The anatomy of *Euphanerops longaevus* Woodward, 1900, an anaspid-like jawless vertebrate from the Upper Devonian of Miguasha, Quebec, Canada

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Janvier P. & Arsenault M. 2007. — The anatomy of *Euphanerops longaevus* Woodward, 1900, an anaspid-like jawless vertebrate from the Upper Devonian of Miguasha, Quebec, Canada. *Geodiversitas* 29 (1): 143-216.

ABSTRACT
The anatomy of the Upper Devonian jawless vertebrate *Euphanerops longaevus* Woodward, 1900, from the Escuminac Formation of Miguasha, Quebec, Canada, is described on the basis of new specimens, some of which display what is regarded here as an extensively mineralized endoskeleton that is essentially made of calcium phosphate, with traces of diagenetic calcite and silicate. Most of the mineralized elements of *E. longaevus* display the same spongiose microstructure, which notably occurs in such undoubtedly endoskeletal elements, as the fin radials, and this suggests that they all are actually endoskeletal elements. Their structure consists of groups of large, generally paired, ovoid spaces that recall the chondrocytes of lamprey cartilage, and are therefore referred to as "chondrocyte spaces". The latter are surrounded by a shell of "mineralized territorial matrix", and cemented by a finely spherulitic "mineralized interterritorial matrix" that extends between them. The question whether this mineralized tissue is an unusual form of biogenic calcified cartilage, or an authigenic, microbially induced *post-mortem* phosphatization, is discussed, but no definite answer is proposed. The snout of *E. longaevus* displays three "head stains" that may be either the imprints of the collapsed median olfactory organ and paired eyes, or traces of cartilaginous plates arming the snout. In large specimens, these are followed posteriorly by a large patch of mineralized tissue tentatively

interpreted as a braincase. The branchial apparatus consists of an elongated, cone-shaped "basket", composed of at least 30 vertical, sinuous gill arches, and extending from beneath the presumed braincase to the anal region. The gill arches bear a large number of more or less horizontal gill ray-like mineralized rods, which probably supported the gill filaments. The gill arches seem to have been attached dorsally and ventrally to series of massive endoskeletal elements, referred to as the "copular elements". The ventral series of copular elements is prolonged anteriorly by a median "anterior ventral rod", which extends to a ring-shaped structure, the "annular cartilage". The homology of the latter to the annular cartilage of lampreys remains uncertain. The position of the heart remains problematical, despite the possible presence of a pericardiac cartilage at the rear of the branchial basket. The viscera were housed dorsal to the branchial apparatus, and comprised a large stomach containing fine-grained sediment, but the organization of the digestive tract and its relations to the branchial apparatus remains unknown in detail. The axial skeleton clearly displays complete dorsal and ventral series of arcualia, ventrally to which extends a series of elements referred to as "haemal series". The anal fin radials are supported by large "anal fin supports". *E. longaevus* is regarded here as having possessed thin paired fin radials, arranged in ventrolateral series, which diverge anteriorly, like in anaspids, but this species is unique among vertebrates in having paired fins that extend ventrolaterally to the branchial apparatus. Many anatomical features of *E. longaevus* remain nevertheless unexplained, such as the "white line" and the "black lines", tentatively interpreted here as blood vessels. Peculiar mineralized elements, referred to as the "intermuscular elements" and "diffuse mineralized matter", have no equivalent in other vertebrates and may either have been endoskeletal elements housed in intermuscular connective tissues of the trunk, or haphazardly distributed authigenically phosphatised soft tissues. The oblique, elongated imprints, variously referred to as "scales", or "myomere imprints" in previous descriptions, are only seen in the smaller and poorly mineralized individuals but their nature remains unknown. The sediment in the stomach contents rather suggests microphagous bottom feeding. The Late Devonian *Endeiolepis aneri* Stensiö, 1939 (a probable junior synonym of *E. longaevus*) and the Middle Devonian *Achanarella trewini* Newman, 2002 and *Cornovichthys blaauweni* Newman & Trewin, 2001 share with *E. longaevus* the same organization of the three "head stains" and the same structure and elongation of the branchial apparatus. These four taxa are thus likely to form a clade, the Euphaneropidae. The Lower Silurian *Jamoytius kerwoodi* White, 1946, may also turn out to belong to this clade. Owing to the uncertainty as to the biogenic or diagenetic nature of the anatomical features described in *E. longaevus*, no character analysis is proposed. Only a few possible homologies are uniquely shared by euphaneropids and either lampreys or anaspids, or both.

KEY WORDS
Vertebrata,
Euphaneropidae,
Devonian,
taphonomy,
anatomy,
homologies.

RÉSUMÉ
*L'anatomie d'*Euphanerops longaevus *Woodward, 1900, un vertébré sans mâchoires ressemblant à un anaspide et provenant du Dévonien supérieur de Miguasha, Québec, Canada.*
L'anatomie du vertébré sans mâchoires du Dévonien supérieur *Euphanerops longaevus* Woodward, 1900, de la Formation d'Escuminac, Miguasha, Québec, Canada, est décrite à partir de nouveaux spécimens, dont certains présentent des structures considérées ici comme un endosquelette complètement minéralisé et

constitué essentiellement par du phosphate de calcium, avec quelques traces de calcite et de silicates d'origine diagénétique. La plupart des éléments minéralisés d'*E. longaevus* présentent la même microstructure vacuolaire, que l'on trouve principalement dans des éléments aussi indiscutablement endosquelettiques que les radiaux des nageoires. Tous les éléments présentant cette structure sont donc également endosquelettiques. Leur structure consiste en des groupes de grands espaces ovoïdes, généralement pairs, qui rappellent les chondrocytes du cartilage des lamproies et sont donc ici appelés « lacunes chondrocytaires ». Ces derniers sont tapissés par une couche de « matrice territoriale minéralisée » et cimentés par une « matrice interterritoriale minéralisée » finement sphérulitique qui remplit les espaces les séparant. La question de l'origine de cette minéralisation, qu'elle soit une forme inhabituelle de cartilage calcifié d'origine biogénique ou une calcification authigénique *post-mortem* d'origine microbienne, est discutée, bien qu'aucune réponse définitive n'y soit apportée. L'extrémité antérieure de la tête d'*E. longaevus* présente trois « taches céphaliques » qui peuvent être soit les empreintes d'un organe olfactif médian et de capsules optiques paires, soit les traces de plaques cartilagineuses armant le museau. Chez les spécimens de grande taille, leur fait suite postérieurement une importante masse de tissu minéralisé interprété avec réserves comme un neurocrâne. L'appareil branchial est constitué d'une « corbeille branchiale » en forme de cône allongé et composée d'au moins 30 arcs branchiaux verticaux et sinueux qui s'étendent depuis le neurocrâne présumé jusqu'à la région anale. Les arcs branchiaux portent un grand nombre de baguettes minéralisées plus ou moins horizontales, qui évoquent des rayons branchiaux et soutenaient probablement les filaments branchiaux. Les arcs branchiaux semblent avoir été attachés dorsalement et ventralement à des séries d'éléments endosquelettiques massifs nommés ici « éléments copulaires ». La série ventrale d'éléments copulaires se prolonge antérieurement par une « barre ventrale antérieure » médiane qui atteint une structure annulaire, le « cartilage annulaire ». L'homologie de cette dernière avec le cartilage annulaire des lamproies reste incertaine. La position du cœur reste problématique, en dépit de la présence possible d'un cartilage péricardique à l'arrière de la corbeille branchiale. La masse viscérale était située dorsalement par rapport à l'appareil branchial et comprenait un estomac volumineux contenant un sédiment à grain fin, mais l'organisation du tube digestif et ses relations à l'appareil branchial restent inconnues dans le détail. Le squelette axial présente clairement des séries dorsale et ventrale d'arcualia, ventralement auxquelles s'étend une série d'éléments appelés ici « série hémale ». Les radiaux de la nageoire anale sont articulés sur de grands « éléments de soutien de la nageoire anale ». *E. longaevus* est considéré ici comme ayant de fins radiaux des nageoires paires, disposés en séries ventro-latérales et divergeant antérieurement, comme chez les anaspides ; cependant cette espèce est singulière parmi les vertébrés par le fait que ses nageoires paires s'étendent ventro-latéralement à l'appareil branchial. De nombreux caractères anatomiques d'*E. longaevus* restent néanmoins inexpliqués, comme la « ligne blanche » ou les « lignes noires », interprétées avec réserves comme des vaisseaux sanguins. D'étranges éléments minéralisés appelés ici « éléments intermusculaires » et « matière minéralisée diffuse » n'ont pas d'équivalents chez d'autres vertébrés et pourraient être soit les éléments endosquelettiques logés dans les tissus conjonctifs du tronc, soit des tissus mous calcifiés authigéniquement et distribués au hasard. Les empreintes allongées et obliques considérés soit comme des « écailles », soit comme des « traces de myomères » dans les descriptions

antérieures, ne sont observées que sur les petits spécimens faiblement minéralisés, mais leur nature demeure inconnue. Le sédiment formant le contenu stomacal suggère plutôt un régime alimentaire microphage limivore. *Endeiolepis aneri* Stensiö, 1939 (synonyme junior probable d'*E. longaevus*), du Dévonien supérieur, ainsi qu'*Achanarella trewini* Newman, 2002 et *Cornovichthys blaauweni* Newman & Trewin, 2001, du Dévonien moyen, partagent avec *E. longaevus* la même organisation des trois « taches céphaliques » et la même élongation de l'appareil branchial. Ces quatre taxons appartiennent donc probablement à un même clade, les Euphaneropidae. *Jamoytius kerwoodi* White, 1946, du Silurien inférieur, pourrait également s'avérer appartenir à ce même clade. En raison de l'incertitude quant à l'origine biogénique ou diagénétique des structures décrites chez *E. longaevus*, aucune analyse de caractère ne peut être sérieusement proposée. Seules quelques homologies possibles sont partagées uniquement par les Euphaneropidae ou par ces derniers et soit les lamproies, soit les anaspides, soit ces trois taxons.

MOTS CLÉS
Vertebrata,
Euphaneropidae,
Dévonien,
taphonomie,
anatomie,
homologies.

CONTENTS

INTRODUCTION

Euphanerops longaevus was first described by Woodward (1900), on the basis of a single specimen (BMNH P.6813, Figs 1; 2) collected by Mr. Jex from the Upper Devonian (lower Frasnian) Escuminac Formation at the Miguasha cliff (Quebec, Canada), and presented to the Natural History Museum, London. Woodward considered at first that *E. longaevus* could be referred to either the "Cephalaspida" (Osteostraci) or the Anaspida, a taxon described one year earlier by Traquair (1899) from the Silurian of Scotland. Shortly after, Woodward (1902) clearly referred it to the Anaspida, but he still oriented it upside down (Fig. 1), as did Traquair for the Scottish anaspids. Both authors considered that, by analogy with many other Palaeozoic fishes,

anaspids possessed an epicercal tail. The hypocercal condition of the anaspid tail was demonstrated later by Jaekel (1911). Then, the systematic position of *E. longaevus* among the Anaspida was not subsequently questioned (Kiaer 1924; Stensiö 1939, 1958, 1964; Moy-Thomas & Miles 1971; Jarvik 1980) until more recently, when a precise definition of the Anaspida was required in the framework of phylogenetic analyses (e.g., Janvier 1981a, 1996b, c; Forey 1984; Maisey 1986; Gagnier 1993a, b; Forey & Janvier 1994; Donoghue *et al.* 2000; Donoghue & Smith 2001).

Euphanerops longaevus has long remained known only by its holotype, until a second, well preserved specimen was discovered in 1982 (Figs 3; 18), and a third, imperfect one shortly after (Fig. 4A, B). However, owing to some differences in the relative position of the anal fin, development of the presumed "squamation" and alleged presence of a dorsal fin, now regarded as artefacts of preservation, Arsenault & Janvier (1991; see also Janvier 1996a) referred them to a new genus and species, *Legendrelepis parenti*. This taxon is considered as a junior synonym of *E. longaevus*.

Euphanerops longaevus has been referred to as an anaspid, chiefly because of its distinctive hypocercal tail and anal fin (Figs 1-3), which are in many respects similar to those of the Anaspida from the Silurian of Scotland (*Birkenia*, *Lasanius*) and Norway (*Pharyngolepis*, *Pterygolepis*, *Rhyncholepis*), known from complete, articulated specimens (see e.g., Traquair 1899; Kiaer 1924; Simpson 1926; Stetson 1928; Heintz 1958; Parrington 1958; Ritchie 1964, 1980; Blom *et al.* 2001). However, since it apparently has no mineralized dermal skeleton, *E. longaevus* lacks evidence for the tri-radiate postbranchial spine, which Forey (1984) proposed as the defining character of the Anaspida. Consequently, it is now often treated in recent phylogenetic analyses as a separate terminal taxon, alongside other scale-less (or "naked") jawless vertebrate taxa also once regarded as anaspids, namely *Endeiolepis aneri* Stensiö, 1939 and *Jamoytius kerwoodi* White, 1946. Arsenault & Janvier (1991) pointed out the presence of an extremely elongated branchial apparatus (with about 30 gill bars), in *E. longaevus* ("*Legendrelepis parenti*") (ga, Fig. 3) and regarded

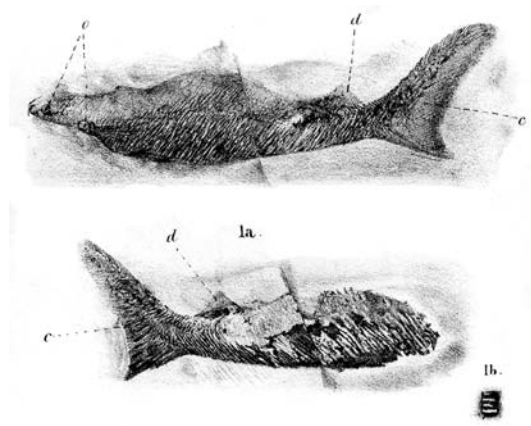


FIG. 1. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; holotype (BMNH P.6813), facsimile of Woodward's (1900) original illustration (part and counterpart ["1a"], and detail of a "scale" ["1b"]). Notice the upside down orientation of the specimen, as the caudal fin was thought to be epicercal. Original abbreviations: **o**, orbits; **c**, caudal fin; **d**, dorsal fin.

this condition as derived. As will be discussed below, such a very elongate branchial apparatus, reaching to the anal region, may be more widespread among the Palaeozoic "naked" jawless vertebrates than previously believed.

Despite the recent discovery of several, outstandingly preserved specimens, the anatomy of *E. longaevus* remains largely enigmatic. The present study rests on what we can infer mainly from the morphology of the Anaspida and lampreys, which remain the closest fossil and living "proxies", respectively, for this species, and despite the lack of any information about the internal anatomy of anaspids (the alleged evidence for an axial skeleton in anaspids [Smith 1956] is now known to be erroneous, as it refers to a displaced branchial plate observed in radiographs). However, many of the structures observed on the available specimens of *E. longaevus* remain unexplained or, at the best, ambiguous. Notably, there is much uncertainty as to the nature of the mineralized anatomical structure that some of them display; that is, whether they are biomineralized structures, or fabrics due to *post-mortem* authigenic mineralization (see Structure and nature of the mineralized tissues, p. 154). Therefore, we generally avoid here referring to these

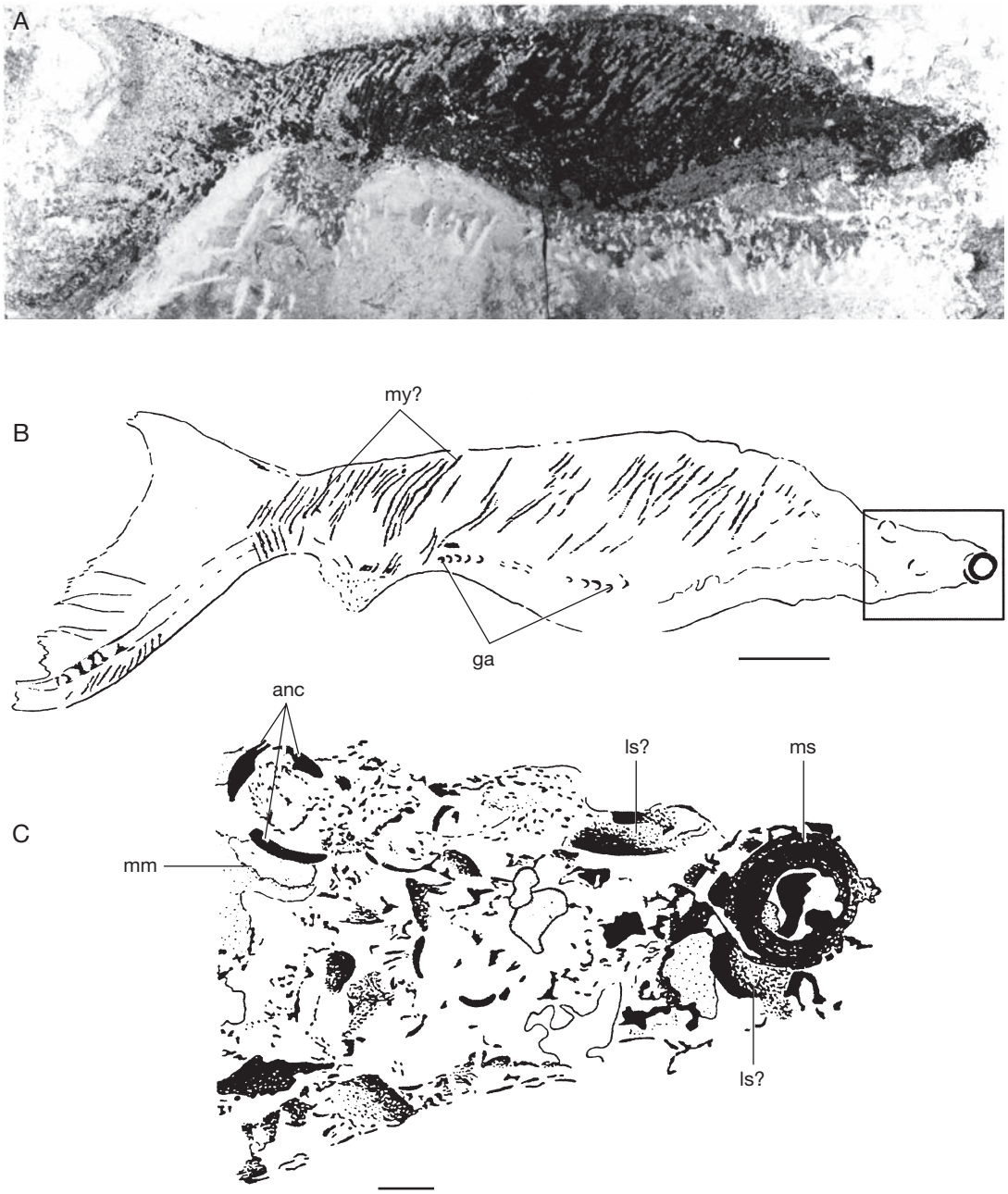


FIG. 2. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; holotype (BMNH P.6813): **A**, photograph of one part of the specimen (P.6813a); **B**, explanatory drawing; **C**, camera lucida drawing of the anterior end of the specimen (framed in B). Scale bars: A, B, 10 mm; C, 1 mm. B, C, after Arsenault & Janvier 1991: figs 2a; 3a, abbreviations modified.

