of, 1 (**RMCA-9724**); Temvo, 1 (RMCA-5847).

APPENDIX 2

Gazetteer

The distributional localities cited are listed alphabetically below. Abbreviations are as follows : CM, Cameroon ; CAR, Central African Republic ; C, Congo ; EG, Equatorial Guinea ; G, Gabon ; N, Nigeria ; Z, Zaire.

Ajos Höhe (Ayos Heights), CM, 03°54′N, 12°31′E ; Akak, CM, 02°25′N, 10°E ; Akenge, Z, 02°54′N, 26°48′E ; Akonangi, CM, 02°12′N, 11°21′E ; Amadjabe, Z, 00°04′N, 25°17′E ; Avakubi, Z,01°20′N, 27°35′E ; Balondo, CAR, 03°58′N, 16°45′E ; Bambesa, Z, 03°28′N, 25°43′E ; Bambio, CAR, 03°57′N, 16°58′E; Basho, CM, 06°08′N, 09°26′E ; Bata, EG, 01°51′N, 09°49′E ; Batiakuya, Z, 00°36′N, 23°59′E ; Beni, Z, 00°30′N, 29°28′E ; Benito R., estuary, EG, 1°35′N, 9°37′E ; Bipindi, CM, 03° 05′N, 10° 25′E ; Bokuma, Z, 02°26′N, 27°57′E ; Bolobo, Z, 02°10′S, 16°17′E ; Bomboko, CAR, 03°54′N, 18°35′E ; Buta, Z, 02°48′N, 24°47′E ; Butuhe, Z, 00°13′N, 29°16′E ; Cameroon River, estuary, CM, 03°56′N, 09°33′E ; Dali, Z, 03°49′N, 23°40′E ; Debundsha, Cape, CM, 04°07′N, 08°58′E ; Deng Deng, CM, 05°10′N, 13°30′E ; Djaposten, CM, 03°25′N, 13°32′E ; Douala, CM, 04°04′N, 09°43′E ; Edea, CM, 03°48′N, 10°08′E ; Efoulan, CM, 03°00′N, 10°55′E ; Ekom, CM, 03°20′N, 13°02′E ; Etoumbi, C, 00°01′N, 14°57′E ; Faradje, Z, 03°44′N, 29°42′E ; Fougamou, G, 01°16′S, 10°30′E ; Gamangui, Z, 02°10′N, 27°45′E ; Ibembo, Z, 02°38′N, 23°41′E ; Impfondo, C, 01°36′N, 18°00′E, Idenau, CM, 04°14′N, 08°59′E ; Inkongo, Z, 04°53′S, 23°15′E ; Irangi, Z, 01°55′S, 28°27′E ; Irumu, Z, 01°15′N, 29°40′E ; Ituri River, 80 km SW of Irumu, Z, 01°15′N, 29°40′E ; Kango, G., 0°09′N, 10°08′E ; Kasongo Lunga Falls-Tembo Falls, Z, 07°34′S, 17°17′E ; Kinkala, C, 04°18′S, 14°49′E ; Kisangani, Z, 00°33′N, 25°14′E ; Kongana, CAR, 02°47′N, 16°25′E ; Koteli, Z, 02°52′N, 24°33′E ; Kotto-Barambi, CM, 04°28′N, 09°15′E ; Kribi, CM, 02°56′N, 09°56′E ; Kundelungu, Z, 09°50′S, 27°47′E ; Kunungu, Z, 02°06′S, 16°26′E ; Lac Tumba, Z, 01°05′S, 18°09′E ; La Maboké, CAR, 03°54′N, 17°53′E ; Lesse, Z, 00°45′N, 29°48′E ; Lolodorf, CM, 03°14′N, 10°44′E ; Lomie Distr., CM, 03°30′N, 13°30′E ; Londo, CAR, 03°37′N, 17°04′E ; Longji, CM, 03°04′N, 09°59′E ; Lukafu, Z, 10°31′S, 27°33′E ; Mabwe, Upemba NP, Z, 08°41′S, 26°31′E ; Mainyu Bridge, Mamfe, CM, 05°46′N, 09°17′E ; Makaia N'Tete, Z, 05°37′S, 13°05′E ; Makoua, C, 00°15′S, 15°40′E ; Mamfe, CM, 05°46′N, 09°17′E ; Manguredjipa, Z, 00°21′N, 28°44′E ; Mankaketi, near Bolobo, Z, 02°11′S, 16°20′E ; Mawambi, Z, 01°05′N, 28°35′E ; M'Bigou, G, 01°53′S, 11°56′E ; Medje, Z, 02°25′N, 27°18′E ; Metet, CM, 03°26′N, 11°45′E ; Minkan, near Kiango, CM, 03°01′N, 10°55′E ; Molegbwe, Z, 04°12′N, 20°53′E ; Moloundou, CM, 02°03′N, 15°14′E ; Mueli, CM, 04°23′N, 09°07′E ; Mundame, CM, 04°35′N, 09°31′E ; Mushi (or Muschie), Z, 03°01′S, 16°55′E ; N'Djole, G, 00°07′S, 10°45′E ; Niaji, N, 05°19′N, 08°34′E ; Niapu, Z, 02°25′N, 26°31′E ; Ndiki, CM, N'Djolé, G, 0°11′S, 10°45′E ; Niangara, Z, 03°42′N, 27°52′E ; Niede River, near Nkali, CM, 02°40′N, 11°50′E ; Nkolefong, N. W. of Sangmelima, CM, 02°56′N, 11°58′E ; Obala, Betouri Distr., CM,