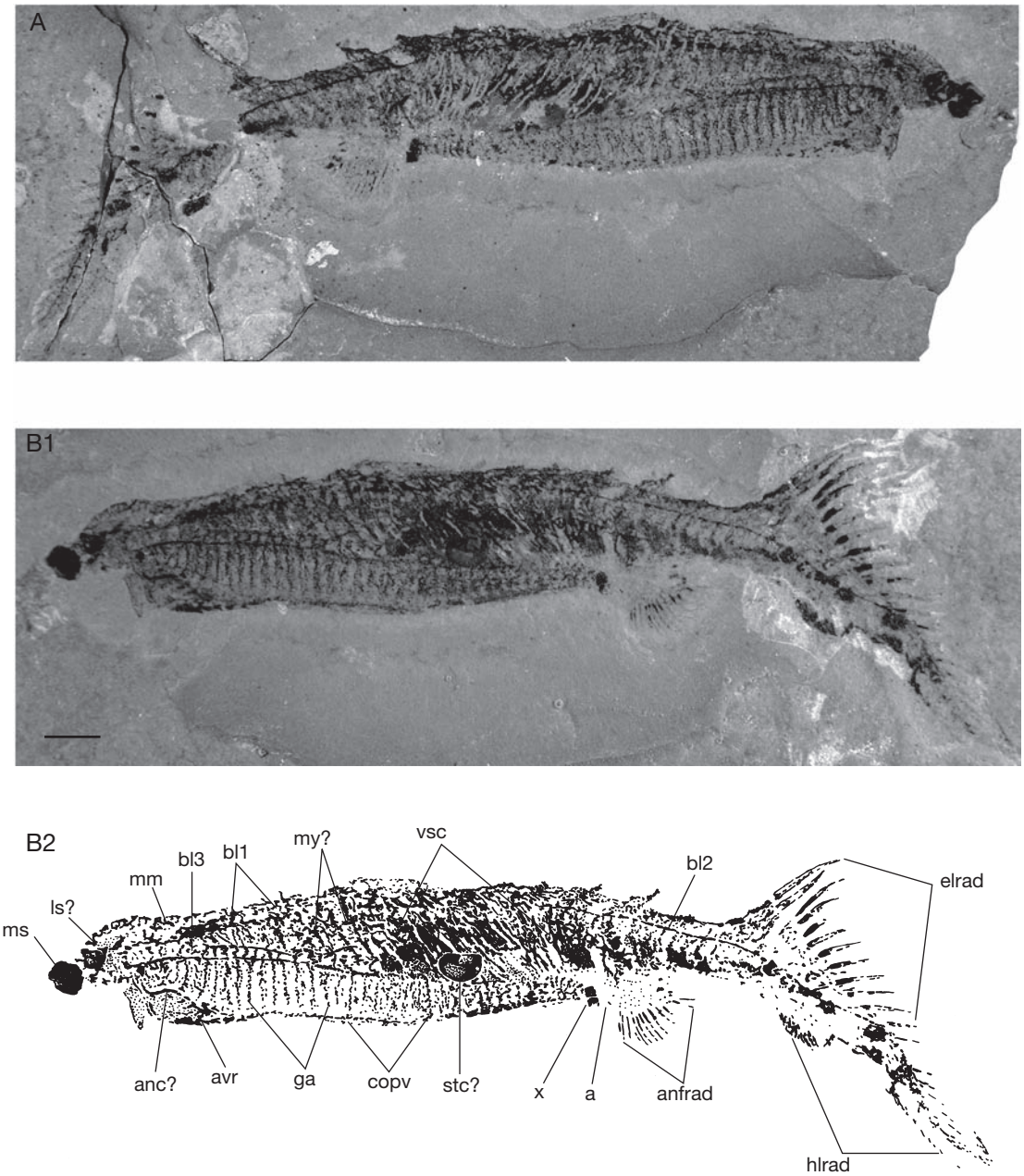


FIG. 3. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: part (**A**) and counterpart (**B1**) of a complete specimen presumably collapsed in lateral aspect [MHNM 01-02, designated by Arsenault & Janvier (1991) as the holotype of *Legendrelepis parenti*], photographed in immersion in water, and explanatory drawing based on the counterpart (B2). Scale bar: 10 mm. B2, from Arsenault & Janvier 1991, abbreviations modified.

structures with names that could misleadingly suggest a hypothesis of homology, as its has been done in earlier articles (e.g., Arsenault & Janvier 1991; Janvier 1996a-c), and we only suggest possible interpretations for some of them.

We also allude to the possibility that another anaspid-like form from Miguasha, *Endeiolepis aneri* Stensiö, 1939, could be, if not a junior synonym of *E. longaevus*, at any rate a closely similar species, preserved in different types of sediment. The so-called "ventrolateral scale series" (Stensiö 1939) of *E. aneri* is in fact either the impression, or the internal natural cast of the elongated and polybranchic branchial apparatus (Janvier *et al*. 2006).

The most impressive discovery in the new material of *E. longaevus* described here is the evidence for extensively mineralized structures in the larger – and presumably aged – individuals. These mineralized structures have been regarded as calcified cartilage by Janvier & Arsenault (2002), but, owing to its unusual aspect, their interpretation at an early stage of this study has raised questions. Initially, and before the most extensively mineralized specimens (e.g., MHNM 01-123) could be studied in detail, we even wondered if some of these mineralized structures (namely those now referred to the branchial apparatus) could not be some kind of scales. After the discovery of MHNM 01-69 (later referred to as the paratype of "*Legendrelepis parenti*"; Fig. 5A, B), one of us (MA) pointed out to the other (PJ) the still enigmatical doughnut-shaped structure described below (see Enigmatic structures, p. 193), as well as the first evidence for mineralized tissues in this form. Namely, he noticed that the area in MHNM 01-69 that corresponds to the anterior part of the branchial apparatus in the then just studied specimen MHNM 01-02 (Arsenault & Janvier 1991; Figs 3; 18) did not look the same as in the latter. Instead, this area was, in MHNM 01-69, filled with minute, vermicelli-like mineralized elements that showed a "tubular and striated structure" (MA pers. comm. to PJ 1989) and were first thought to be scales. As we shall see below, it is now probable that these structures, alongside many others observed in MHNM 01-98, 123 and 135, and other more recently discovered specimens, are in fact endoskeletal, and thus not scales. The "tubular and striated structure" referred to above is the characteristic garland-like aspect of the mineralized elements referred to here as gill arches and "gill rods" (see Structure and nature of the mineralized tissues, p. 154).

Notwithstanding the uncertainty which remains as to the cause of this mineralization, and thus as to the nature of the mineralized tissue that can be observed, we assume here that the mineralized structures described herein do provide some anatomical information.

Abbreviations

Institutional abbreviations

BMNH	Natural History Museum [formerly British Museum (Natural History)], London;
MHNM	Musée d'Histoire naturelle de Miguasha, Parc national de Miguasha, Quebec;
NHRM	Naturhistoriska Riksmuséet (Swedish Museum of Natural History), Stockholm.

Figure abbreviations

a	presumed position of the anus;
ahs	"anterior haemal series";
anc	"annular cartilage";
anfrad	anal fin radials;
anfsd	dorsal "anal fin supports";
anfsv	ventral "anal fin supports";
arc	arcualia;
arcd	dorsal acualia (basidorsals and interdorsals);
arcv	ventral arcualia (basiventrals and interventrals);
avr	"anterior ventral rod";
bl1-3	"black lines" 1 to 3;
blv?	possible imprints of blood vessels;
bra	branchial apparatus;
brc	"braincase";
brst	branching structure supporting the rearmost caudal radials;
chs	"chondrocyte spaces";
cl	compact layer mineralized lining the surface of some skeletal elements;
conprv	processes connecting the ventral "copular elements";
copd	dorsal "copular elements";
copv	ventral "copular elements";
dl	dark line along the diffuse mineralized matter;
dmm	"diffuse mineralized matter";
dss	"doughnut-shaped structure";
elrad	epichordal lobe radials;
f	longitudinal canals of fibres in the "white line";
ga	gill arch;
ga+gr	mixed fragments of gill arches and "gill rods";

gcont?	possible gut contents;
gr	"gill rods";
grl	growth lines;
hema	anterior hemibranch;
hemp	posterior hemibranch;
hlrad	hypochordal lobe radials;
hs	"head stains" (i.e. undistinguished "median" and "lateral head stains");
ime	"intermuscular elements";
ls	"lateral stains";
mitm	"mineralized interterritorial matrix";
mm	patch of "mineralized matter" in the presumed otic region;
ms	"median stain";
mtm	"mineralized territorial matrix";
my?	possible imprints of either myomeres or scales;
nch	space occupied by the notochord;
otg	outgrowth in the lumen of the "doughnut-shaped structure";
pcard?	possible pericardiac cartilage;
pfrad	paired fin radials (pfrad 1, 2, left and right series, respectively);
phs	"posterior haemal series";
sbr	side-branches of the "black lines";
sed	sediment;
sk	possible imprint of the skin lining the snout and oral region;
sp?	possible spinous processes of the gill arches;
sph	microspherulitic (globular) structure;
stc	stomach contents;
vsc	imprint of the visceral cavity;
wl	"white line";
x	carbonaceous imprints at the posterior end of the branchial apparatus;
z	enigmatic lamellar structure.

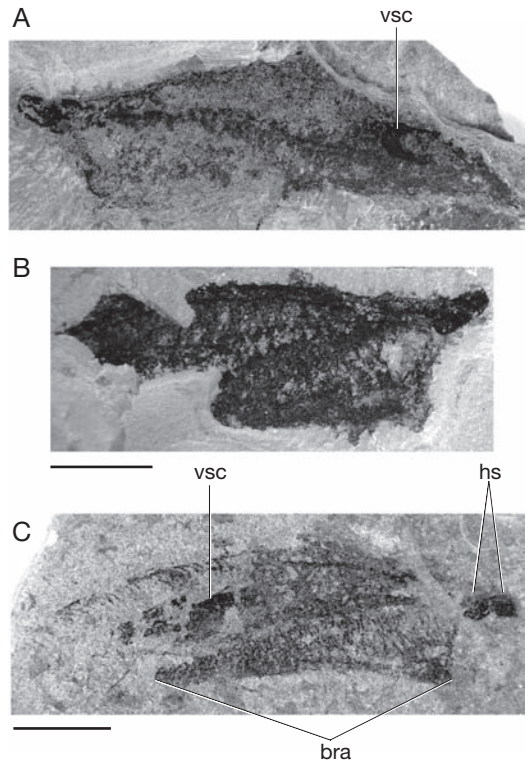


FIG. 4. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; specimens photographed in immersion in water, and showing the characteristic aspect of the anterior part of the head when collapsed in lateral aspect, with the "head stains" overhanging the anterior limit of the branchial apparatus: part (**A**) and counterpart (**B**) of an imperfect specimen (MHNM 01-69A,B), designated by Arsenault & Janvier (1991) as the paratype of *Legendrelepis parenti* (see details of the "head stains" in Figure 38); **C**, imperfect specimen (MHNM 01-130). Scale bars: 10 mm.

MATERIAL AND METHODS

Most specimens of *Euphanerops longaevus* from Miguasha have been discovered incidentally, as the cliff falls down, and this explains why some specimens, such as the exquiste MHNM 01-123 (Figs 5; 16), have no counterpart. Most of the specimens described herein have been collected by patrols of the Parc national de Miguasha, which make remarkably efficient daily surveys of the fossils fallen off from the cliff or found by the visitors.

The specimens of *E. longaevus* described to date are the holotype (BMNH P.6813, part and counterpart; Figs 1; 2; Woodward 1900: fig. 1; Arsenault & Janvier 1991: figs 2, 3, pls 1, 2A; Janvier 1996a: figs 1b, 3, 6B), MHNM 01-02 (part and counterpart, holotype of "*Legendrelepis parenti*"; Figs 3; 18; 33; 34; 36A; Arsenault & Janvier 1991: fig. 4, pl. 3; Janvier 1996a: figs 4, 6A) and MHNM 01-69A,B (part and counterpart, referred to as the paratype of "*Legendrelepis parenti*"; Figs 4A, B; 32; Arsenault & Janvier 1991: pl. 2B).

The new and hitherto unpublished specimens are listed below:

– MHNM 01-79A,B: a relatively large, but poorly preserved specimen (part and counterpart), showing traces of calcification. The tail, however is

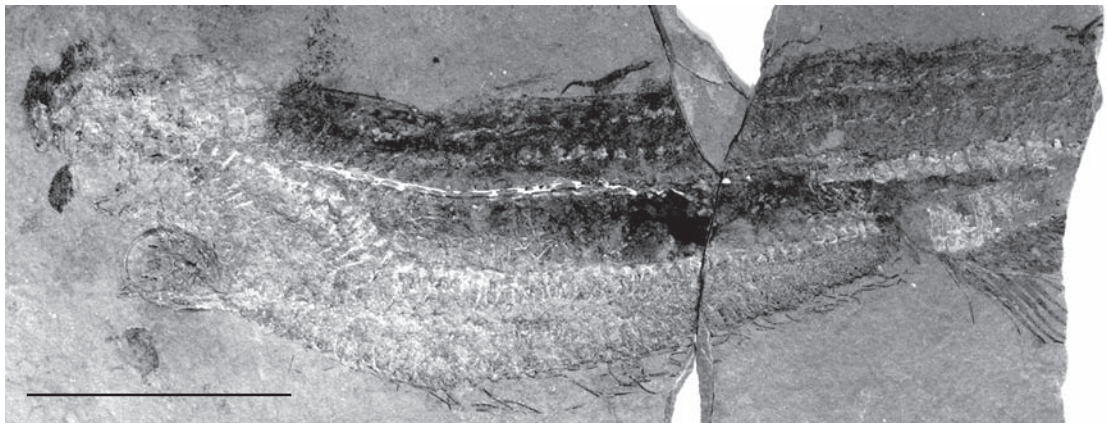


FIG. 5. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; specimen MHNM 01-123 showing an extensively mineralized skeleton (see also Figure 16 for details), and photographed in immersion in alcohol in order to enhance the carbonaceous imprint of the non-mineralized tissues of the body and the "head stains" (dark zones at the anterior end of the head and in the dorsal half of the body). Scale bar: 50 mm.

remarkably preserved and displays the rearmost radials (Fig. 29);
– MHNM 01-89A,B: a small specimen (part and counterpart), exposed in either dorsal, or ventral view and showing the best evidence for the organization of the three "head stains" (Figs 13A; 15F);
– MHNM 01-98: an almost complete, medium-sized specimen, somewhat obliquely collapsed and with partly mineralized branchial apparatus (Figs 12; 36B; 37);
– MHNM 01-101A,B: a small, poorly preserved specimen (part and counterpart), exposed in either dorsal, or ventral view, and showing a faint trace of the "head stains" (Fig. 15E);
– MHNM 01-123: a large specimen with extensively mineralized endoskeleton (Figs 5; 16; 17; 21; 22; 27A; 28; 30; 39). The tail is missing, but the foremost radial of the epichordal lobe is visible. Samples from this specimen have been used for histological studies of the "braincase" and "white line" (Figs 10; 11);
– MHNM 01-124A,B: a small portion of a large specimen, showing a well mineralized endoskeleton (not illustrated here);
– MHNM 01-125A,B: a relatively large, obliquely collapsed specimen (part and counterpart, anterior part of the body only) showing an extensively mineralized branchial apparatus and the best evidence for the paired fin radials (Figs 32; 33);
– MHNM 01-126A,B: a very small, poorly preserved specimen (part and counterpart), exposed in either dorsal, or ventral view (Fig. 13B);
– MHNM 01-130: a poorly preserved, medium-sized and weathered specimen, showing a trace of the head stains, branchial apparatus and visceral cavity (Fig. 4C);
– MHNM 01-135A,B: a large, deformed specimen (part and counterpart) with an extensively mineralized endoskeleton (Figs 23-25; 27B; 31). The counterpart (B) only shows a small portion of the body (Fig. 25). The part (A) distinctly shows the branchial apparatus, the paired fin radials, part of the "annular cartilage" and part of the axial skeleton. The head stains and axial skeleton are poorly preserved. Samples from this specimen have been used for histological studies of the mineralized tissue of the branchial and axial skeleton (Figs 6-8; see also Janvier & Arsenault 2002: fig. 2);
– MHNM 01-136: a faint imprint of a relatively large specimen, clearly showing the three "head stains" (Fig. 15G);
– MHNM 01-137: a poorly preserved, unmineralized, medium-sized specimen showing the head stains in either dorsal or ventral view, and a vague trace of the body (Figs 14A; 15C);

– MHNM 01-150A,B: an imperfect, more or less dorsoventrally collapsed specimen. The branchial apparatus is broken up into several portions spread either sides (Figs 19; 20), possibly as a consequence of the disruption of the visceral cavity during decay. The degree of calcification of the endoskeleton is very low, approximately as in MHNM 01-02. The "black lines" are conspicuous and quite suggestive of blood vessel imprints, with side-branches;
– MHNM 01-158: a small specimen showing essentially the "head" stains in either dorsal or ventral view, and a shadow of the body, but distinct paired patches of mineralized matter posterior to the "head stains" (Figs 14B; 15B).

Most specimens have been photographed in immersion in either water or alcohol in order to enhance the contrast between the imprint and the matrix. In specimens that display mineralized structures, the latter appear conspicuous because of their pinkish colour that contrasts with the greyish-blue colour of the surrounding matrix. Unfortunately, and despite attempts at using various techniques, black and white photographs may not always show the shape and distribution of all these elements. Therefore, the photographs of these specimens, aimed at showing particular details, are accompanied here by explanatory camera lucida drawings. For histological studies, small samples have been embedded in transparent resin before being thin-sectioned. These sections have been photographed with a transmission light microscope equipped with Nomarski optics. Other samples have been mounted on a plug for SEM study, and slightly etched with 5% formic acid for one hour, or included in resin and polished for microprobe analysis by means of a scanning electron microscope equipped with a Camera SX100 Castaing microprobe.

TAPHONOMY

The new material of *Euphanerops longaevus* described herein consists of both smaller (e.g., MHNM 01-126; Fig. 13B) and much larger (e.g., MHNM 01-123; Figs 5; 16) specimens than those previously described by Woodward (1900) and Arsenault & Janvier (1991), which were about the same size. Although the holotype described by Woodward (1900) is of uncertain derivation, but undoubtedly from the Miguasha cliff, all other specimens recorded to date are from one particular outcrop of this cliff, located about 100 m west of the Miguasha museum, which consists of fine-grained laminite beds, sometimes including concretions. It is referred to the Unit 1 of the Escuminac Formation (Prichonnet *et al*. 1996; Parent & Cloutier 1996). All what is known to date of the taphonomy of the Escuminac Formation has been reviewed by Parent & Cloutier (1996: 73-76), but no particular attention has been paid to the case of *E. longaevus*. However, considering the diversity of the states of preservation of the specimens referred to this taxon, it is probable that they reflect a wide range of decay states. The specimens described herein display a highly variable aspect, probably because of differences in the way the decaying carcasses have collapsed before fossilization (Purnell & Donoghue 1999), but each of them enlightens the interpretation of the others. Most of them look as if exposed in more or less lateral aspect, but in fact display overprinted structures of the right and left sides. Others are dorsoventrally or obliquely collapsed, or are preserved in a way that suggests sudden obruption of the visceral cavity or the stomach during decay. A striking feature of these specimens, when appearing in a more or less lateral aspect, is the fact that the tip of their head (marked by dark stains) very often tapers anteriorly, at a right angle with the anterior margin of the branchial region (e.g., Figs 3-5; 18; 38). This vaguely gives their head the overall aspect of that of a basking shark. As it will be discussed below, it is uncertain whether this reflects the actual shape of the anterior part of the head, but the repeated occurrence of this head outline may indicate that the snout was more or less overhanging the presumed oral region.

These specimens show various degrees of mineralization, essentially in the endoskeleton, the *pre-* or *post-mortem* origin of which is a matter of debate (see discussion below). The endoskeleton of the smaller specimens (up to the size of MHNM 01-02; that is, about 10 cm) is almost entirely preserved as a blackish, presumably carbonaceous, imprint, but traces of incipient mineralization in the form

of a characteristic pinkish mineralized matter, may occur here and there, generally behind the "head stains", and sometimes also at the level of the gill arches (mm, Figs 2C; 3B2; 13B; 14B; 18B; 20A). Larger specimens display an increasingly mineralized skeleton, and in such specimens as MHNM 123 and 135 (with an estimated total length of about 33 cm), none of the endoskeletal elements remains in the form of a carbonaceous imprint (Figs 5; 16; 23).

Considering these differences in the mode of preservation, one might also raise the question of why should all these specimens, which can differ considerably in size, be referred to the same species. This is admittedly an approximation based on the supposedly similar organization of the head stains, branchial apparatus and fins. Further findings may provide evidence for several different *Euphanerops* species, but to date no character hints at such a specific diversity.