04°15′N, 14°15′E ; Oban, N, 05°17′N, 08°33′E ; Okoiyongo, CM, Ossa Lake, between Sanaga and, CM, ca 03°49′N, 10°08′E ; Panga, Z, 01°51′N, 26°25′E ; Pemba Nyambi, G, 01°54′S, 09°27′E ; Poko Welle, Z, 03°09′N, 26°53′E ; Sakbayémé, CM, 04°02′N, 10°34′E ; Salo2, CAR, 03°10′N, 16°03′E ; Sangmelima, CM, 02°56′N, 11°59′E ; Souanké, C, 02°05′N, 14°03′E ; Temvo, Z, 05°30′S, 13°01′E ; Victoria, CM, 04°10′N, 09°10′E ; Yaoundé, CM, 03°52′N, 11°31′E ; Yaoundé District, CM, ca 03°45N, 11°30′E ; Yenagoa, N, 04°55′N, 06°15′E ; Yombi, G, 02°14′S, 11°56′E.

APPENDIX 3

Institutions housing study specimens

AMNH American Museum of Natural History, New York, NY, USA
BMNH The Natural History Museum, London, UK
MC Marc Colyn Collection, Paimpont, France
FMNH Field Museum of Natural History, Chicago, IL., USA
IRSNB Royal Institute of Natural Sciences, Brussels, Belgium
MCZ Museum of Comparative Zoology, Cambridge, MA, USA
MHNC Musée d'Histoire naturelle, La Chaux-de-Fonds, Switzerland
MHNG Muséum d'Histoire naturelle, Genève, Switzerland
MNHN Musée National d'Histoire naturelle, Paris, France
MNHU Museum für Naturkunde der Humboldt-Universität Berlin, Berlin, Germany
NMNH National Museum of Natural History, Washington, D.C., USA
NRST Riksmuseet Stockholm, Stockholm, Sweden
PCM The Powell-Cotton Museum, Birchington, UK
RMCA Royal Museum for Central Africa, Tervuren, Belgium
SMF Forschungsinstitut & Naturmuseum Senckenberg, Frankfurt, Germany
SMNS Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
ZFMK Zoologisches Forschungsinstitut & Museum A. Koenig, Bonn, Germany
ZSM Zoologische Staatssammlung, München, Germany

APPENDIX 4A

Basic statistics (in mm) of 17 skull characteristics of Xenogale naso.

	X. n. naso (« NASO »)						*X. n. almodovari* (« ALMO »)					
VAR	N	MIN	MAX	MEAN	SD	SE	N	MIN	MAX	MEAN	SD	SE
GSL	15	104.7	115.4	109.6	3.57	0.92	47	104.2	122.4	111.3	4.27	0.62
CBL	14	100.8	111.0	106.0	3.45	0.92	45	100.0	118.6	107.5	3.81	0.57
ROL	21	39.4	40.3	37.8	1.73	0.38	50	34.7	42.5	37.7	1.74	0.25
PAL	19	51.8	60.9	56.0	2.78	0.64	49	52.7	63.6	56.7	2.49	0.36
MAX	21	36.3	41.6	38.7	1.61	0.35	51	35.0	41.6	38.4	1.23	0.17
TYM	15	18.4	21.7	19.8	0.95	0.24	47	18.1	22.7	20.6	1.02	0.15
CAN	19	19.0	24.2	21.8	1.30	0.30	51	19.7	25.6	22.3	1.37	0.19
ROB	17	25.2	29.8	27.1	1.45	0.35	51	24.2	31.7	27.3	1.54	0.22
IOB	17	19.3	23.5	21.2	1.22	0.30	50	18.1	24.8	21.6	1.48	0.21
PAB	21	27.9	34.8	30.9	1.52	0.33	51	26.4	34.8	30.6	1.69	0.24
ZYG	16	48.5	60.4	55.6	3.16	0.79	48	48.5	66.4	56.6	3.62	0.52
BRB	16	34.1	38.5	35.7	1.11	0.28	50	32.9	38.4	35.6	1.29	0.18
MAS	14	38.3	44.1	40.6	1.61	0.43	47	38.0	46.8	41.6	2.27	0.33
BRH	15	28,2	31.4	29.9	0.91	0.24	48	27.3	31.7	29.7	1.11	0.16
MAL	21	68.8	79.0	73.4	2.89	0.63	50	68.6	78.8	73.2	2.40	0.34
MAN	21	42.2	48.0	44.5	1.65	0.36	50	41.3	48.0	44.5	1.55	0.22
CMH	19	27.3	32.0	29.6	1.39	0.32	50	27.3	34.6	30.0	1.55	0.22

APPENDIX 4B

	X. n. microdon (« MICR »)						*X. naso* ssp. (« SSP ? »)					
VAR	N	MIN	MAX	MEAN	SD	SE	N	MIN	MAX	MEAN	SD	SE
GSL	18	97.2	115.0	106.5	4.73	1.12	27	96.7	115.7	103.4	4.58	0.88
CBL	15	97.0	110.8	104.3	4.28	1.11	26	94.0	106.9	100.8	3.44	0.68
ROL	21	32.0	39.4	35.6	1.95	0.43	29	27.5	36.8	34.2	1.75	0.33
PAL	21	49.3	60.4	53.9	2.77	0.60	29	47.9	58.6	53.2	2.35	0.44
MAX	21	33.5	39.8	37.0	1.66	0.36	29	33.8	38.6	35.7	1.22	0.12
TYM	16	19.4	21.6	20.3	0.57	0.14	26	18.0	21.4	19.8	0.87	0.17
CAN	21	18.4	24.6	21.3	1.88	0.41	29	17.4	23.2	20.3	1.67	0.31
ROB	18	24.0	27.7	25.8	1.17	0.28	29	21.7	28.3	25.2	1.53	0.28
IOB	17	18.2	22.9	20.4	1.48	0.36	29	17.3	22.6	19.6	1.45	0.27
PAB	22	28.4	33.0	30.7	1.35	0.29	29	27.7	32.1	29.9	1.17	0.22
ZYG	19	49.1	60.2	54.0	4.79	0.87	29	46.5	60.1	51.5	3.69	0.68
BRB	20	31.5	36.1	34.5	1.29	0.29	29	31.6	36.0	33.2	0.94	0.18
MAS	14	38.2	43.0	39.9	1.25	0.33	26	34.5	41.9	37.8	1.83	0.36
BRH	17	27.8	33.0	29.9	1.27	0.31	28	26.3	30.3	28.1	1.11	0.21
MAL	21	64.7	75.1	70.5	3.30	0.72	29	61.6	72.8	67.7	2.68	0.50
MAN	21	38.7	46.5	43.0	2.06	0.45	29	37.6	44.2	41.0	1.39	0.26
CMH	21	26.6	33.0	29.7	1.87	0.41	29	23.5	30.9	27.2	1.72	0.32

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ALBIONELLA KABATAI BENZ & IZAWA, 1993 (COPEPODA : LERNAEOPODIDAE) FROM *APRISTURUS PROFUNDORUM* (GOODE & BEAN, 1896) (CHONDRICHTHYES : SCYLIORHINIDAE) IN THE NORTHWEST ATLANTIC OCEAN

by

WILLIAM E. HOGANS[1] and FERNANDO MARQUES[2]
[1]Atlantic Reference Centre
Huntsman Marine Science Centre
St. Andrews, New Brunswick
Canada EOG 2XO
[2]University of Toronto
Department of Zoology
Toronto, Ontario
Canada M5S 1S5

SUMMARY

A specimen of *Albionella kabatai* found on the cat shark *Apristurus profundorum* collected on the continental shelf in the Northwest Atlantic is described in detail. The specimen constitutes a new host and geographical record. Comparison is made between *A. kabatai* from the Northwest Atlantic and the only other known specimen of this species collected from the spatulasnout cat shark *Apristurus platyrhynchus* in the Sea of Kumano, off Japan. Aspects of the biogeography, and host specificity of *Albionella* are discussed.