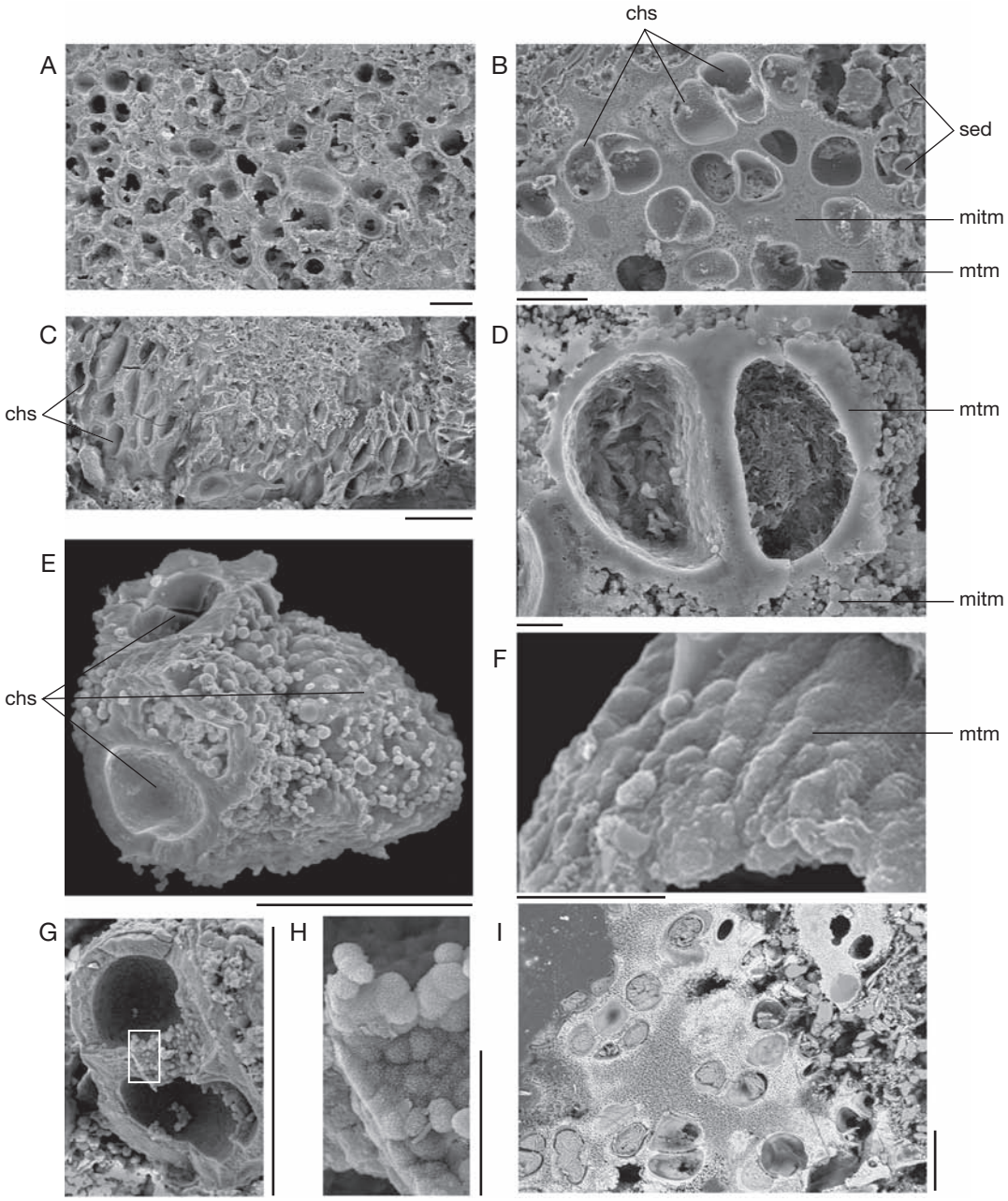
The highly variable state of preservation of the specimens referred to *E. longaevus* is suggestive of the process referred to as "scaumenellization" by Béland & Arsenault (1985), who provided an explanation for the long enigmatic soft-bodied fossil *Scaumenella mesacanthi* Graham-Smith, 1935, from the Escuminac Formation. *Scaumenella* is a vague carbonaceous imprint, which somewhat recalls the Middle Devonian *Achanarella* (Newman 2002; and see below) but sometimes displays traces of fin spine-like structures. Béland & Arsenault (1985) showed that all kinds of intermediate morphologies can be found between *Scaumenella* and perfectly preserved specimens of the acanthodian *Triazeugacanthus affinis* (Whiteaves, 1887), from the same beds of the Escuminac Formation. Therefore, they considered *Scaumenella* as the ultimate state of degradation of this particular acanthodian, through presumably an early diagenetic process which they called "scaumellization". This process should perhaps be reconsidered in the light of recent advances in taphonomy, and it may turn out to involve the role of decay before fossilization. Scaumenellization may also be invoked to explain the fact that, despite their medium size, some specimens of *E. longaevus* from the laminite beds of Miguasha appear as barely more than a shadow on a slab, and are only identified thanks to their three head stains. The latter are never observed in typical *Scaumenella*. Various degrees of scaumellization have also been noticed in small specimens of other fish taxa from Miguasha, notably the sarcopterygian *Eusthenopteron* and the antiarch *Bothriolepis*.

STRUCTURE AND NATURE OF THE MINERALIZED TISSUES

It is admittedly unusual to begin the description of an articulated fossil vertebrate by that of its tissue structures, but the condition in *Euphanerops longaevus* is so unusual that any conclusion that may be drawn about the anatomy and systematic position of this taxon inevitably depends on whether the morphology of the mineralized structures observed in some specimens actually represent skeletal elements, or are a fortuitous assemblage of diverse tissues that have undergone *post-mortem* mineralization.

Most of the interpretations presented in this article rest on the assumption that the mineralized structures observed in certain specimens of *E. longaevus* are actual cartilages, regarded by Janvier & Arsenault (2002) as made up by an *in vivo* calcified form of lamprey-like cartilage. However, in the light of stimulating comments made by the reviewers of an earlier version of this article, and considering the very unusual aspect of this mineralization, which does not resemble classical vertebrate calcified cartilage, one must raise the question of whether it is actually a biomineralization that has developed in

FIG. 6. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; structure and composition of the mineralized elements in MHNM 01-135: **A**-**H**, SEM micrographs of samples etched with 5% formic acid (the surface of samples in A, B, D has been polished before etching); **A**, typically spongiose aspect of the mineralized matter in the larger elements (e.g., arcualia or "copular elements"); **B**, close-up view of the same kind of structure, showing sections of the "nests" of "chondrocyte spaces"; **C**, garland-like structure of an elongated element (probably a "gill rod"); **D**, section through a pair of "chondrocyte spaces", showing the compact shell of "mineralized territorial matrix", surrounded by the microspherulitic "interterritorial mineralized matrix"; **E**, intact, isolated shell of a "chondrocyte space", with portions of two adjacent shells (the lower



one shows an incomplete septum), and scattered minute globules of the "mineralized interterritorial matrix"; **F**, external surface of the shell of a "chondrocyte space", showing the bosses that are regarded as traces of an initially spherulitic structure of the "mineralized territorial matrix"; **G**, broken shell of an ensemble of three or four "chondrocyte spaces", showing the microspherulitic structure of the internal surface of one of the "spaces"; **H**, detail view of the area framed in G; **I**, SEM micrograph of the polished surface of a mineralized element (ventral "copular element"), tested with microprobe for F, MgO, SiO_2, Al_2O_3, Cl, K_2O, CaO, TiO_2, Cr2O3, MnO, FeO, NiO, and P_2O_5. Calcium phosphate predominates in the light grey areas, and silicates in the dark grey areas. Scale bars: A-C, E, G, I, 100 µm; D, F, H, 10 µm.

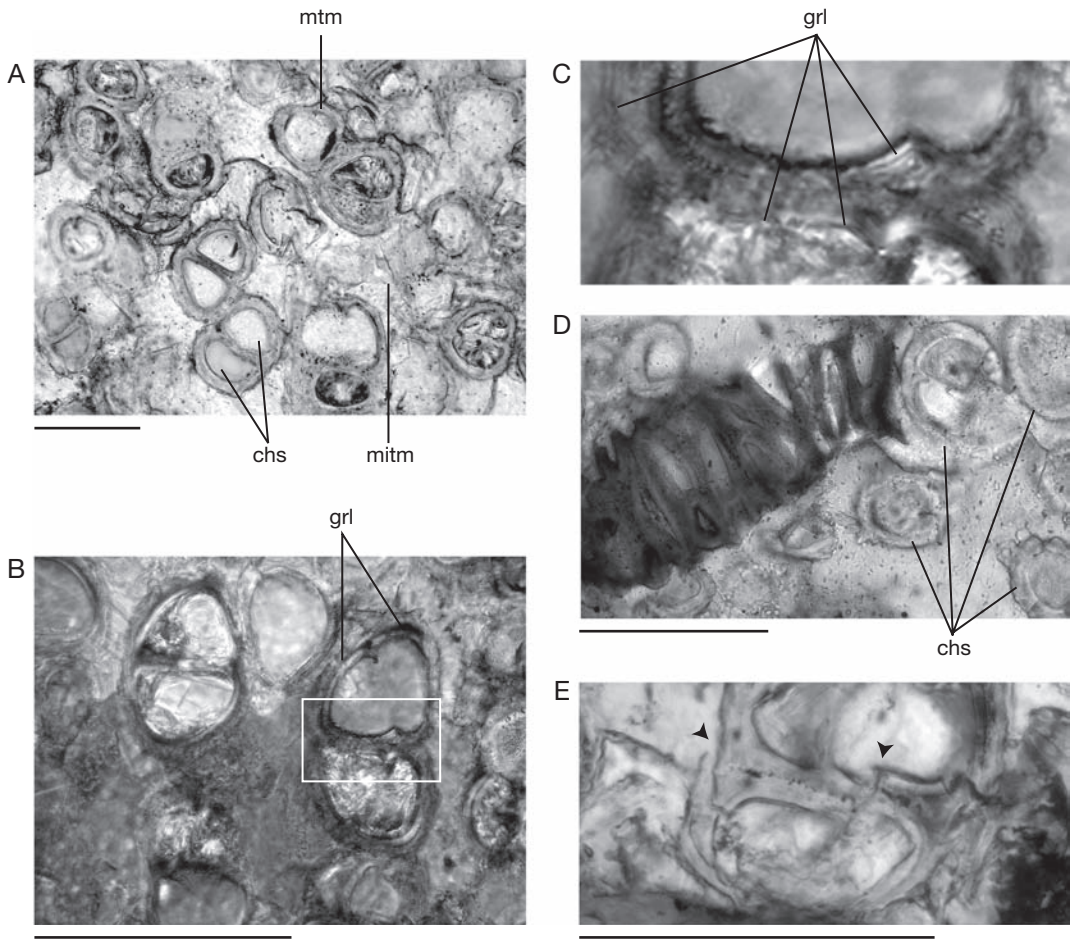


FIG. 7. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; sections through mineralized endoskeletal elements sampled from MHNM 01-135A (A, D, E, optical micrographs in normal light; B, C, Nomarski interference optical micrographs): **A**, transverse section through a "copular element"; **B**, detail view of a different zone of the same sample showing transverse sections of "chondrocyte spaces" with well marked growth lines; **C**, detail view of the area framed in B, showing the thinner growth lines in the "mineralized territorial matrix"; **D**, Section through an assemblage comprizing a "gill rod" (left) and isolated "chondrocyte space" shells; note the typically dark stain of most of the elongated elements, notably "gill rods"; **E**, section through an isolated "chondrocyte space" shell showing microfractures (arrowheads). Scale bars: 100 µm.

aged individuals, or a *post-mortem* fabric resulting from either permineralization, or authigenic phosphatization induced by microbes during decay (Briggs 2003; Donoghue *et al.* 2006).

Whether or not the structures described below can be referred to as "histological structures" depends thus on the confidence one may have in their biological derivation. These mineralized structures are best observed in the largest specimens known to date, notably MHNM 01-123 and 135 (Figs 5; 16; 23), on which are based the present descriptions. However, the series of specimens that is currently available suggests that the extension of the mineralization is size-related, and does not proceed randomly (see below). In the most extensively mineralized specimens, some of the skeletal elements are readily identified (e.g., axial skeleton, arcualia, radials, gill arches; see Anatomy, p. 169), whereas

others, whose homology is unclear, are referred to below with non-committal names or/and between quotation marks (e.g., "braincase", "haemal series", "annular cartilage", "copular elements", "gill rods"; see Anatomy p. 169). However, all of them, except for the "white line" (see Enigmatic structures, p. 193) display virtually the same structure, which appears as highly vacuolar or spongiose (Figs 6A, B; 7A; 8). The most massive elements (e.g., arcualia, "copular elements", "anal fin supports", median fin radials) display large, bubble-shaped, hollow bodies, often lying side-by-side, lined with a mineralized shell (Fig. 6B), and loosely cemented by minute spherules. The thinner, elongated, elements (e.g., paired fin radials, "gill arches", "gill rods") are made up by series of lens-shaped cavities, the walls of which is more massively mineralized and resemble the structure of an unfolded garland (Figs 6C; 8). For the sake of convenience, we shall use here the same terms as those used by Janvier & Arsenault (2002) in the first description of these mineralized, presumably endoskeletal structures, but between quotation marks that indicate the lack of definite evidence for their biogenic nature. The only difference is the use of "mineralized" instead of "calcifed", as microprobe analysis now reveals some local accumulations of silicates. It must be clear to the reader that the terms "chondrocyte space", "mineralized territorial matrix", or "mineralized interterritorial matrix", in part taken from Langille & Hall's (1993) description of the *in vitro* calcified lamprey cartilage, are merely descriptive and entail no conclusion as to the nature of the described features.

Microprobe analysis of these mineralized structures showed that they essentially consist of calcium phosphate (apatite), sometimes mixed with clay minerals to various extents. The "mineralized territorial matrix" (mtm, Fig. 6) of the "chondrocyte spaces" (chs, Fig. 6) is consistently made of calcium phosphate (max.: CaO = 50%; P_2O_5 = 33.8%), but the lumen of these spaces is variably filled with either calcite, silicate, or both (max.: SiO_2 = 53.2%; Al_2O_3 = 21.17 %). The finely spherulitic "mineralized interterritorial matrix" (mitm, Fig. 6), which fills the space between the "chondrocyte spaces", as well as the more compact, amorphous layer, which lines the surface of certain elements, is also composed of calcium phosphate, in about the same proportion as the "mineralized territorial matrix", but locally contains large amounts of silicate (possibly kaolinite; max.: SiO_2 = 40.2%; Al_2O_3 = 11.7%) and calcite. The distribution of the silicates (dark grey areas in Figure 6I), relative to the calcium phosphate (light grey areas in Figure 6I), shows no particular pattern, but silicates seem to be more frequent in the "mineralized interterritorial matrix", and probably fill the space that is not occupied by the microspherules of calcium phosphate. This analysis does not allow us to decide whether the calcium phosphate results from a *pre-* or *post-mortem* mineralization, but the local enrichment in silicate is certainly diagenetic, presumably derived from the surrounding matrix (sed, Fig. 6B), which is composed of quartz grains, feldspars and clay minerals.

Description

"Chondrocyte spaces" and "mineralized territorial matrix"

The most widespread structure in the presumed endoskeletal elements of *Euphanerops longaevus* consists of a foam-like tissue, which displays, in section, an assemblage of hollow, mineralized bodies referred to here as "chondrocyte spaces" (chs, Figs 6A, B, D; 7). The wall of these elements, referred to as the "mineralized territorial matrix" is made up by a generally thin layer of calcium phosphate. The "chondrocyte spaces" generally appear as more or less rounded shells divided into two oval chambers by a somewhat thinner septum, and their shape recalls that of a horse chestnut husk (Figs 6D; 7A, B). In some cases, they can also be grouped four-by-four, and strikingly recall the "cell nests" formed by the large chondrocytes of lampreys (Langille & Hall 1993: fig. 4). Moreover, their large size (about 30 to 50 µm in diametre) agrees with that of the lamprey chondrocytes (Langille & Hall 1993: figs 6, 7).

In general, the mineralized shells of the "chondrocyte spaces" are loosely attached by a diffuse "interterritorial matrix", made up by minute spherules of calcium phosphate (mitm, Figs 6D; 7A), and by calcite and silicates of diagenetic origin. When the largest endoskeletal elements (e.g., the arcualia or the "copular elements"; see Anatomy, p. 169) are

slightly etched with 5% formic acid, the diagenetic calcite that holds together the "chondrocyte spaces" and the spherules of the "mineralized interterritorial matrix" is dissolved. Consequently, the core of these skeletal elements falls apart into minute grains which appear to be the small, ovoid, mineralized shells of the "chondrocyte spaces" (Figs 6E; 7D). However, the densely mineralized peripheral part of the endoskeletal elements remains intact. Such isolated "chondrocyte spaces" show the external surface of the shell, which displays bosses and ridges (mtm, Fig. 6F). Although the "mineralized territorial matrix" that forms the shell's wall looks rather compact, the aspect of its external (and sometimes internal, Fig. 6G, H) surfaces suggests that its mineralization began in the form of globules that then fused into a compact layer around the chondrocytes. In thin section, the "mineralized territorial matrix" shows a few very conspicuous concentric lines (grl, Fig. 7B) that may represent either growth lines or incremental lines, but there are, in addition, much thinner lines (grl, Fig. 7C), whose sinuous aspect recalls Liesegang waves.

In the elongated skeletal elements, such as the gill arches, "gill rods", or radials (see Anatomy, p. 169), the "chondrocyte spaces" are lens-shaped and their equatorial plane is perpendicular to the axis of the elements (chs, Figs 6C; 8; 9). Moreover, these lens-shaped spaces seem to be arranged spirally; consequently, the structure of the elongated elements looks like an unfolded garland (Figs 6C; 8A-C; 9). In the larger elongated elements, such as gill arches or radials, only the peripheral "chondrocyte spaces" are lens-shaped, whereas those in the core of the element are somewhat spherical in shape and resemble those of the more massive elements (Figs 8D-G; 9). The "mineralized territorial matrix" of the elongated elements seems to be more densely mineralized than that of the other elements, and the "mineralized interterritorial matrix" is practically lacking (Figs 6C; 8). Moreover, the elongated elements generally appear darker in colour than the other elements. Thin sections confirm this darker coloration even in the core of the elements (Fig. 7D), but it is likely to be a consequence of weathering.

"Interterritorial matrix"

The small spherules of calcium phosphate that form the "mineralized interterritorial matrix" sometimes grade into larger ones in the vicinity of the "chondrocyte space" shells (mitm, Fig. 6D-F). It seems thus that, despite differences in compactness, the "mineralized interterritorial matrix" is basically of the same nature as the "mineralized territorial matrix". In most samples examined, the space that extends between the shells of the "chondrocyte spaces" is filled with variably dense clusters of spherules. Where these spherules are lacking, the space is filled with calcite and, locally, some silicate.

Near the periphery of the presumed endoskeletal elements, the shells of the "chondrocyte spaces" are smaller, more closely packed, and fused side-by-side to form a more compact zone (Fig. 6B). However, this higher degree of compactness is not only due to thicker "mineralized territorial matrix", but also a higher density of spherules in the "mineralized interterritorial matrix". The most extreme condition is found immediately beneath the amorphous compact layer that lines the surface of certain elements (e.g., the "braincase" and "posterior haemal series"). Here, there are still deformed traces of the "mineralized territorial matrix"(chs, mtm, Fig. 10A), but the "mineralized interterritorial matrix" is filled with minute, densely packed spherules (mitm, sph, Fig. 10A), which also invade the lumen of the "chondrocyte spaces". Whether this structure is due to a *pre-mortem* reworking of the "chondrocyte spaces", linked to cartilage growth, or a *post-mortem* diagenetic process is still undecided.

"Compact layer"

The superficial layer of certain elements ("braincase", "posterior haemal series") is remarkably compact and, when broken, shows an apparently lamellar structure under the binocular microscope. This is probably an artefact due to conchoidal fracture, because the minute fragments of this mineralized matter, which have been sampled from the braincase and sectioned (Fig. 10; 1, 2, Fig. 17), display a peculiar structure, which is clearly different from that of the rest of the mineralized skeletal elements. In thin section their most compact layer shows no evidence of a lamellar structure, cell spaces or vascular canals and only

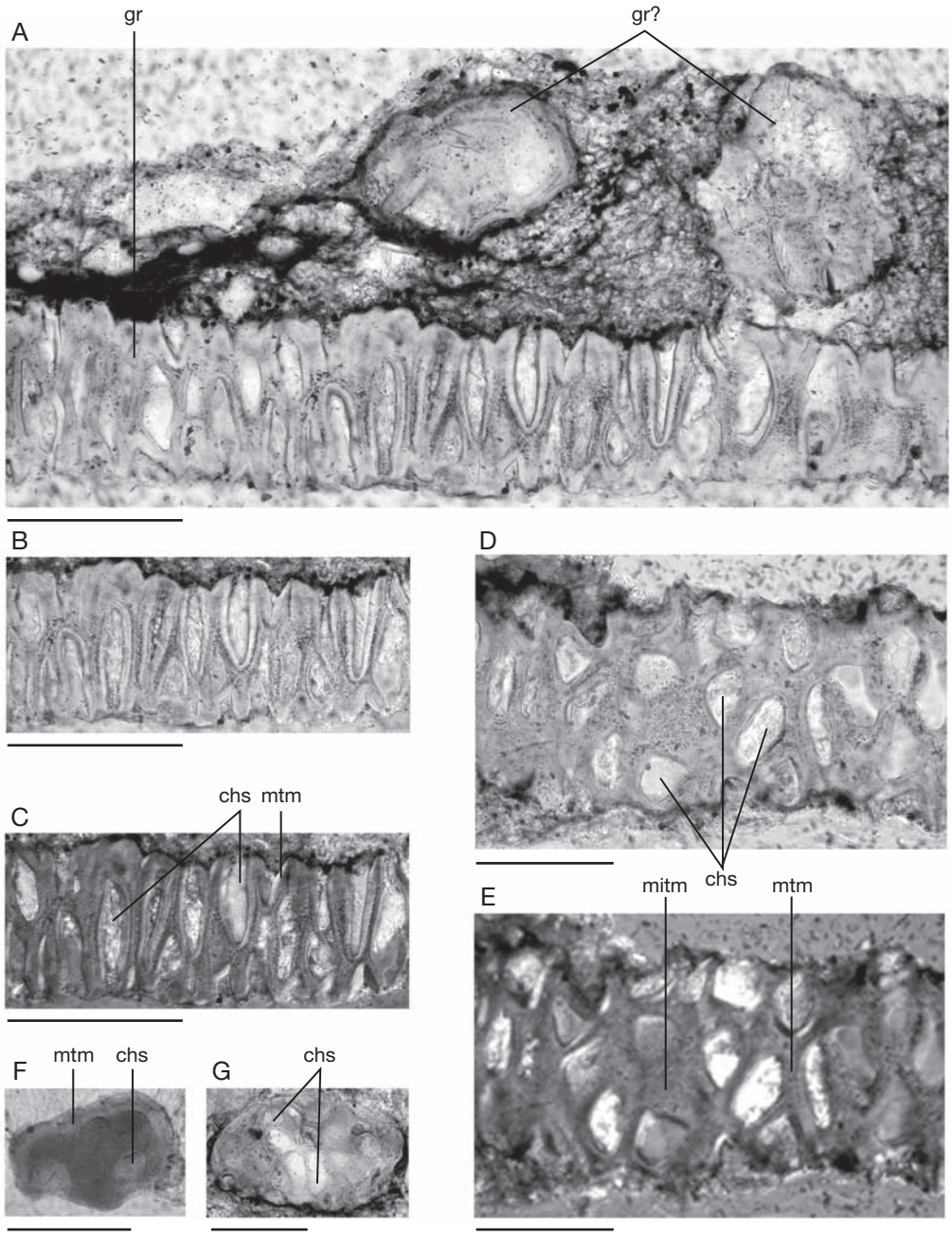


FIG. 8. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; sections through mineralized endoskeletal elements sampled from MHNM 01-135A; **A**, longitudinal (below) and transverse (above) sections through "gill rods"; **B**, **C**, portion of one of the "gill rods" in A, optical micrograph in normal light (B) and Nomarski interference optical micrograph (C); **D**, **E**, portion of a larger elongated element (presumably a gill arch) optical micrograph in normal light (D) and Nomarski interference optical micrograph (E); **F**, **G**, transverse sections through a "gill rod" (F) and a larger elongated element, presumably a gill arch (G); optical micrograph in normal light. Scale bars: 100 µm.