Keywords : Albionella kabatai, systematics, biogeography, host record, parasitic copepod.

INTRODUCTION

The genus *Albionella* was erected by KABATA (1979) to receive four species of *Lernaeopoda* BLAINVILLE, 1822. The creation of this genus was justified entirely by differences in morphology between *Albionella* and *Lernaeopoda* males (KABATA, 1979). In describing a fifth species of *Albionella*, RUBEC and HOGANS (1988) noted that *Albionella* could be separated from *Lernaeopoda* based on the setation pattern of the first maxilla and maxilliped of females. BENZ and IZAWA (1990) elevated to six the number of *Albionella* species with the description of *A. kabatai* collected from the spatulasnout cat shark, *Apristurus platyrhynchus* (TANAKA, 1909) captured off Japan. Biogeographic data and host records for species of *Albionella* are limited.

Our find of *A. kabatai* on *Apristurus profundorum* is the first record of *Albionella kabatai* from the Northwest Atlantic and is also a new host record for this parasite.

This paper presents a detailed description of *Albionella kabatai* from the cat shark *Apristurus profundorum*. A comparison between the two known specimens of *Albionella kabatai* is made and arguments are presented to justify the species assignment of the newly found specimen. Biogeographical and host records for *Albionella* are also discussed.

MATERIAL AND METHODS

The shark host, *Apristurus profundorum*, was caught at a depth of 1250 m, on the continental slope of the Scotian Shelf, off the southern end of Georges Bank in August 1981. The parasite and host were fixed in 10 % formalin and later transferred to 70 % ethanol for storage. After dissection from host tissues, gross morphology of the copepod was studied under a dissecting microscope at magnifications of up to 400 ×. The specimen was cleared and mounted whole in 85 % lactic acid ; fine structural details of appendages were studied at magnifications up to 950x under phase contrast microscopy. Terminology follows that of Kabata (1979). Measurements are in millimeters and drawings were made with the aid of a camera lucida.

Albionella kabatai BENZ & IZAWA, 1990

(Figs 1-2)

Host : Apristurus profundorum (Scyliorhinidae)

Site of infection : bulla embedded in host's skin at base of second dorsal fin.

Locality : Continental slope of Scotian Shelf, southern end of Georges Bank, Northwest Atlantic.

Material examined : Single ovigerous female ; British Museum (Natural History) Cat. No. 1987.72.

Description :

Lernaeopodidae : Cephalothorax (Fig. 1A) short, dorsoventrally flattened, subovoid, narrow anteriorly, broadly rounded posteriorly with distinct dorsal shield. Cephalothorax separated from trunk by narrow transverse constriction. Trunk subtriangular, slightly longer than wide, narrow anteriorly, becoming progressively wider posteriorly, with rounded posterolateral corners. Uropods (UR, Fig. 1A) near center of dorsal posterior margin. Uropods (Fig. 2E) poorly developed, armed with one long naked apical seta and two short naked lateral basal setae. Egg sac (one missing) long, broad, cylindrical with rounded posterior end ; ventrolateral to uropods. Eggs multiseriate. Dimensions of specimen : total length (exclusive of egg sac) 2.83 mm ; cephalothorax length 1.27 ; trunk length 1.56, width 1.54 ; egg sac length 1.80, width 0.58 ; second maxillae length 2.63.

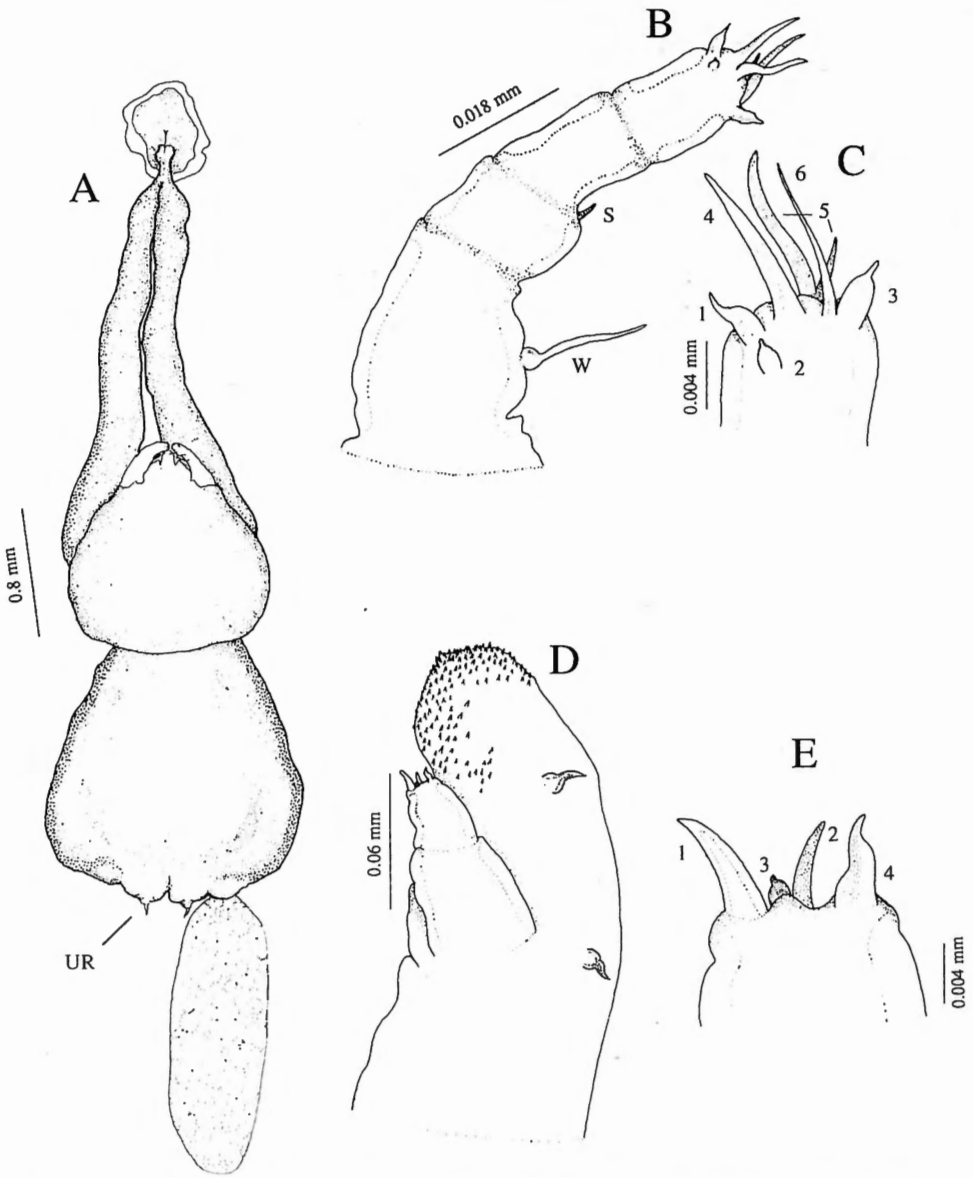

Fig. 1. — *Albionella kabatai* — (A) Habitus dorsal — (B) First antenna — (C) Same, tip — (D) Second antenna — (E) Same, tip.

First antenna (Fig. 1B and 1C) indistinctly four-segmented ; basal segment inflated, whip and solus present (W and S, Fig. 1B) ; apical armature (Fig. 1C) comprising tubercles (1, 2, and 3), digitiform seta (4), slender seta (6), and complex (5) of two setae. Second antenna (Fig. 1D and 1E) sympod indistinctly segmented ;