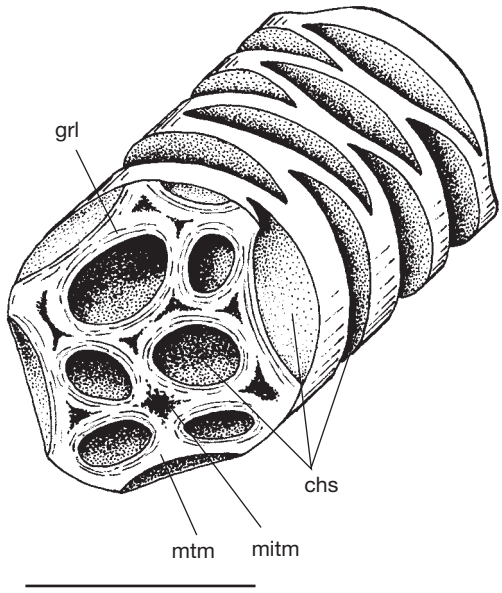


FIG. 9. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; attempted three-dimensional reconstruction of the structure of a mineralized gill arch (the transverse section is slightly oblique, to show the more spherical shape of the internal chondrocyte spaces). Scale bar: 1 mm.

displays an amorphous structure and a brownish colour (cl, Fig. 10). There is no evidence for any external ornamentation, and no resemblance to the dermal bones described in anaspids (Gross 1938, 1958; Märss 1986a; Blom *et al*. 2001). Moreover, it shows no evidence for Liesegang waves or rings. The limit between this compact layer and the underlying vacuolar mineralized tissue is clear-cut, but the latter is also more densely mineralized than elsewhere (Fig. 10). The amorphous structure of this compact layer is suggestive of an early diagenetic mineralization. Nonetheless, the fact that the walls of the immediately underlying "chondrocyte spaces" are strongly deformed may suggest reworking in a biologically active tissue.

"Diffuse mineralized matter"

We term here "diffuse mineralized matter" a strand of diffuse, granulous matter, which mainly extends along the dorsal margin of MHNM 01-123, from the back of the "braincase" to approximately mid-length of the preserved part of the body (dmm, Figs 16; 17). In the first 2.5 cm behind the braincase, this strand seems to be lined with a thin, straight dark line (dl, Fig. 17), which is in fact only superficial (it does not extend into the sediment) and continuous with the adjacent, "diffuse mineralized matter". This dark layer is merely the stained surface of the "diffuse mineralized matter". The latter has much the same aspect as the mineralized endoskeletal elements, such as the arcualia, but the "grains" (in fact the shells of the "chondrocyte spaces") look loose and sometimes scattered in the surrounding sediment. Assuming *pre-mortem* mineralization this "diffuse mineralized matter" may have retained some flexibility, since its mineralization seems to have been restricted to the "territorial matrix" of the "chondrocyte spaces", but we ignore which anatomical structure it may correspond to in other vertebrates. In lampreys, the same area of the mid-dorsal line is occupied by a thick median band of connective tissue, termed as the *tela perimeringealis* (Marinelli & Strenger 1954: fig. 39), which overlies the spinal cord and separates the two adjacent series or myomeres. One may thus imagine that the same structure in *E. longaevus* contained cartilaginous nodules, which could become mineralized to some extent. Another mass of such "diffuse mineralized matter" is also found immediately behind the branchial apparatus, in the anal region (dmm, Fig. 30).

Mineralized tissue of the "white line"

The "white line" is a strand of whitish, fibrous, mineralized matter that extends along most of the body in MHNM 01-123 (wl, Figs 16; 17; 21; 39) and is tentatively interpreted here as a large calcified blood vessel (see Enigmatic structures, p. 193). No microprobe analysis has been made on the white line. However, it is not dissolved by weak acids, but is by HCl, and is probably made of calcium phosphate. The structure of the mineralized tissue of the "white line" is entirely different from that of the presumed endoskeletal elements described above. In transverse section, it shows on the one hand a compact and amorphous layer (cl, Fig. 11) that recalls the compact layer of the endoskeletal elements described above, and, on the other, a more heterogeneous layer which displays numerous black

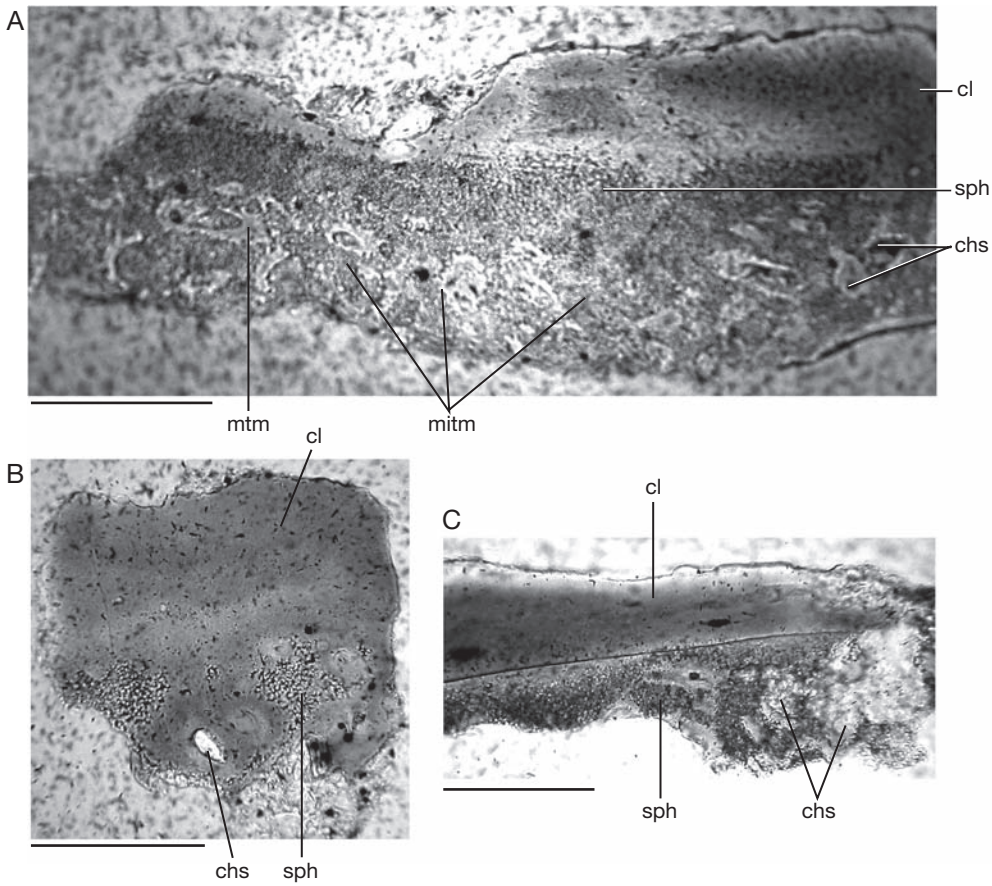


FIG. 10. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; vertical sections through the compact mineralized matter of the "braincase" of MHNM 01-123; **A**, **B**, fragments extracted from area 1 in Figure 17; **C**, fragment extracted from area 2 in Figure 17. Optical micrograph in normal light. Scale bars: 0.1 mm.

dots that could suggest small cell spaces (f, Fig. 11A). However, longitudinal sections clearly show that these are in fact sections of thin, parallel canals (f, Fig. 11B), which give the "white line" its fibrous aspect, when seen under a binocular microscope. What was housed in these canals is unknown. If the "white line" is a phosphatized artery (and whatever the origin of the phosphatization), as suggested here, these canals might be the trace of necrosed muscle fibres of the *tunica media*. At any rate, they seem too large for having housed collagen fibres. Thin sections of the "white line" have been demineralized by L. Zylberberg (CNRS, Denis-Diderot University, Paris), with the aim of finding traces of collagen fibres. Although this provided evidence for abundant organic matter, vaguely arranged in bundles, it provided no evidence for even "ghosts" of collagen fibres.

ARGUMENTS SUPPORTING *PRE-MORTEM* MINERALIZATION

The arguments in favour of the *pre-mortem* (i.e. biogenic) calcification of the cartilage in *E. longaevus* were initally based on a comparison with the histological structure of the normal and *in vitro* calcified cartilage of living lampreys (Langille & Hall 1993; Janvier & Arsenault 2002). Firstly, the shape, size and arrangement of the "chondrocyte

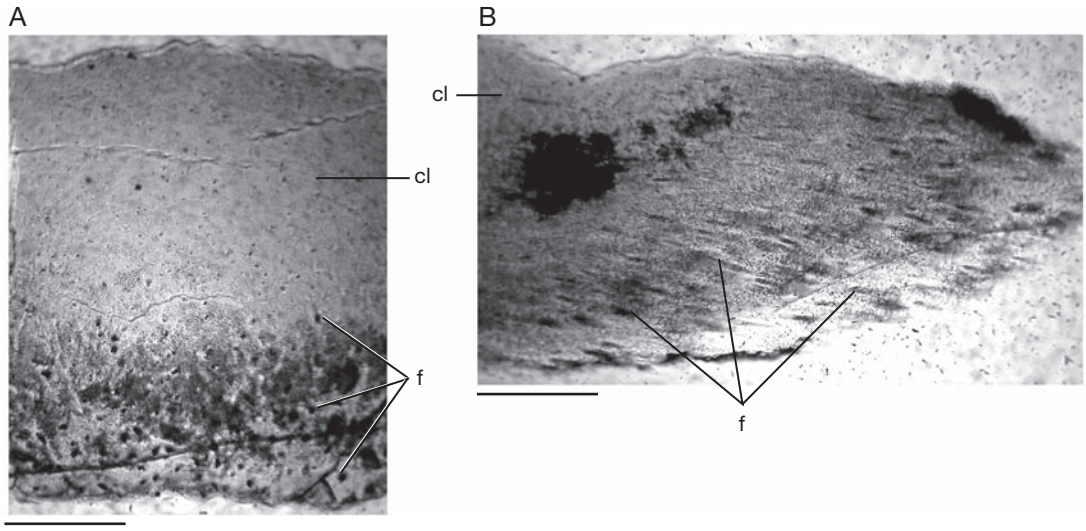


FIG. 11. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: transverse (**A**) and longitudinal (**B**) sections through the "white line" of MHNM 01-123. Optical micrograph in normal light. Scale bars: 0.1 mm.

spaces" of *E. longaevus* are strikingly similar to the chondrocytes of lampreys, notably in the way they form "nests" of closely set cells, generally grouped two-by-two or four-by-four (Fig. 6B). Second, the pattern of mineralization of the extracellular matrix, with a dense mineralized shell, or "mineralized territorial matrix", surrounding the "chondrocyte spaces", and a loose "mineralized interterritorial matrix", recalls that of *in vitro* calcified adult lamprey cartilage (Langille & Hall 1993: fig. 7).

Apart from the fibrous structure of the mineralized "white line" observed in a single specimen, the structure of the mineralized elements in *E. longaevus* is always the same, whether preserved in concretions or in the laminite beds, although within the same specimen, the organization of the "chondrocyte spaces" shows some differences, depending whether the skeletal elements are elongated in shape or not (see above). It is worth pointing out here that in the elongated and curved elements (e.g., gill arches, "annular cartilage") the arrangement of the "chondrocyte spaces" at the level of a curve is modified to accommodate the shape of the element (Fig. 6C). The "mineralized territorial matrix" surrounding the "chondrocyte spaces" is thus not arranged randomly, but its organization is imposed by the morphology of the elements, and this strongly supports, if not the biogenic nature of the mineralization (in fact essentially a calcification) proper, at any rate the biogenic nature of the observed structures (i.e. they are actually cell spaces).

An additional structural argument in favour of the *pre-mortem* mineralization is perhaps the trace of deformed "chondrocyte spaces" walls in the vicinity of the compact layer that lines certain endoskeletal elements in the most extensively mineralized specimens (Fig. 10). It may be argued that the compact layer is in fact a late diagenetic fabric, possibly superimposed on an earlier authigenic fabric, but this would not explain why the walls of the "chondrocyte spaces" appear so extensively reworked (chs, Fig. 10A). Finally, the compact layer is only observed in particular elements, notably part of the "braincase", the larger "anal fin supports" and the "posterior haemal elements" (see Anatomy, p. 169), and there is no taphonomic explanation to this restricted distribution.

None of the acanthodians, which abound in the same laminite beds as *E. longaevus*, shows any mineralized tissue structure that would compare to

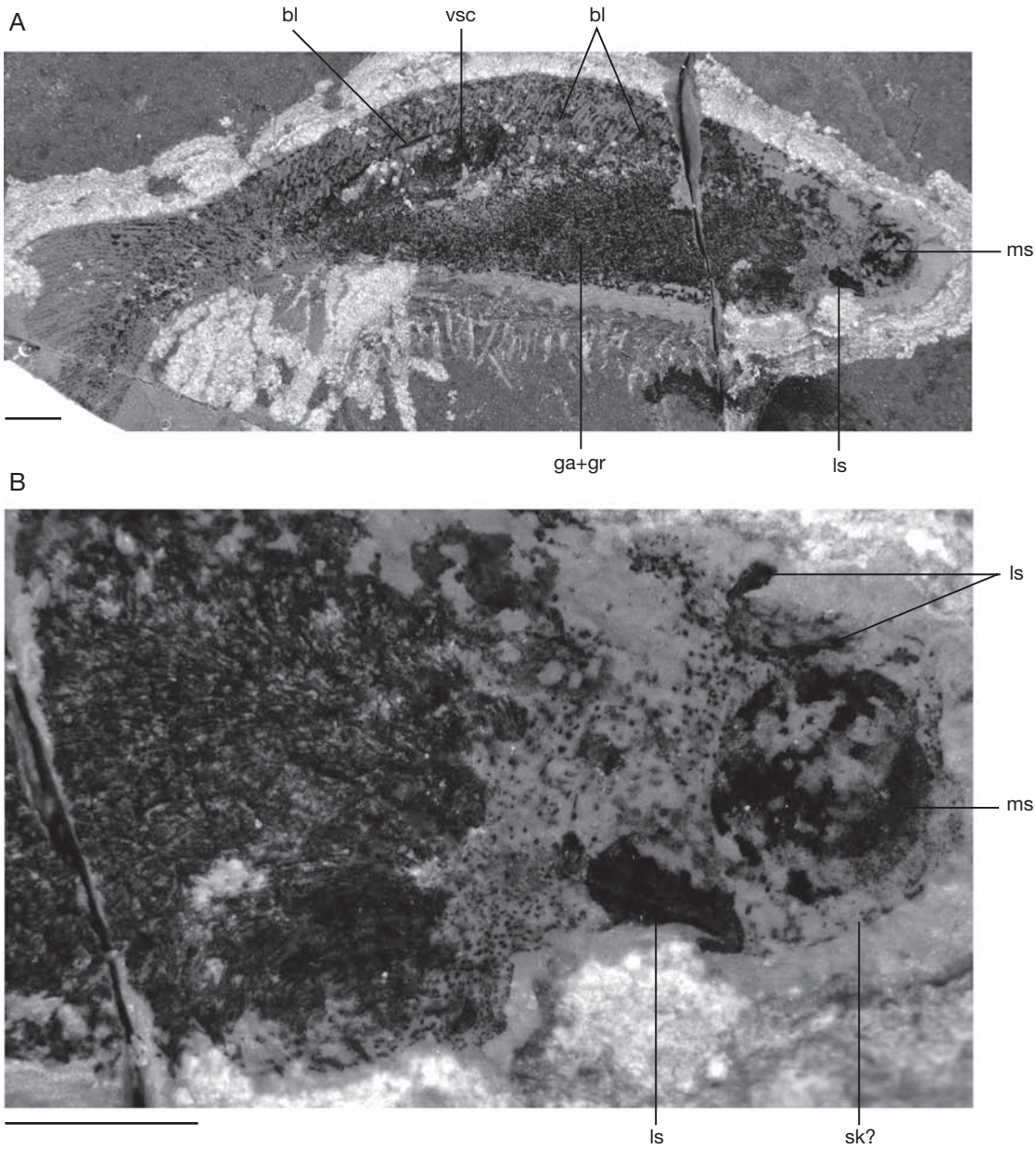


FIG. 12. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: **A**, almost complete specimen, the head of which is dorsolaterally collapsed and shows the three head stains (MHNM 01-98); **B**, detail of the anterior part of the head of the same specimen. Photographed in immersion in water. Scale bars: 5 mm.

that of *E. longaevus*. Moreover, no such structure has ever been met with elsewhere in the calcified cartilage of the other fish taxa from Miguasha, notably in the arthrodire *Plourdosteus canadensis* (Woodward, 1892), various osteichthyans and the osteostracan *Escuminaspis laticeps* (Traquair, 1890)

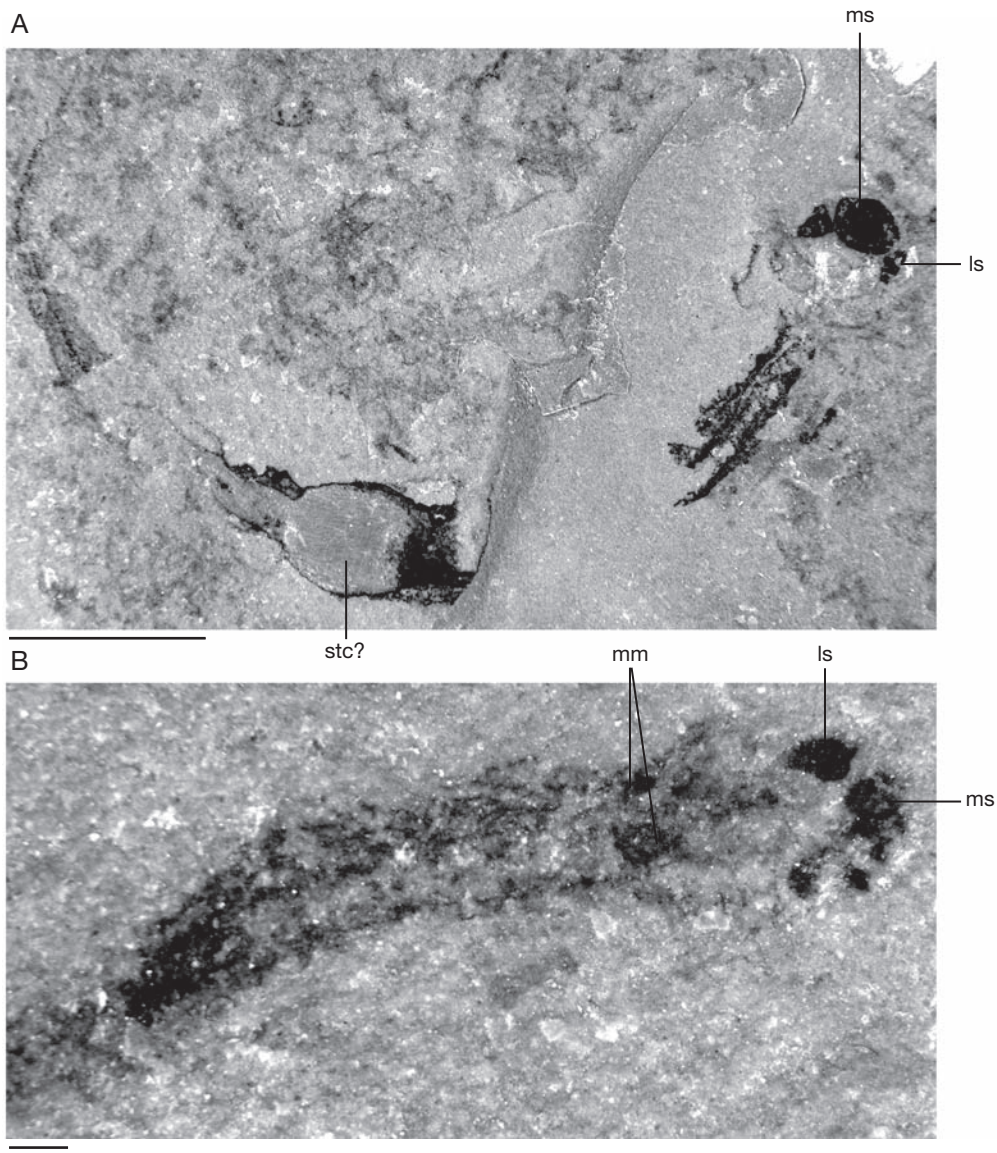


FIG. 13. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; small and presumably juvenile, dorsoventrally collapsed individuals, showing the three "head stains"; photographed in immersion in water: **A**, MHNM 01-89B, single specimen, the body of which is interrupted by a break in the concretion; the sediment that fills the presumed, horizontally broken, stomach contents is extremely fine-grained, and clearly differs from that of the surrounding matrix; **B**, MHNM 01-126A, smallest known individual, showing a pair of stains (one of which displays a slight trace of mineralized matter) behind the "head stains". Scale bars: A, 10 mm; B, 1 mm.

(Ørvig 1951; Cloutier & Schultze 1996; Janvier *et al*. 2004). The calcified cartilage preserved in the pectoral fins of two specimens of *Escuminaspis laticeps* derived from two different layers of the Escuminac Formation displays numerous cell spaces embedded in a calcified matrix, which shows traces of succes-

sive calcification fronts and Liesegang waves. The shape of its cell spaces and the overall structure of its calcified cartilage matrix agrees with the condition described by Ørvig (1951: fig. 15) in the calcified Meckelian cartilage of *Plourdosteus*, but differ from the structure of the mineralized endoskeletal elements in *E. longaevus* described here, notably by the lack of the characteristic pairs of large "chondrocyte spaces". One may assume that, if *post-mortem* calcification of the cartilage and soft tissues were a widespread phenomenon in the fossil fishes of the Escuminac Formation, it would be found in a wide range of different taxa. Finally, assuming that the mineralized elements in *E. longaevus* are essentially cartilages (at any rate in the case of the median fin radials, whose anatomical identification is unambiguous), it should be pointed out that no case of *post-mortem* authigenic phosphatization of fish cartilage has ever been recorded, despite the numerous cases of authigenic phosphatization of other soft tissues (muscles, gill filaments, blood vessels) known in vertebrates (D. Martill pers. comm. 2005). The only peculiarity that can be noticed in the histological structure of the vertebrates from Miguasha are the enigmatic spherules described by Ørvig (1968: fig. 1; see also Donoghue *et al*. 2006: fig. 3:5) in the dermal skeleton of the osteostracans *Escuminaspis laticeps* and the Antiarch *Bothriolepis canadensis* Whiteaves, 1880, and which could recall in size the minute spherules of the "mineralized interterritorial matrix" of *E. longaevus*. These spherules have been regarded by Ørvig (1967, 1968) as a primary mode of calcification of the vertebrate dermal skeleton, but failed to be observed in either osteostracans or antiarchs from other localities. However, microspherulitic acellular dermal bone has been described in galeaspids by Wang *et al*. (2005).

Regarding taphonomy, it is clear that the mineralization of both the "territorial" and "interterritorial matrix" has occurred before the lithification of the sediment. This is evidenced by the numerous elements (e.g., paired fin radials; pfrad, Figs 22; 31) that are sometimes broken into series of slightly displaced chunks. In some cases, the break passes through the mineralized shell of the "chondrocyte spaces" and the two parts of the same "chondrocyte

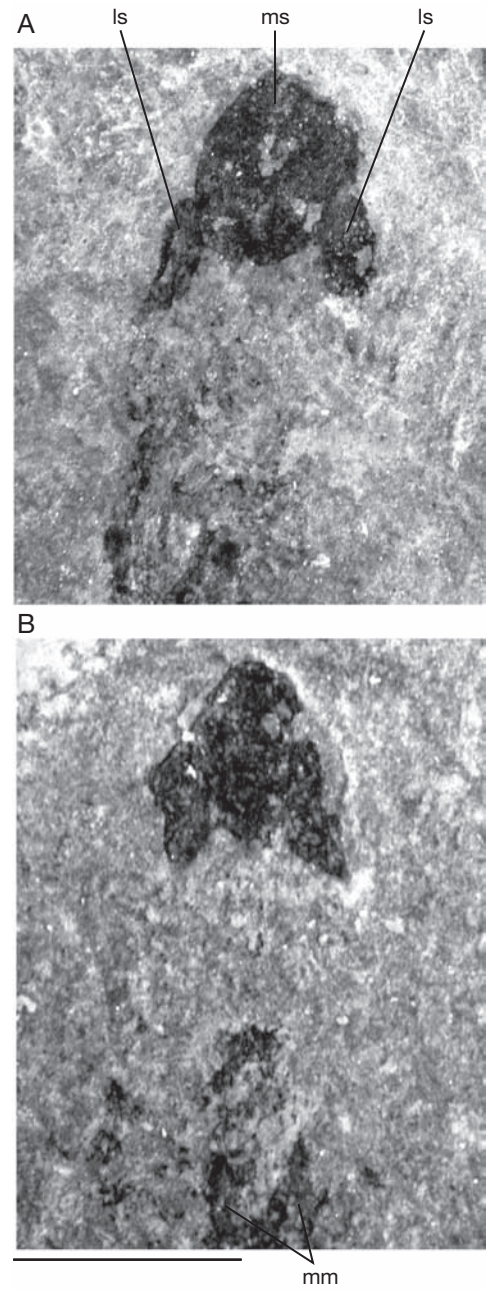


FIG. 14. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; anterior part of the head in two small, dorsoventrally collapsed individuals: **A**, MHNM 01-137; **B**, MHNM 01-158, notice the presence of two small patches of mineralized matter in exactly the same position as in MHNM 01-126A (see Figure 13B). Scale bar: 5 mm.

space" can be traced on both sides of the break. In other cases, broken "chondrocyte spaces" are in contact with the sediment and filled with fine sediment particles (sed, Fig. 6B), or the two parts of their broken wall of the same "chondrocyte space" only show a slight relative displacement (Fig. 7E). However, we should concede that the presence of elongated and sinuous mineralized elements that remain intact despite the compaction of the sediment (e.g., the gill arches and "intermuscular elements"; ime, Fig. 21) is difficult to explain when assuming *pre-mortem* calcification. Such very brittle mineralized elements would have been easily damaged during the collapse and compaction of the carcass, unless they retained some flexibility. The latter possibility cannot be ruled out, since in some of the mineralized elements, notably the larger ones, the shells of the "chondrocyte spaces" are very loosely attached by a barely consolidated "mineralized interterritorial matrix" (chs, Fig. 7D).

Post-mortem calcification would probably entail some differences in the degree of calcification of the specimens of approximately the same size, depending on the nature of the sediment or the ion concentration of the surrounding water. Although all the specimens of *E. longaevus* come from the basal part of the Escuminac Formation and from the same outcrop, most of them come from several, different layers. Some specimens are preserved in very fine-grained concretions, whereas others are preserved in the laminite beds that include these concretions (Parent & Cloutier 1996: 73-76). However the two sets of specimens, provided that they are approximately similar in size, show no marked difference as to the degree of mineralization and the structure of the mineralized elements. The only difference lies in the fact that the non-mineralized, carbonaceous, imprints are more conspicuous and better defined in the specimens preserved in the concretions (e.g., BMNH P.6813, MHNM 01-02, 01-150, 01-98; Figs 2; 3; 12; 19; 20) than in those preserved in the laminite beds (e.g., MHNM 01-123, 01-125; Figs 5; 16; 32).

Assuming that we are dealing with individuals of a single species, yet another argument in favour of the *pre-mortem* mineralization is that the extent of the mineralization in *E. longaevus* not only depends on the size of the specimens, but seems to proceed in a well defined sequence. In general, the larger the individuals, the more mineralized the presumed endoskeleton. In MHNM 01-123 and 01-135, for example, all elements referred here to the endoskeleton are completely mineralized, and none of them is preserved in the form of carbonaceous imprints (Figs 5; 16; 23), contrary to, e.g., MHNM 01-02, 01-69, 01-89, 01-98, 01-126, or 01-150 (Figs 2-4; 12-14; 18-20), where most, if not all elements are carbonaceous imprints. In the smallest, supposedly younger individuals, such as MHNM 01-101, 01-126 or 01-89 (Figs 13; 14), the endoskeleton is only in the form of a diffuse, blackish imprint, and practically no particular element can be identified, apart from the "head stains". Incipient mineralization can, however, be observed in such specimens. Notably, it appears in the form of small pinkish areas of characteristic foam-like mineralized matter, which shows the same structure as that found in more extensively mineralized specimens. Interestingly, one of the first traces of mineralization that appears in a site-specific position in small specimens always occurs somewhat behind the "head stains" (mm, Figs 2C; 3B2; 13B; 14B; 18B; 20A; 38). In dorso-ventrally collapsed specimens, it is paired and situated on either sides of the midline (Figs 13B; 14B). Its position corresponds approximately to that of the posterior part of the "braincase" in MHNM 01-123 (brc, Fig. 17). A pair of stains occur in exactly the same position in *Achanarella trewini* Newman, 2002 (Newman 2002: pl. 2, figs 5, 6), and we suspect that they correspond to the same skeletal structure. Assuming that this is the result of incipient biomineralization, it is possible that the otic capsule induced the early stage of mineralization in this region of the head. Patches of mineralized matter are also found here and there in the gill-arches of otherwise unmineralized specimens, where they display a banded aspect (e.g., Fig. 18) that clearly recalls the garland-like structure of the mineralized gill arches and "gill rods" of MNHM 01-123 and 01-135 (Figs 8; 9).

When considering all the available specimens, there appears thus a trend towards an increasing mineralization in larger and larger specimens.

There are nevertheless some exceptions among the average-sized specimens, ranging from about 10 to 15 cm in estimated total length, some slightly larger specimens showing less traces of mineralized matter than slightly smaller ones (e.g., Figs 3; 12). Although the number of relatively well preserved specimens is small, the mineralization seems to proceed as follows: in the smaller specimens, it only affects the presumed otic region; then, in the medium-sized specimens, the gill arches and "gill rods", and possibly the "annular cartilage", "copular elements" and "anterior median ventral rod". Finally, in the largest specimens, it extends to the "head stains", "braincase", axial skeleton, "anal fin supports", and paired and unpaired fin radials (see Anatomy, p. 169). To date, no specimen displays, for example, mineralized radials, but an unmineralized branchial apparatus.

Decay experiments show that authigenic phosphatization begins in the tissues that are more readily penetrated by microbes and generally closer to the body surface (Briggs 2003). In the case of *E. longaevus*, this would not agree with the very late mineralization of the radials. In this connection, it is worth noticing here that none of the mineralized tissue samples observed by means of SEM shows clear evidence for autolithified microbes, which are generally abundant in certain types of authigenically phosphatised tissues (but not in substrate or intermediate microfabrics; Briggs 2003). Although the minute spherules of calcium phosphate that compose the "mineralized interterritorial matrix" or, in some cases, the surface of the "mineralized territorial matrix" (Fig. 6D, E, H) could agree in average size with that of the autolithified microbes in a microbial microfabric, they differ from the latter in being remarkably regular in shape and showing a wide range of different sizes.

Arguments supporting *post-mortem* mineralization

The first argument that can be raised in support to the interpretation of the mineralized elements of *E. longaevus* as the result of a *post-mortem* mineralization rests on the fact that their structure is strongly at odds with what we know of the biological process of cartilage calcification in extant vertebrates. Admittedly, we have no extant model for jawless vertebrates, since hagfishes and lampreys lack calcified cartilage, with a possible exception in some lamprey specimens mentioned by Bardack & Zangerl (1971), but never investigated further. The only proxies we have are experiments of *in vitro* calcification of larval and adult lamprey cartilage (Langille & Hall 1993). Nevertheless, some fossil jawless vertebrates informally referred to as "ostracoderms", or jawless stem gnathostomes, display spherulitic calcified cartilage, whose structure and growth seems identical to that of extant gnathostomes (Ørvig 1951, 1967; Denison 1967; Janvier *et al*. 2004; Wang *et al*. 2005). Typical spherulitic calcified cartilage develops in the extracellular matrix, in the form of spherules centred about a nucleus, which may not necessarily be a chondrocyte (Ørvig 1967). The invasion of the extracellular matrix by the spherules proceeds centrifugally; that is, towards the surface of the cartilage. At later stages, the spherules become coalescent and the calcification front surrounds the chondrocytes, which finally die. From what can be seen in *E. longaevus*, the shell of "mineralized territorial matrix" that surrounds the "chondrocyte spaces" seems to have been the first zone of the cartilage to become mineralized (Fig. 6A, B). Then, minute spherules of calcium phosphate formed in the "interterritorial matrix" and more or less loosely cemented the mineralized shells of the "chondrocyte spaces" (Fig. 6D). In all the elements observed in thin section or by means of SEM, these spherules are particularly dense near the surface of the presumed endoskeletal elements, and much less so deeper inside them; that is, the reverse of what is observed in typical spherulitic calcified cartilage. Moreover, assuming that the "chondrocyte spaces" actually contained chondrocytes, the latter would not have survived when completely enclosed in a mineralized shell.

There are several ways of explaining this discrepancy between the condition in *E. longaevus* and what we know of biogenic cartilage calcification. One is that calcification occurred late in the life of the individuals (possibly as a pathologic process) and that the death of the chondrocytes slowed down cartilage growth. Another one is that the calcification of the walls of the "chondrocyte spaces" (the

"mineralized territorial matrix") is biogenic, but that the "interterritorial matrix" became mineralized *post-mortem*. A more radical explanation is that the entire calcification occurred *post-mortem*, during decay.

Post-mortem mineralization that allows soft-tissue preservation involves a wide range of processes, which have been reviewed by Briggs (2003). We can rule out permineralization, which generally concerns silicifications, but this process may have been involved to some extent in the particular case of *E. longaevus*, if the traces of silicates found here and there in the "interterritorial matrix" can be proven to have occurred very soon after deposition. Considering the predominance of the calcium phosphate in the mineralized structures of *E. longaevus*, the choice is essentially between two possible processes: either microbially induced calcification, which generates substrate microfabrics, or calcifications that are due to the autolithification of the bacteria, which invade the carcasses during decay. Intermediate conditions involving both processes (i.e. intermediate microfabrics) can also occur (Briggs 2003).

In the case of *E. longaevus*, there seems to be no characteristic autolithified microbes, unless the microspherules of the "mineralized interterritorial matrix" are in fact all autolithified microbes (Martill & Wilby 1994; Briggs 2003; Briggs *et al*. 2005). These microspherules do bear some resemblance to autolithified coccoid microbes (Fig. 6H; Briggs *et al*. 2005: fig. 4C, D), but differ from the latter by a wide range of different sizes and their perfectly rounded shape. Conversely, if autolithified microbes are actually absent, a microbially induced mineralization (substrate microfabric) may have occurred. A key argument in favour of authigenic mineralization in *E. longaevus* is that there are at least two different kinds of phosphatized tissues, at any rate in MHNM 01-123: one is the widespread spongiose structure regarded here as cartilage, because it occurs in elements that are undoubtedly endoskeletal (e.g., radials); the other one is the peculiar, densely calcified and fibrous structure that we refer here to as the "white line" (see Enigmatic structures, p. 193), and which may be a large calcified blood vessel (possibly the dorsal aorta). In addition, the compact layer that lines certain skeletal elements may represent a third type of mineralized structure.

Janvier & Arsenault (2002) invoked the resemblance between the structure of the mineralized elements of *E. longaevus* and the *in vitro* calcified lamprey cartilage, which displays much the same pattern of the calcified matrix (densely calcified "territorial matrix" and loosely calcified "interterritorial matrix"). This, in turn, raises the question of the nature of the calcification process observed by Langille & Hall (1993). The immersion of living lamprey cartilage in a metastable solution of hydroxyapatite at a temperature of 30-37°C for 6-12 days may have in fact induced an early process of permineralization. However, this would be inconsistent with the difference in the calcification processes observed by these authors between larval and adult lamprey cartilage (extracellular in the adult and intracellular in the larva).

If authigenic phosphatization is involved in the case of *E. longaevus*, one may also wonder about what actually became mineralized, at any rate in the case of the presumed cartilage. Substrate microfabrics generally reproduce details at the cellular level, such as cell outline and even cell nuclei (Martill 1990). Here, there is no evidence for calcified intracellular structures, but the presumed "chondrocytes spaces" are perfectly preserved as cell outlines. Assuming that the cartilage of *E. longaevus* had much the same composition as the lamprey cartilage, there is also a striking resemblance between its mineralized structure in the bar-shaped elements (e.g., gill arches and "gill rod"; Figs 6C; 8) and the fibrous matrix of lamprin (an analogue of the collagen that ensures flexibility of the cartilages), which surrounds the chondrocytes in the gill arches of lampreys (Robson *et al*. 1997: figs 3, 5). It is thus possible that, during the decay of the carcass, the invasion of the microbes into the cartilage began at the surface of the skeletal elements and in the "chondrocyte spaces" left empty by the decay of the chondrocytes proper. This would explain why the mineralization is more dense at the surface of the elements and along the wall of the "chondrocyte spaces". Later on, the deposition of calcium phosphate in the extracellular matrix would have

proceeded preferentially along the collagen (or lamprin) fibres, which formed a tougher template than the rest of the matrix. Also, the "mineralized territorial matrix" surrounding the "chondrocyte spaces" shows growth lines (grl, Fig. 7B, C), which suggest that calcium phosphate deposition at this level could last for a longer time than elsewhere.

The fact that the mineralization is more extensive in the larger individuals than in smaller ones also accords with the hypothesis of authigenic phosphatization, which is known to be related to the size of the decaying carcass, as the more phosphorus is available to microbes, the more efficient the deposition of calcium phosphate (Briggs 2003). However, the difference in size is sometimes very slight between barely mineralized specimens and fully mineralized ones (e.g., MHNM 01-02 and MHNM 01-98; Figs 3; 12).

Here we regard as unlikely the possibility that the "chondrocyte spaces" are in fact large autolithified micro-organisms. Generally, the autolithified microbes observed in microbial microfabrics are about 1 µm in diametre; that is, far less than the size of the "chondrocyte spaces". Nevertheless, the "chondrocyte spaces" may agree in size and shape with acritarchs. Although acritarchs are not proven to induce authigenic phosphatization, there are instances of *post-mortem* phosphatized (but probably not autolithified) acritarchs, previously referred to as "mazuelloids" or "muellerisphaerids" (Kremer 2005). However, the latter show traces of the characteristic acritarch spines, for which there is no evidence in the "chondrocyte spaces". In addition, even a bloom of acritarchs in a decaying organism would not show such a selective distribution in the body (B. Kremer pers. comm. 2005).

ANATOMY

The description of the anatomy of *Euphanerops longaevus* is made difficult by the overprinting of structures due to the various ways in which the carcasses collapsed before fossilization. In addition, there are uncertainties about the nature of some elements, here gathered in a particular section (see Enigmatic structures, p. 193). Among the other factors that may bias the description and interpretation is the uncertainty as to whether the mineralized elements observed in the large specimens have undergone *pre-* or *post-mortem* mineralization. As discussed above, this question has important bearings on the interpretation of the preserved elements (i.e. whether they are cartilage or soft tissues). No definite answer can be offered to it, but what is important to anatomists is perhaps not so much the origin of the mineralization, but the identification, or homology, of the organs or elements it preserves. As pointed out above, nearly all the mineralized elements observed in *E. longaevus* display the "chondrocyte spaces", which are almost identical to chondrocytes (particularly lamprey ones) in shape and arrangement, and are notably present in fin radials, whose identification is unambiguous. Therefore, we assume that all the elements showing this stucture are in fact cartilages. We are conscious that the same kind of structure may possibly have formed through authigenic phosphatization or microbial induction in widely different kinds of tissues, and that the "chondrocyte spaces" are misinterpreted, but to date, interpreting this structure as that of cartilage (whatever the origin of its mineralization) remains the most parsimonious solution.

Consequently, the reader must keep in mind that the present description rests on objects, the biological interpretation of which remains speculative. Therefore, unless the structures observed in *E. longaevus* have obvious homologues in other fossil or living taxa (e.g., the fin radials), we refer to them with non-committal names between quotation marks. The attempted reconstruction of this species, which we propose here in Figure 40 is based on cross-observations of the 17 specimens mentioned above (see Material and methods, p. 151).