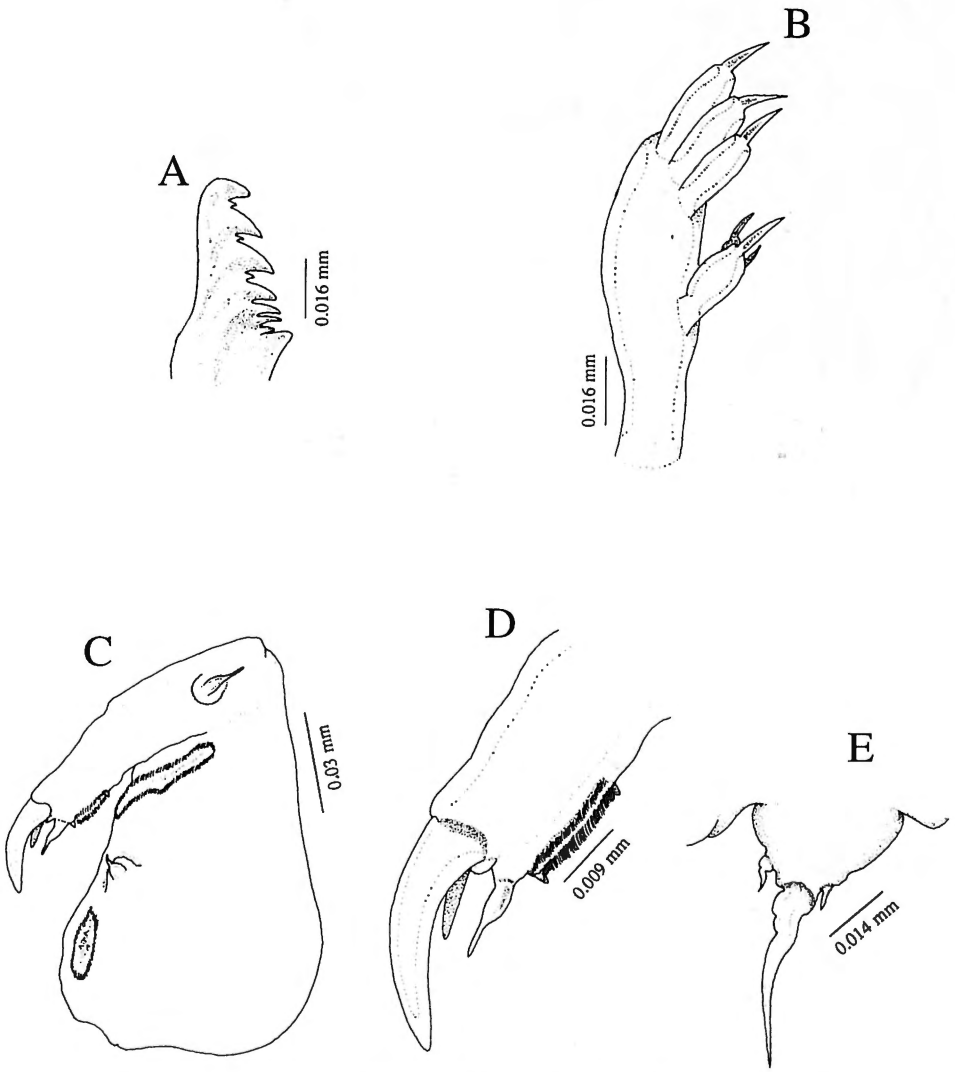

Fig. 2. — *Albionella kabatai* — (A) Mandible — (B) First maxilla — (C) Maxilliped — (D) Apex maxilliped shaft — (E) Caudal ramus.

exopod unsegmented, bulbous, much larger than endopod, bearing two prominent sensory papillae; apical and medial surfaces extensively spinulated. Endopod indistinctly two-segmented, apical armature (Fig. 1E) consisting of reduced hook (1), slender seta (2), dorsal tubercle (3), and ventral process (4). Labrum not viewed. Mandible (Fig. 2A) with narrow base and wide blade, dental formula P1, S1, P1, S1, P1, S1, B4. First maxilla (Fig. 2B) with lateral exopod carrying three naked setae, one long, two short; dorsolateral margin of exopod no spinulated;

endopod with three long, stout terminal papillae bearing short, stout setae. Second maxilla (Fig 1A) slender, cylindrical, much longer than trunk (second maxilla to trunk length ratio 1.7:1), separated from opposite second maxilla except where the inner margins are fused at apex. Bulla expanded distally into flattened subquadrangular plate (Fig. 1A). Manubrium slender. Maxilliped (Fig. 2C and 2D) with stout corpus; myxal area armed with two spinulated pads and a stout spiniform seta; subchela with long shaft bearing one long, stout seta on ventral surface; tip of subchela (Fig. 2D) with large recurved claw, two small processes at each end of two rows of finely arrayed denticles on inner margin; claw with one secondary barb at base.