Anterior head structures and "braincase"

"Head stains"

The anteriorly tapering tip of the head of *Euphanerops longaevus* is always marked by a few, more or less rounded, black stains (e.g., Figs 1-5; 12-20; 23; 32). These have been regarded by Woodward (1900: 2) as the orbits. Arsenault & Janvier (1991: pl. 2A) and Janvier (1996a: fig. 6A) interpreted the foremost of them as an annular cartilage, because of its vaguely

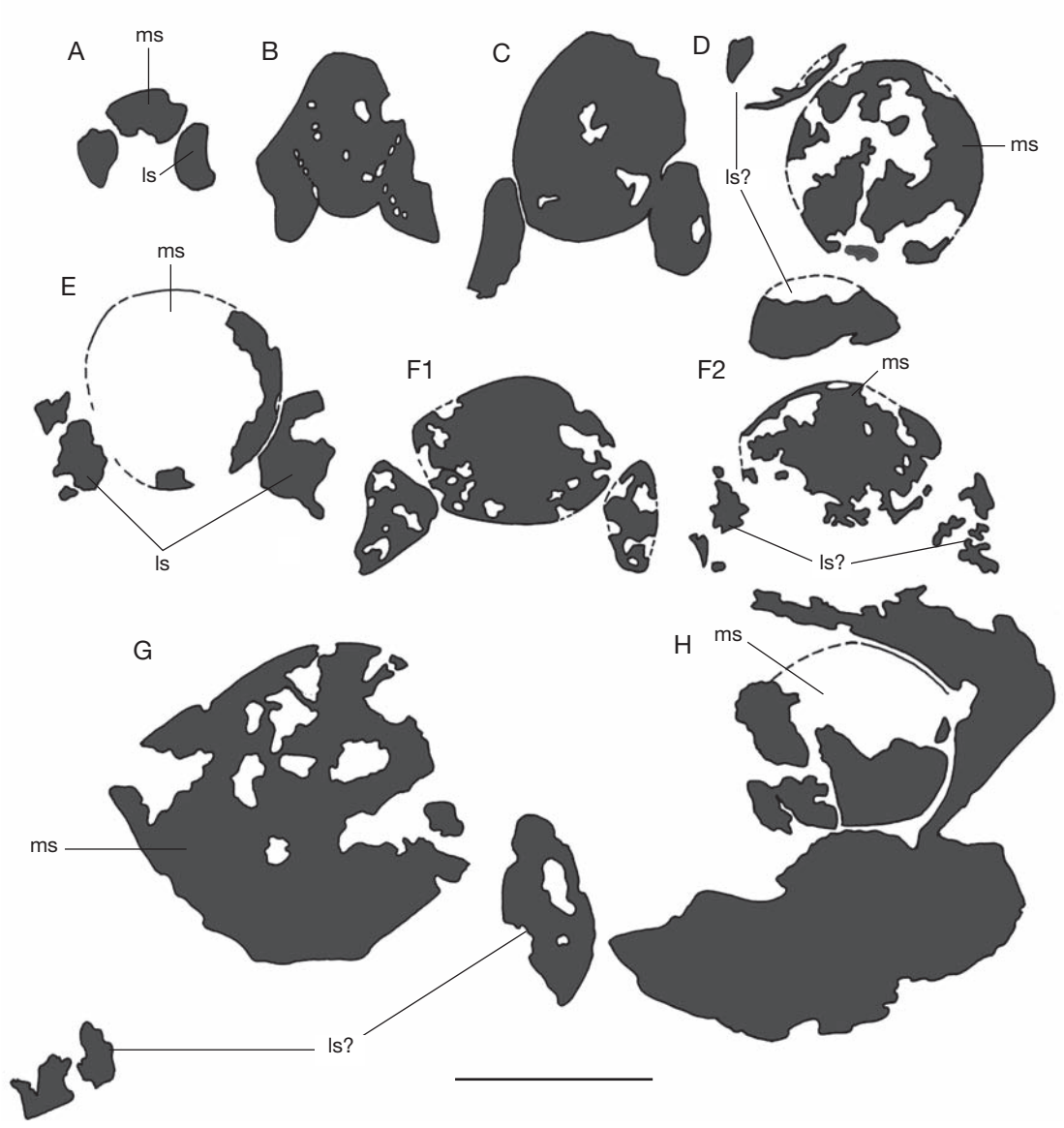


FIG. 15. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; camera-lucida drawings of the "head stains" in all known specimens that are regarded as being dorsoventrally collapsed: **A**, MHNM 01-126; **B**, MHNM 01-158; **C**, MHNM 01-137; **D**, MHNM 01-98; **E**, MHNM 01-101A; **F**, MHNM 01-89A, B; **G**, MHNM 01-136; **H**, MHNM 01-125A. Scale bar: 5 mm.

doughnut-like shape and terminal position in the holotype (ms, Fig. 2C), and erroneously compared it to the "doughnut-shaped structure" in MHNM 01-69 (Figs 4A; 38; see Enigmatic structures, p. 193). Admittedly, in some specimens, there seems to be only two rounded stains, lying side-by-side and suggestive of collapsed paired eye imprints (Figs 3; 4; 18; 23). However, several specimens now enlighten the arrangement of these anterior stains, as they are more or less dorsoventrally collapsed (Figs

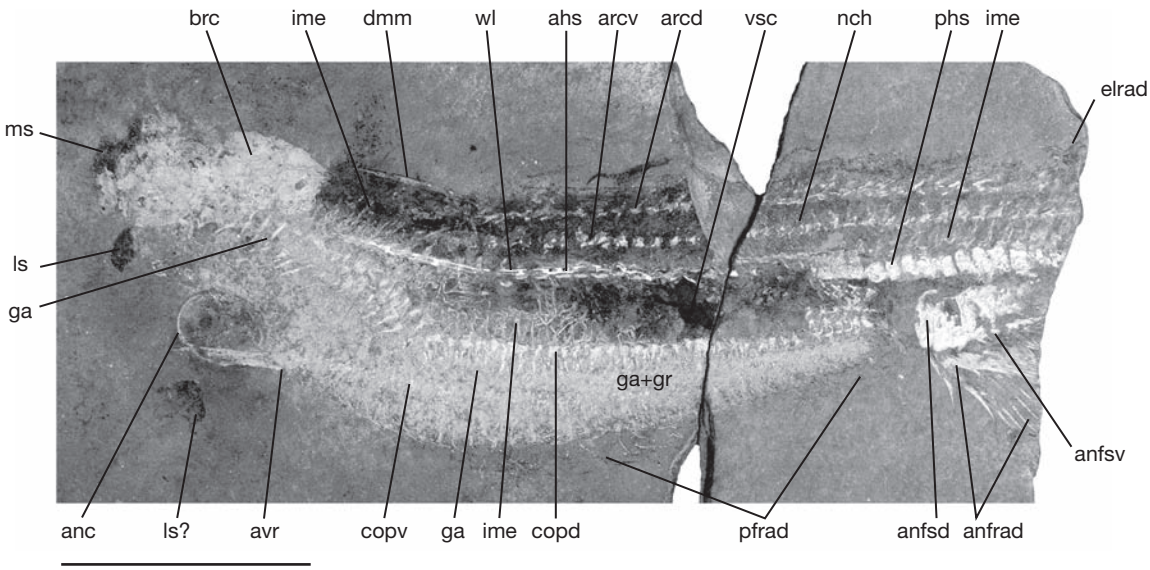


FIG. 16. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; large, laterally or ventrolaterally collapsed specimen (the "braincase" is probably twisted in an either ventral or dorsal aspect), showing and extensively mineralized endoskeleton (MHNM 01-123, same specimen as in Figure 5). Photographed dry. Scale bar: 50 mm.

12-15). In most of them, the anterior end of the head displays in fact three blackish stains: a large, rounded, slightly bowl-shaped one termed here the "median stain" (ms, Figs 2; 3; 12-20), and paired, somewhat triangular ones, termed here "lateral stains" (ls, Figs 12-17). In MHNM 01-89, 01-137 and 01-158 (Figs 14; 15B, C, F), the "lateral stains" clearly meet the posterolateral margins of the "median stain" and sometimes seem fused to the latter. It is thus probable that the large, terminal stain, which, in the holotype, seems to form a circular structure, and was referred to by Arsenault & Janvier (1991: pl. 2A) as the "annular cartilage", is in fact the "median stain" (ms, Fig. 2C), the central part of which is damaged. At any rate, it is also certainly the case for the anteriormost stain in MHNM 01-02 (ms, Figs 3; 18) regarded by Arsenault & Janvier (1991: fig. 4B) as eye imprints. Further examination of the structure referred to by Arsenault & Janvier (1991) as a possible impression of the orbit in the holotype showed that is consists of a partially mineralized ring (anc, Fig. 2C), which is identical to the structure referred to below as the "annular cartilage", and certainly has no relation to the eyes. By comparison with the classical interpretation of another fossil "naked" jawless vertebrates, *Jamoytius kerwoodi* (Ritchie 1968: pl. 3; 1984: pl. 1), the three anterior black stains of *Euphanerops* intuitively suggest the trace of a large, median olfactory organ and/or an annular cartilage, flanked by a pair of eye stains.

Now, this interpretation becomes problematic when one considers the large specimens, in particular MHNM 01-123 (Figs 5; 16), in which the presumed endoskeleton is extensively mineralized. Here, these stains are less distinct, but nevertheless present (Figs 16; 17). There is a large, terminal, blackish area, which is almost certainly the "median stain" (ms, Figs 16; 17) and, by its side, one of the "lateral stains" (ls, Figs 16; 17). Similar stains are also visible, yet to a lesser extent, in the other large, mineralized specimen MHNM 01-135A, but here it is difficult to distinguish the median one from the lateral ones (hs, Fig. 23). However, in both specimens, the surface of these stains has a spongiose aspect, instead of being the amorphous tarry layer

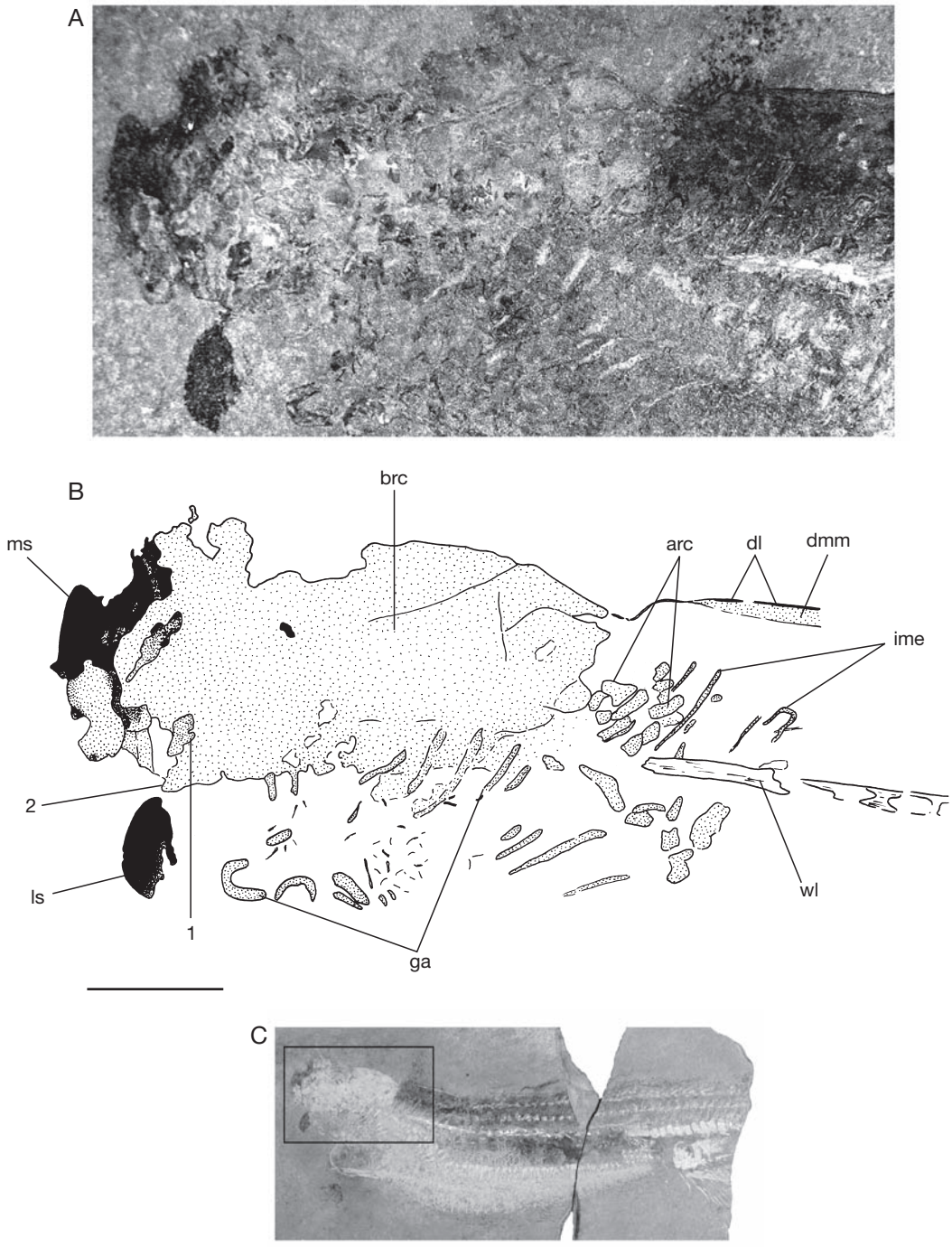


FIG. 17. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; "braincase" and "head stains" of MHNM 01-123: photograph (**A**, in immersion in water) and camera lucida drawing (**B**) of the area framed in **C**. Scale bar: 10 mm.

seen in most of the smaller specimens (e.g., Figs 3; 4; 12-14; 18-20; 32). In places where this stain is superficially worn out, it proves to be continuous with an underlying layer of spongiose mineralized matter. A minute fragment of the "lateral stain" of MHNM 01-123 has been extracted and vertically sectioned and proves to be entirely made up by mineralized matter of the same type as, e.g., the arcualia or radials, with the typical "chondrocyte spaces" (Figs 6-9). Towards its blackish surface (the "stain" in the specimen), the mineralized matter only becomes darker, chocolate-brown in section, as also seen near the surface of certain other endoskeletal elements, such as the paired fin radials, gill arches and "gill rods" (Figs 7D; 33) or the elements of the "posterior haemal series" (phs, Figs 16; 30). This is corroborated by a re-examination of what is presumably one of the "lateral stains" in MHNM 01-02B (ls?, Figs 3B; 18B), which shows, under the microscope, the same, incipiently spongiose and slightly pinkish aspect. Assuming a massive, microbially induced, *post-mortem* mineralization would not preclude the interpretation of these three stains as being soft-tissue structures, such as optic and olfactory capsules, respectively. For some reason, the latter would have become calcified in exactly the same way as such undoubtedly endoskeletal elements, as the fin radials. In contrast, assuming that this spongiose structure of the "head stains" is the result of a biomineralization, the most likely interpretation is that these are in fact cartilages that armed the snout. There remains, however, the possibility that these stains are actually carbonaceous imprints of the collapsed olfactory organ and eyes, but which are overprinted on underlying calcified cartilaginous structures (calcified sclera or nasal capsule).

None of these "head stains" displays any particular morphology which would suggest that they are the nasal capsule and eyes, respectively. In the best preserved non-mineralized specimens exposed in either dorsal or ventral view, the "median stain" is an almost perfectly rounded, tarry imprint, and the "lateral stain" show virtually no variation in shape, as could be expected in collapsed decaying carcasses (Fig. 15). The "median stain" could be interpreted as superimposed eye stains, but this would leave the "lateral stains" unexplained. All three stains seem to be mere plate-shaped elements, much like the tectal cartilages of the lamprey snout (Marinelli & Strenger 1954: fig. 65). We are aware that some specimens may give the impression that the "lateral stains" (e.g., ls, Fig. 12B) are in fact collapsed, cone-shaped, structures, and thus probably the optic capsules, but the combination of the part and counterpart of these specimens shows that this is merely an illusion due to damages in the margins of the carbonaceous layer that constitutes the imprint. The reason why these stains appear as distinct dark stains, even when mineralized, remains unclear. Assuming that they are cartilages, they were perhaps relatively thick and may have trapped more organic matter than other skeletal elements. The largest mineralized fin radials also show quite a similar dark colour (Figs 22; 28; 30; 31A).

"Braincase"

The structure we term here as the "braincase" in *Euphanerops longaevus* is best seen in MHNM 01-123 (brc, Figs 16; 17), and to some extent in MHNM 01-135A (brc, Fig. 23B), in posterior continuity with the "head stains". The term "braincase" used here is admittedly less non-committal than, e.g., "head stains", but this suggests a higher degree of certainty as to the identification of this structure, unless, of course, this large mineralized mass is entirely a substrate or microbial fabric around soft tissues, and does not reflect any particular skeletal structure. Therefore, we refer to it with quotation marks, because there is no guarantee that it actually represents only the braincase proper. It is an oblong mass of mineralized matter and, assuming that it actually represents essentially the braincase, we cannot decide whether it is seen in dorsal or ventral view. Yet its spindle-shaped posterior end suggests that it includes otic and occipital regions, and thus may have enclosed the roots of the glossopharyngeal and vagal nerves, contrary to the braincase of lampreys. It seems partly fused with the "median stain" (ms, Fig. 17), but probably not with the "lateral stains", which are displaced away from it (ls, Fig. 17).

Most of the pink mass, which constitutes the "braincase" is made up by spongiose mineralized

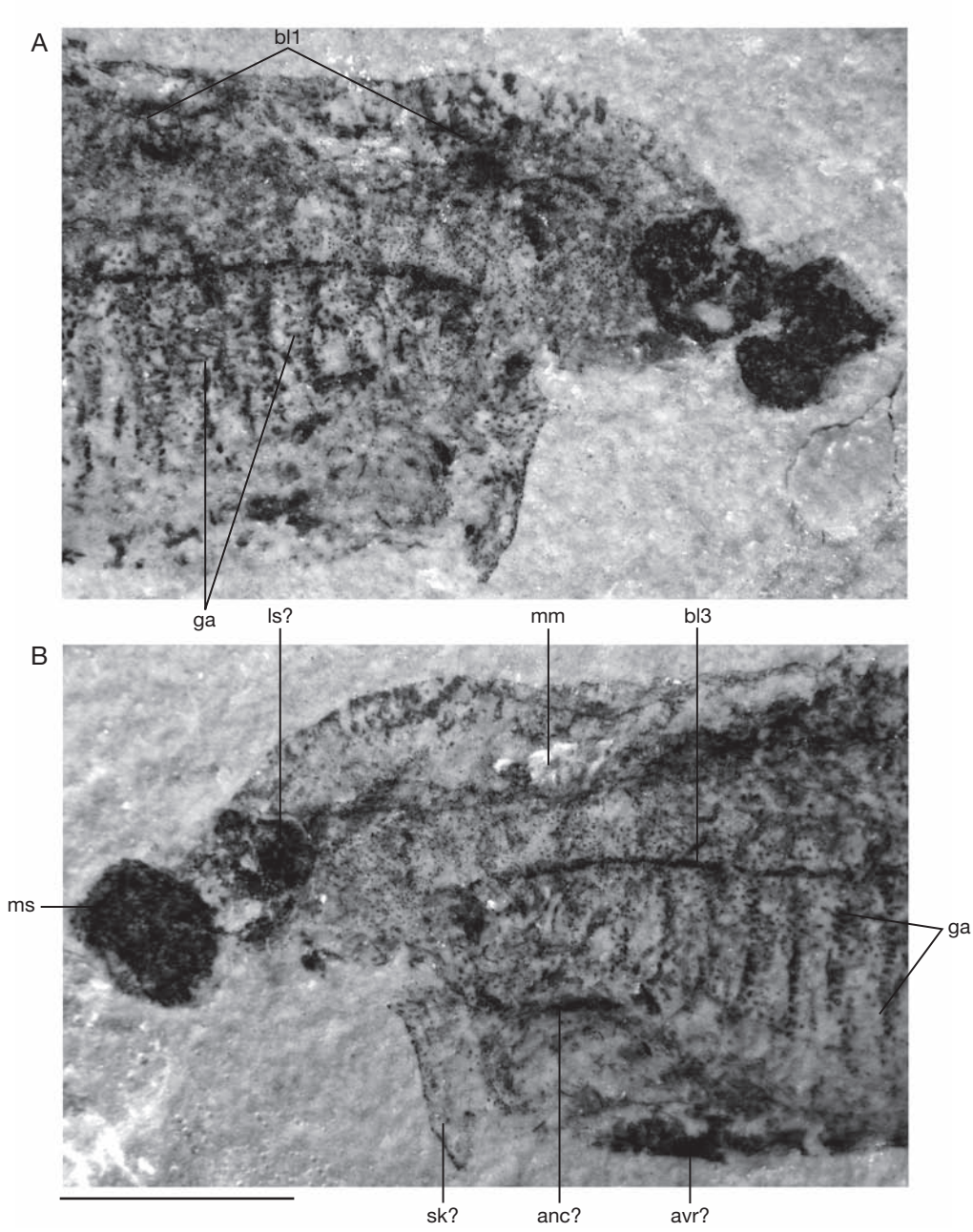


FIG. 18. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; detail of the anterior part of the head of MHNM 01-02 (same specimen as in Figure 3): part (**A**) and counterpart (**B**), photographed in immersion in water. Scale bar: 5 mm.

matter, with "chondrocyte spaces" visible under a binocular microscope, but here and there its surface shows small, apparently superficial, fragments of a more compact layer which, in thin section, shows a dense, amorphous structure (cl, Fig. 10). This compact layer shows no "chondrocyte spaces" and may