DISCUSSION

As described by BENZ and IZAWA (1990), the exopod of the second antenna of *A. kabatai* displays a bluntly rounded denticulous apex with one truncated and one blunt lateral spine. In our specimen, no truncated spine was found; instead two sensory papillae were observed. BENZ and IZAWA (1990) also described the endopod of the second antenna as having a medial denticulous patch and apically bearing one robust and claw-like, and two thin spiniform elements. The Northwestern Atlantic specimen differs by lacking the medial denticulous patch and having an additional dorsal tubercle on the apical armature of the second antenna. The mandible of the specimen described from the Sea of Kumano exhibited the formula P1, S1, P1, S1, P1, S1, B3; whereas the Northwestern Atlantic specimen was characterized by the following formula : P1, S1, P1, S1, P1, S1, B4. However, as pointed out by KABATA (1964) and RUBEC and HOGANS (1988), the mandibular tooth formula of adult male and female lernaeopodids may vary intraspecifically. The exopod of the first maxilla in the Japanese *A. kabatai* specimen bears three apical setae : two long and one short. In our specimen, there is one long and two short setae.

The occurrence of *Albionella kabatai* in the Northwestern Atlantic on *A. profundorum*, does not suggest that the present specimen is a distinct species from that collected in Japanese waters on *A. platyrhynchus* since other species of *Albionella* display similar geographical distribution. For instance, *A. longicauda* (HANSEN, 1923) was found living on *Centrophorus squamosus* (BONNATERRE, 1988) in Iceland, whereas, in Japanese waters this species parasitizes *C. acus* GARMAN, 1906 and *C. granulosus* (BLOCH and SCHNEIDER, 1801). *A. etmopteri* (YAMAGUTI, 1939) was found on *Etmopterus lucifer* JORDAN and SNYDER, 1902 in Japan while found on an unknown species of *Etmopterus* in South Africa (KABATA, 1979). Alternatively, one species of host may be parasitized by more than one species of *Albionella*. For instance, *Centroscyllium fabricii* (REINHARDT, 1825) was found to be parasitized by *Albionella centroscyllii* (HANSEN, 1923) and *A. fabricii* RUBEC and HOGANS, 1988 (KABATA, 1979).

Deep-sea parasitic copepods are infrequently collected and many species are known only from single specimens (BENZ and IZAWA, 1990). At this moment, the

differences observed between the two existing specimens either justify the erection of a species for the Northwestern Atlantic specimen or suggest intraspecific variability. We consider the present specimen as *Albionella kabatai* for two reasons : (*i*), host shifting is not uncommon within *Albionella* ; (*ii*), due to the lack of available specimens which would provide a range of intraspecific variability, we cannot assume that the differences found between two specimens are sufficient to erect a new species.

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BOOK REVIEW

Traité de Zoologie : Tome VII : *Crustacés,* premier fascicule (Éditions Masson, 1994).

Enfin, le premier des trois épais fasicules qui doivent couvrir l'ensemble des Crustacés dans le prestigieux *Traité de Zoologie* de P.-P. Grassé, vient de paraître. Les Zoologistes francophones et européens attendaient avec impatience la sortie de presse de cet important volet de l'impressionnant *Traité de Zoologie,* devenu ouvrage de référence par excellence. Mis en chantier il y a 15 ans, l'ouvrage connut pas mal de viscissitudes avant d'arriver à sa conception actuelle et à l'édition finale. Il faut savoir gré à Jacques Forest du Musée d'Histoire Naturelle de Paris, d'avoir mené à bien le travail ingrat d'éditeur scientifique, et d'avoir obtenu des auteurs une mise à jour *up to date* de leurs contributions.

Ce premier fascicule, fort de 917 pages et de 434 figures, concerne les aspects généraux de la biologie des Crustacés, c'est-à-dire la morphologie, la physiologie, la reproduction et l'embryologie. Deux autres fascicules, probablement de volume égal à celui-ci, traiteront de la systématique des Crustacés, ainsi que de l'écologie, l'éthologie et la biogéographie.

Après un court chapitre introductif, sous la plume de l'éditeur Jacques Forest, qui justifie la notion de « Super classe des Crustacés » et résume les grandes étapes de leur classification, on trouve un chapitre d'une quarantaine de pages, rédigé par H.-E. Gruner de Berlin, qui décrit en détail les particularités morphologiques permettant de relier le développement ontogénique des Crustacés à leur phylogénie et à leur classification, à savoir la notion de tagmes, les étapes de la segmentation et la morphologie des appendices.

Le chapitre « Tégument : morphologie et biochimie », par G. Goffinet et Ch. Jeuniaux, présente une synthèse de nos conceptions les plus actuelles concernant l'architecture ultrastructurale de la cuticule, cette cuticule chitinoprotéique « qui fait l'arthropode », synthèse illustrée par de très nombreuses microphotographies au microscope électronique à transmission. Ce chapitre aborde également les modifications cycliques du tégument au cours du cycle de mue. Un aspect particulier de la biologie du tégument, à savoir la pigmentation et la nature des changements de couleur, est envisagé ensuite par Y. Noël (CNRS) et C. Chassard-Bouchaud (Paris VI) en un court chapitre synthétique.

Un gros chapitre de près de 90 pages est consacré à la mue, à l'autotomie et à la régénération, sous la plume de M^{me} G. Vernet et de M^{me} Charmantier-Daurès, de Montpellier. On y trouvera évidemment la définition et la caractérisation des stades de mue dans les principaux groupes de Crustacés, et une analyse approfondie des aspects physiologiques de la mue et de la régénération des appendices, notam-

ment leur contrôle hormonal. L'étude de la mue conduit tout naturellement à celle de la croissance et à l'origine des allométries de croissances, sujet traité par A. Mayrat.

La partie consacrée au système nerveux (110 pages) est subdivisée en deux chapitres. La cytologie, l'histologie et l'anatomie sont décrites par J. Chaigneau, de Poitiers, tandis que les neurohormones sont envisagées par G. Martin, lui aussi de Poitiers, et on retrouve ici toute la compétence de l'école de Poitiers. C'est également J. Chaigneau qui présente, en une belle synthèse, l'état des connaissances sur les organes des sens mécanorécepteurs et chémorécepteurs, sans oublier l'énigmatique « organe de Bellonci ». Un court chapitre, traité par H.-E. Gruner, de Berlin, est dévolu aux organes lumineux et à la luminescence.

L'anatomie de l'appareil circulatoire et celle du système digestif font l'objet de deux chapitres traités de manière classique, l'un par A. Mayrat, l'autre par H.-J. Ceccaldi, où on regrettera peut être le maigre développement de la physiologie et de la biochimie de la digestion (3 pages). Par contre, les aspects biochimiques de l'osmorégulation et de la régulation osmotique intracellulaire sont largement développés dans le chapitre « osmorégulation », dû à la collaboration de E. Schoffeniels et G. Dandrifosse, de Liège, où on trouvera notamment un grand tableau exhaustif de la pression osmotique comparée de l'hémolymphe et de l'urine par rapport à celle du milieu extérieur, à travers l'ensemble de la classe des Crustacés (ce tableau s'étend sur 12 pages !).

Après un chapitre sur les organes endocriniens, fort bien traité par M^{me} Charmantier-Daurès et Guy Charmantier, de Montpellier (organe Y, organes mandibulaires, glandes antennaires), le reste du volume, soit environ 260 pages, est réservé au sexe et à la reproduction. On y trouve un vaste panorama de la physiologie sexuelle, de la vitellogenèse et du contrôle de l'expression des caractères sexuels secondaires (sous la plume des spécialistes de l'école de Poitiers, J.-J. Legrand et P. Juchault) ainsi qu'une minutieuse description des gamétogenèses et des mécanismes de la fécondation dans les différents groupes de Crustacés, par M^{me} Pochon-Masson, de Paris VI. L'ouvrage s'achève par un vaste chapitre (80 pages) sur le développement embryonnaire, dû à P. Weygoldt, de Freiburg, qui décrit les différentes variantes du mode de segmentation de l'œuf fécondé et du mode de formation des feuillets germinatifs, ainsi que les modalités de la morphogenèse.

Le tome consacré aux Crustacés parachève ainsi l'œuvre magistrale entreprise par P.-P. Grassé, il y a bientôt 50 ans, ce « Traité de Zoologie » qui porte son nom et qui reste, plus que jamais, l'ouvrage de référence obligé et indispensable pour les chercheurs comme pour les enseignants.

Ch. JEUNIAUX.

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