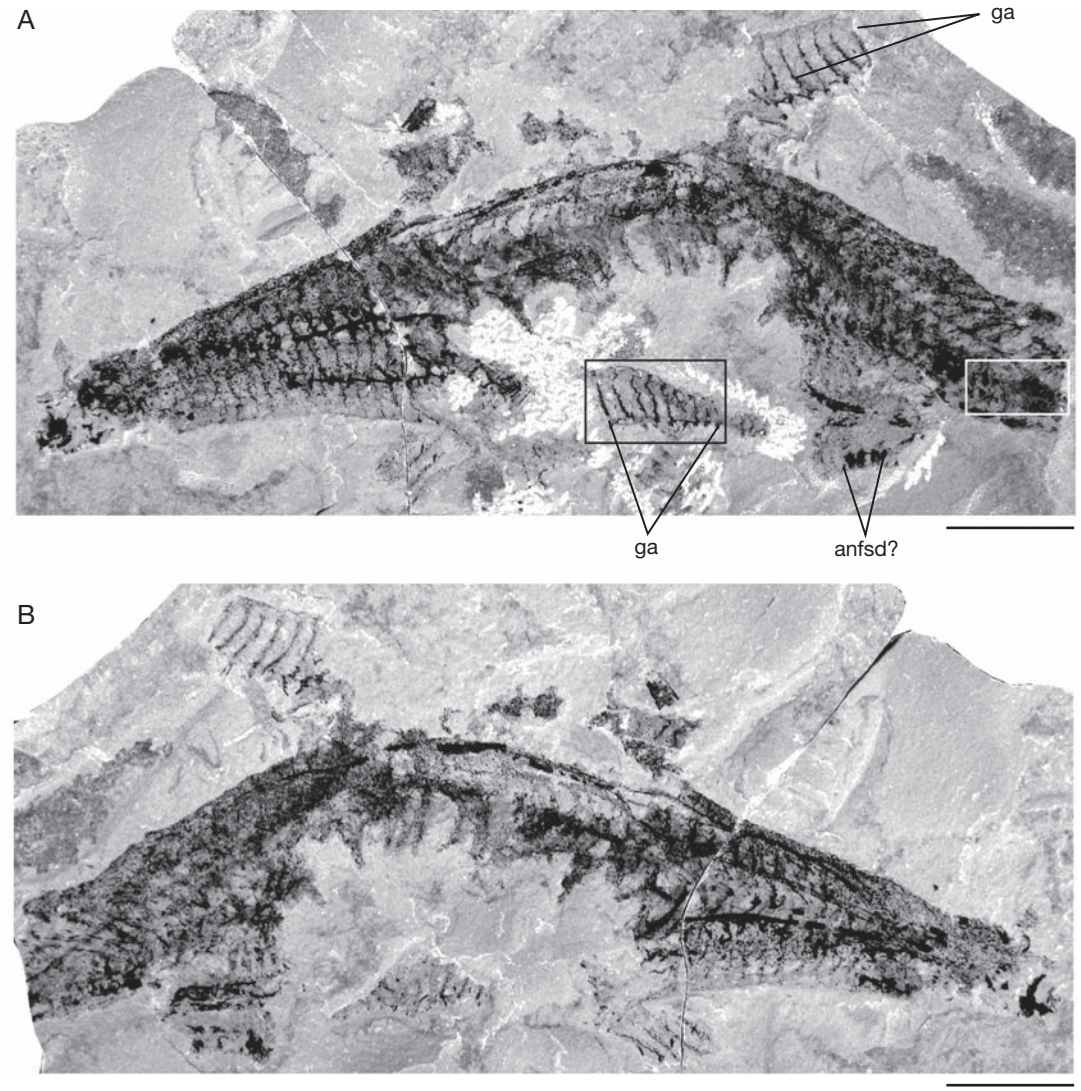


FIG. 19. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; imperfectly preserved specimen, presumably collapsed more or less dorsoventrally, and showing the sinuous gill arches and possible imprints of afferent branchial blood vessels; specimen MHNM 01-150; part (**A**) and counterpart (**B**), photographed in immersion in water. Framed areas in A are illustrated in Figure 20C, D. Scale bars: 10 mm.

be either of diagenetic origin, or compact calcified cartilage derived from the braincase wall (see Structure and nature of the mineralized tissues, p. 154).

A radiograph of the "braincase" of MHNM 01-123 has been made in order to check if any internal structure was preserved, but shows no evidence for any distinct internal structure, apart from a vaguely symmetrical pattern, which does not match the symmetry of its external outline and may be merely fortuitous.

Behind the presumed occipital region of MHNM 01-123 occur a number of scattered, separate elements, which are most probably the foremost arcualia (arc, Fig. 17).

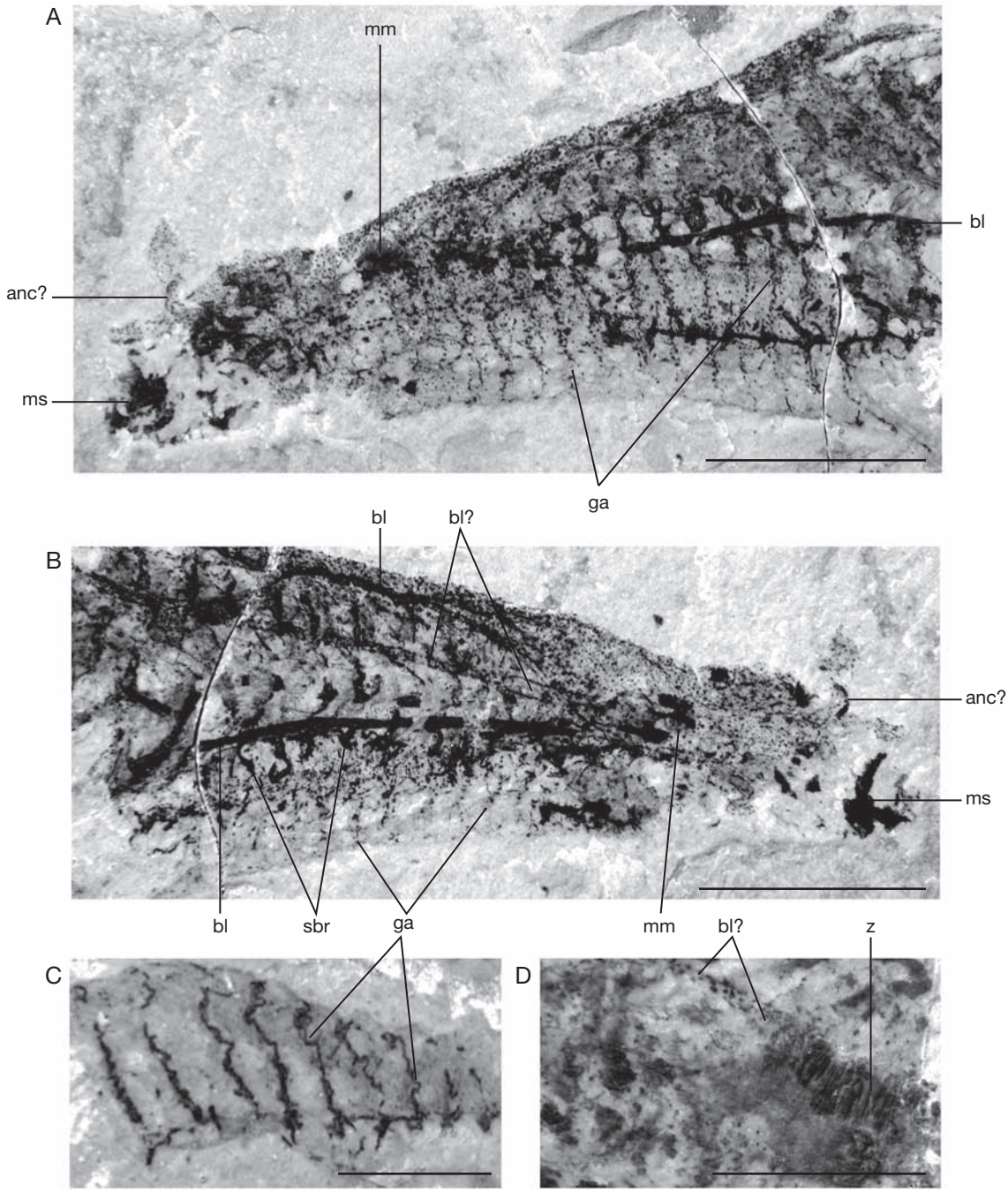


FIG. 20. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; details of specimen MHNM 01-150: **A**, **B**, head region in the part (**A**) and counterpart (**B**); **C**, detail view of the posterior gill arches of one side (area framed in Figure 19A); **D**, detail view of the lamellar mineralized structure at the posterior end of the lighter "black line" (area framed in Figure 19A). Scale bars: A, B, 10 mm; C, D, 5 mm.

Branchial apparatus

The branchial apparatus of *Euphanerops longaevus*, which extends from a short distance behind the "head stains" to immediately in front of the anal fin, was probably more or less cone-shaped, as suggested by its three-dimensionally preserved natural cast in specimens referred to as *Endeiolepis aneri* (Janvier *et al*. 2006). It is best visible in MHNM 01-02 (Fig. 3), but is also quite conspicuous in MHNM 01-98 (Fig. 12), 01-123 (Figs 5; 16), 01-135 (Figs 23-25), and 01-150 (Figs 19; 20), but its structure is more or less clear, depending on the degree of mineralization of its components. In unmineralized or poorly mineralized specimens that are collapsed in a roughly lateral aspect (e.g., MHNM 01-02 and 01-130; Figs 3; 4), only its numerous (at least 30) vertical, sinuous, gill bars are clearly visible (ga, bra, Figs 3; 4C). Then, in larger and more extensively mineralized specimens, there appear additional elements, termed here as "gill rods" (see below), which considerably obscure its organization, all the more so when the specimen is dorsoventrally or obliquely collapsed, such as in MHNM 01-98 (Fig. 12), 01-123 (Fig. 16), 01-135 (Fig. 23), and 01-125 (Fig. 32). In such cases, the entire branchial apparatus appears as a mass of packed vermicelli, made up by the broken mineralized gill arches, and the innumerable, more or less anteroposteriorly oriented "gill rods".

We term here as gill arches the larger, strongly sinuous, vertical elements that Arsenault & Janvier (1991: fig. 4B, "l.br") erroneously regarded as possible imprints of the gill filaments (ga, Figs 3; 18-20). These elements bear some resemblance to the gill arches of lampreys, which show much the same sinuous pattern (Holmgren & Stensiö 1936: fig. 226; Marinelli & Strenger 1954: fig. 64), and we assume here that they are actual gill arches and therefore not referred to here between quotation marks. The sinuous shape of the gill arches could be regarded as a consequence of the shrinkage of the musculature during decay (Briggs & Kear 1994; Briggs 2003), but we consider this unlikely, because no comparable distortion affects other elongated elements, such as paired and unpaired fin radials, and the "gill rods" when well exposed (with a single exception in MHNM 01-125, where the "gill rods" are much deformed; Figs 32; 33). These are best visible in MHNM 01-02 (ga, Figs 3; 18), where they show traces of incipient mineralization in the form of a pink transverse banding, and in 01-150 (ga, Figs 19; 20). In all other specimens, only portions of these arches are preserved here and there, and more or less covered with bundles of "gill rods" (ga+gr, gr, Figs 8; 12; 16; 21; 23-25; 32; 33). The mid-part of the gill arches is sinuous (ga, Figs 18-20; 40), but their dorsal and ventral portions seem to become almost straight (ga, Figs 17; 23; 24A; 26A; 40). It is thus probable that the crescent-shaped structures described in the holotype of *E. longaevus* by Arsenault & janvier (1991: fig. 2, "cr"), and then interpreted as possible dermal elements bordering the external gill openings, are in fact the loops of the sinuous portion of the gill arches, covered by the tarry layer of the so-called "myomere imprints" or "scales" (ga, Fig. 2B). Similar loops are visible along the dorsal margin of the branchial apparatus in MHNM 01-123 and 01-125 (ga, Figs 17; 30; 33A). Like in lampreys, the rearmost gill arches seem to be produced anteriorly and posteriorly into spinous processes (sp?, Fig. 35A2), but there is no clear evidence for the longitudinal epitrematic and hypotrematic *teniae*, which, in lampreys, unite the gill arches laterally.

How these gill arches were connected dorsally and ventrally remains obscure. However, MHNM 01-123 and 01-115 throw some light on this question. These specimens show longitudinal series of large, apparently paired, mineralized elements, many of which send off laterally an elongated process (ga, Figs 21; 23; 24A), whose extremity sometimes shows an incipient sinuous shape. These series of elements extend along the dorsal and ventral limits of the area occupied by the branchial apparatus, respectively. We assume here that they are probably paired, median series of elements, to which the gill arches were connected dorsally and ventrally. Therefore, they are termed here as dorsal and ventral "copular elements" (copd, copv, Figs 16; 21-24; 26; 30; 31; 40). In the rearmost part of the branchial apparatus of MHNM 01-123, the successive "copular elements" of the ventral series seem interconnected by a horizontal process, much as in the branchial basket of lampreys (conprv, Fig. 22).

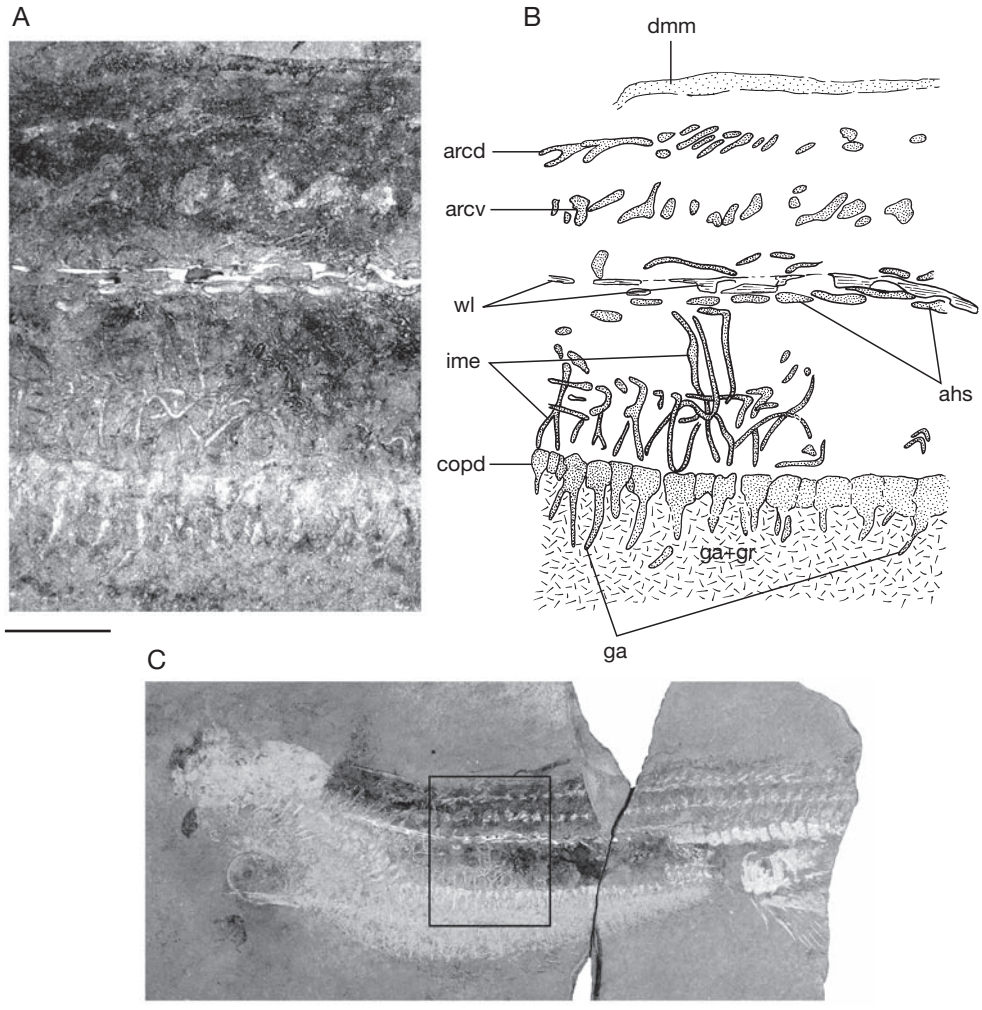


FIG. 21. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: photograph (**A**) and camera lucida drawing (**B**) of the mid-dorsal part of the body of MHNM 01-123 (area framed in **C**). Scale bar: 10 mm.

This interpretation may be corroborated by the fact that, in MHNM 01-02 and 01-150, at any rate, the gill arches seem also interconnected ventrally by means of a horizontal bar (Figs 3; 18-20), and this compares with the *taenia longitudinalis ventralis* of lampreys (Marinelli & Strenger 1954: figs 16, 64). In addition, in MHNM 01-150 (Figs 19; 20), which is more or less dorsoventrally collapsed, the branchial apparatus is partly dismantled on either sides of the specimens, but the gill arches of its displaced portions remain attached together and retain a normal spacing (ga, Fig. 20C), thereby suggesting that they were rigidly connected in some way. It is also worthy noticing that the rearmost five dorsal "copular elements" of MHNM 01-123, which are exposed in either dorsal, or ventral view, send off lateral processes on both sides (copd, ga, Fig. 30). This provides further evidence for the median position of the pairs of copular elements, and their probable connection with the gill arches of either

sides. Nevertheless, the reconstruction proposed here for the branchial apparatus of *E. longaevus* differs from the condition in lampreys (Fig. 26). Notably, lampreys show no median dorsal *taenia* (thus no equivalent, or homologue of the dorsal series of "copular elements"), and the dorsal end of the gill arches is free, extending along the ventrolateral surface of the notochord (Marinelli & Strenger 1954: fig. 39).

In MHNM 01-135A and less clearly so in 01-123, the presumed ventral series of "copular elements", is continued anteriorly by an elongated rod, termed here the "anterior ventral rod" (avr, Figs 3; 16; 23; 24; 27), which reaches to, and even seems to pass through, the ring-shaped element termed here as the "annular cartilage" (anc, Figs 3; 16; 23; 27; see below).

From what can be seen in 01-123, the series of dorsal "copular elements", reaches anteriorly to the level of the rear of the "braincase" (copd, Figs 16; 40). Posteriorly, both the dorsal and ventral "copular element" series end just anteriorly to the anal region, as also does the series of gill arches (copd, copv, Figs 16; 22; 30; 40).

The innumerable, minute cylindrical fragments of mineralized elements, which, in addition to the more or less complete gill arches, fill the area occupied by the branchial apparatus are referred to here as the "gill rods", in order to avoid any allusion to their homology with the gill rays of the jawed vertebrates; yet it is admittedly what they suggest most closely (ga+gr, gr, Figs 12; 16; 23; 25; 26; 30; 32; 33; 35A; 36; 40). The actual shape and position of the "gill rods" in *E. longaevus* is difficult to reconstruct, as they are closely packed, mixed up with gill arch fragments, and often distorted. In most cases, they appear as short rods, but they may sometimes be curved, and even form loops (gr?, Fig. 25B). In MHNM 01-98 and 01-135, however, they seem to form more or less anteroposteriorly oriented bundles, giving the aspect of a hairy covering (Figs 12; 25A). In some places, namely the dorsal and ventral parts of the branchial apparatus, they seem to diverge dorsally and ventrally, respectively (Fig. 12B). Curiously, in MHNM 01-125 (Figs 32; 33), which is obliquely collapsed, this arrangement into longitudinal bundles is not visible, and all the "gill rods" appear as randomly distributed and deformed. In MHNM 01-123 (Figs 5; 16), they are so closely packed that they form a large, pink mass, in which no particular orientation can be observed (yet this may also be due to the superficial weathering of the specimen).

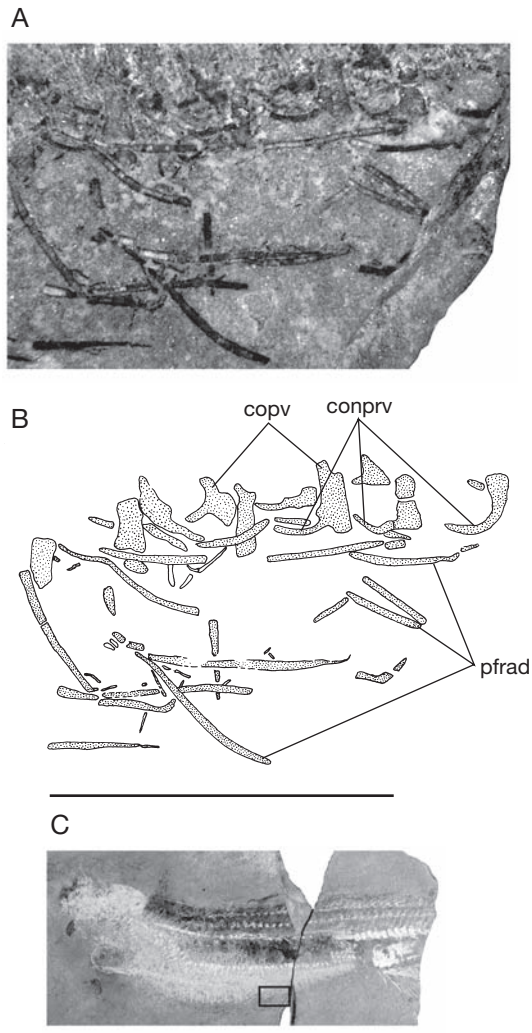


FIG. 22. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: photograph, in immersion in water (**A**), and camera lucida drawing (**B**) of the posterior part of the ventral series of "copular elements" in MHNM 01-123, showing the processes possibly connecting the ventral "copular elements" (area framed in **C**). Scale bar: 10 mm.

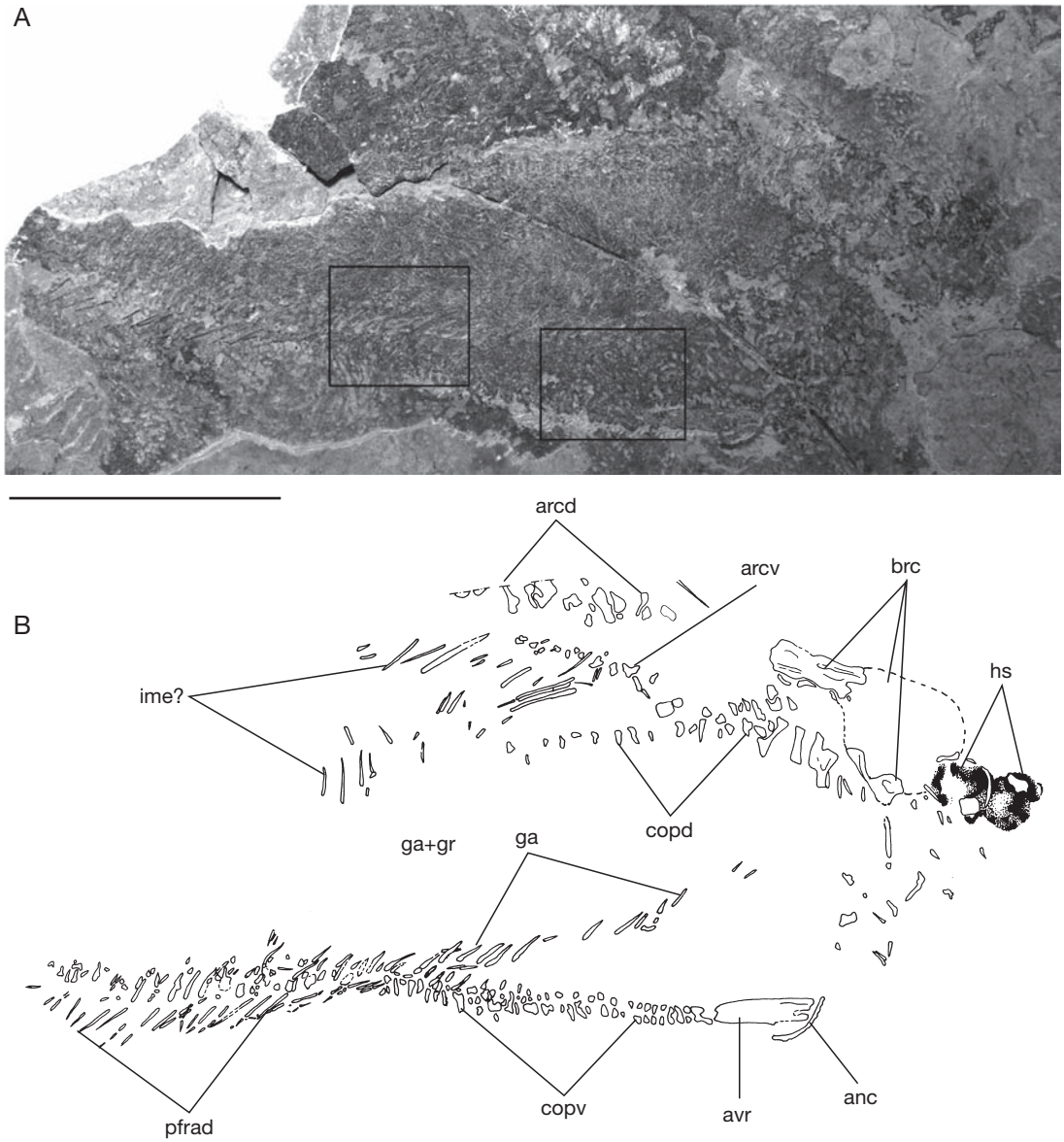


FIG. 23. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; specimen MHNM 01-135A, showing the head and paired fin skeleton, and the part of the disarticulated axial skeleton: **A**, photograph in immersion in water (detailed view of the branchial apparatus and ventral copular series in framed areas are shown in Figure 24); **B**, explanatory drawing ("gill rods" and middle part of gill arches omitted). Scale bar: 50 mm.

In contrast, in the posterior part of the branchial apparatus of MHNM 01-135A, the "gill rods" as distinctly arranged in anteroposteriorly oriented bundles, but some are curved and form roughly parallel, transverse series (gr?, Fig. 25B), thereby recalling the pattern of rounded fish scales. This peculiar shape can be interpreted in two ways, the curved, transverse elements being either part of the

"gill rods" (and this would suggest that the rods were somehow possibly united by loops), or overprinted portions of the sinuous gill arches of the right and left side. The position of the "gill rods" relative to the gill arches is currently impossible to tell. In MHNM 01-98 (Fig. 12), they sometimes overlie, and sometimes underlie the gill arches. We are thus only left with the possibility to speculate that, since the gills of lampreys are medial to the gill arches, those of *E. longaevus* and their supporting "gill rods" were probably also in the same position; that is, oriented toward the pharynx, and housed either in the gill filaments, or the interbranchial septum (gr, Fig. 26B1, B2). However, recently discovered specimens referred to *Endeiolepis aneri* throw some light on the role and position of these "gill rods" (Janvier *et al*. 2006). The three-dimensionally preserved branchial region of these specimens shows series of longitudinal grooves on the lateral surface of the internal cast of the branchial compartments (Stensiö's [1939] "ventrolateral scales"). In addition, one of these specimens (MNHM 01-154) shows the internal cast of the successive individual gill pouches, separated by narrow clefts. The surface of each of these clefts displays series of more or less parallel impressions, which strikingly resemble the gill rays in the gill filament impressions of *Eusthenopteron foordi* Whiteaves, 1881 (Jarvik 1980: fig. 114B), and even more so those of a Late Devonian cladoselachid from USA (Maisey 1989: fig. 3). We assume that these parallel impressions are either those of the "gill rods", or those of the soft tissues of the gill filaments, notably the afferent branchial arteries. If these impressions are actually those of the "gill rods" that are found mineralized in the large specimens of *E. longaevus*, then the latter were oriented anteromedially relative to the gill arches and body wall, and armed either the gill filaments proper (gr, Fig. 26B1), or the interbranchial septa between two adjacent gill pouches (gr, Fig. 26B2). They would thus be in much the same position as the gill filaments of an adult lamprey (Janvier *et al*. 2006). Again, these observations based on this particular specimen of *E. aneri* are inconsistent with the third, though unlikely, interpretation proposed here, that the "gill rods" armed the lateral wall of the gill chamber (gr, Fig. 26B3).

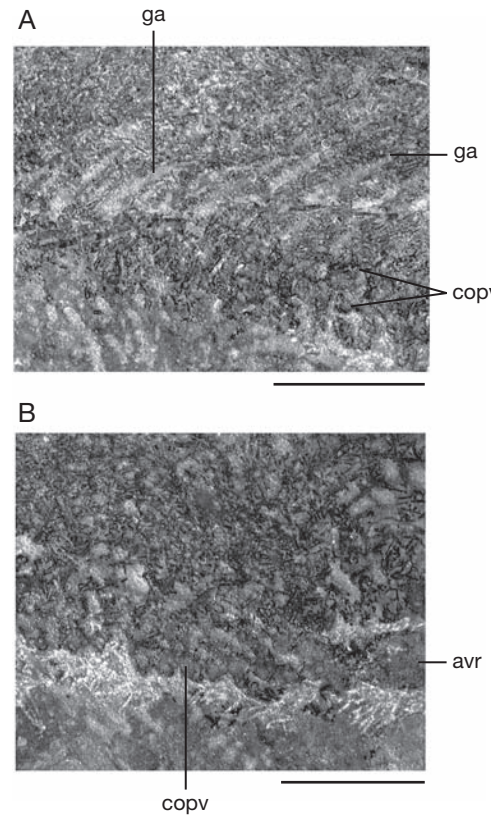


FIG. 24. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; details of the ventral copular elements and gill arches of MHNM 01-135A in the areas framed in Figure 23A: **A**, posterior part of the ventral series of "copular elements"; **B**, anterior part of the ventral series of "copular elements" and posterior extremity of the "anterior ventral rod". Photographed in immersion in water. Scale bars: 10 mm.

It is undecided whether these "gill rods" can be regarded as homologous to the gill rays of the gnathostomes (the only living vertebrates having gill rays), or homoplastic and unique to *Euphanerops* and perhaps *Endeiolepis*. Among fossil jawless vertebrates, the only – though remotely - comparable condition is found in the Lower Cambrian Myllokunmingiida, in which the six gill arches bear series of thin filamentous gill supports, or "gill rays" (Hou *et al*. 2002: figs 1, 2; Shu *et al*. 2003: fig. 1G, K; Janvier 2003: fig. 2E). Filamentous gill supports vaguely recalling gill rays also occur in the enigmatic Lower Cambrian Yunnanozoa, regarded

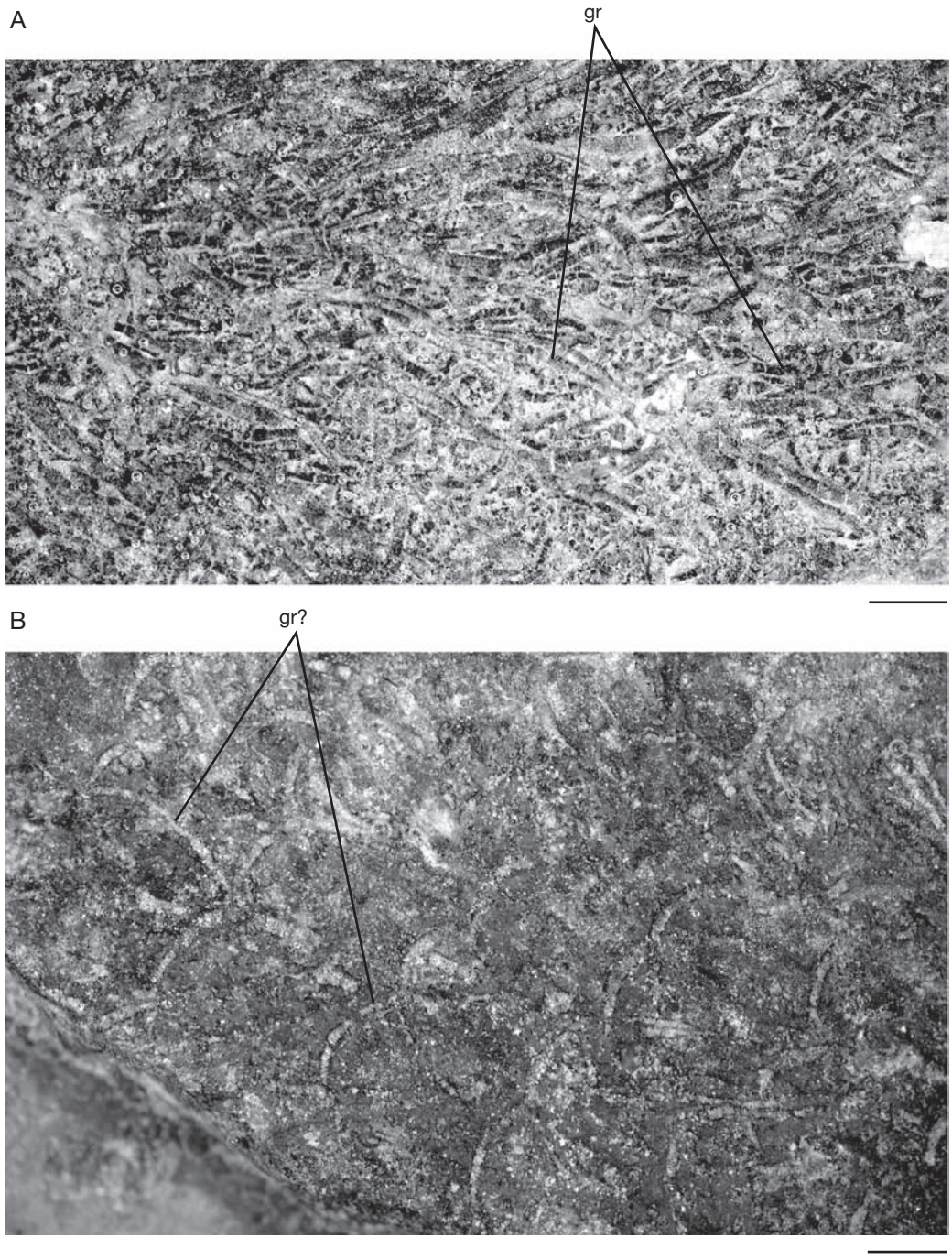


FIG. 25. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; detail view of the posterior region of the branchial apparatus of MHNM 01-135B, showing the numerous and closely packed "gill rods" (**A**) and the regular arrangement of certain curved elements, regarded here as either looping "gill rods", or overprinted portions of right and left sinuous gill arches (**B**). Photographed in immersion in water. Scale bars: 2 mm.

by some as basal vertebrates (Mallatt & Chen 2003: figs 5; 12; 15), but these gill supports are far less numerous and display a different structure than the "gill rods" of *E. longaevus*. Moreover, the gill ray-like structures of myllokunmingiids and yunnanozoans seem to be lateral to the gill arches, as in jawed vertebrates.

"Annular cartilage"

We refer here to as the "annular cartilage" a ring-shaped (in fact, slightly oval) element of *Euphanerops longaevus*, which is particularly conspicuous in MHNM 01-123 (anc, Figs 16; 27A). Again, we refer to this structure with quotation marks, because there is no evidence that it is homologous to the annular cartilage which strengthens the oral funnel of lampreys. Its relations to the neighbouring structures are unclear, but at least two specimens show that it is situated at the anterior end of the "median ventral rod" that prolongs the "ventral copular series" (avr, Figs 23B; 27). In turn, there is no evidence that the "median ventral rod" is the homologue of the piston cartilage of lampreys. The "annular cartilage" (assuming that it is actually a cartilage, and not another kind of diagenetically mineralized tissue) seems to be situated well behind the level of the "head stains", whereas the annular cartilage of lampreys in the anteriormost cartilage of their head skeleton. Its position in the best preserved specimens of *E. longaevus* seems to correspond to the anterior end of the branchial skeleton and to be oriented obliquely, relatively to the dorsoventral axis (anc?, anc, Figs 3B; 16; 18). In MHNM 01-123 (Fig. 27A), its lumen looks as if filled with dark outgrowth, but preparation reveals that these are merely scattered fragments of "gill rods". In this specimen, as in MHNM 01-135 (Fig. 27B), it is also traversed by the anterior portion of the "anterior ventral rod" (avr, Figs 16; 23; 27). Some traces or portions of this ring-shaped cartilage can also be seen MHNM 01-69, and possibly in 01-02, 01-150 and the holotype (anc, anc?, Figs 2C; 3B2; 38B).

There is thus no clear indication that the "annular cartilage" is homologous to the much thicker and anteriorly placed annular cartilage of lampreys (Marinelli & Strenger 1954: fig. 64). However, it may be noticed that, at metamorphic stage 8 of lampreys, the annular cartilage is much thinner than in the adult, and forms from a blastema which is in continuity with that of the piston and apical cartilages of the lingual apparatus (Johnels 1948: fig. 39). It is uncertain how much this may relate to the apparently close association of the "annular cartilage" and the "anterior ventral rod" in *E. longaevus*, and we can offer no interpretation for the

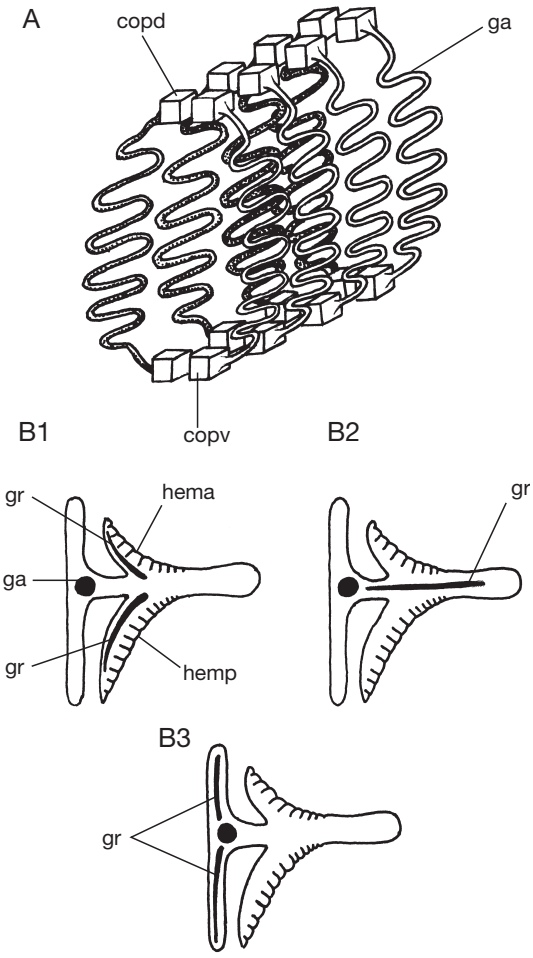


Fig. 26. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: **A**, attempted reconstruction of the branchial apparatus, showing the relations between the gill arches and the dorsal and ventral "copular elements", diagrammatically figured here as cubic; the "gill rods" are omitted; **B**, horizontal section of a gill unit, showing three possible reconstructions of the position of the "gill rods". Not to scale.

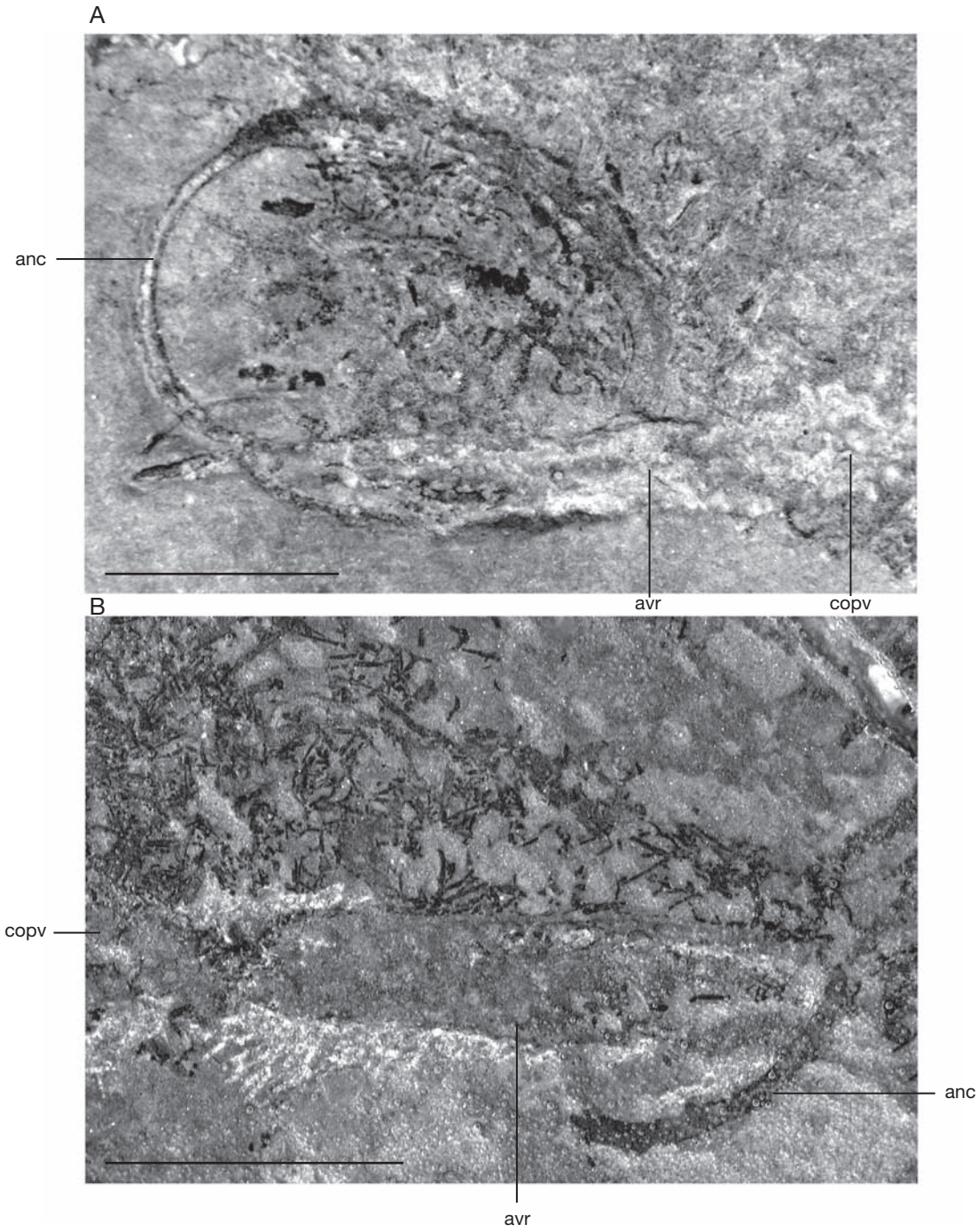


Fig. 27. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; elements referred to here as the "annular cartilage" and the "anterior ventral rod" in MNHN 01-123 (**A**) and 01-135A (**B**). Photographed in immersion in water. Scale bars: 10 mm.

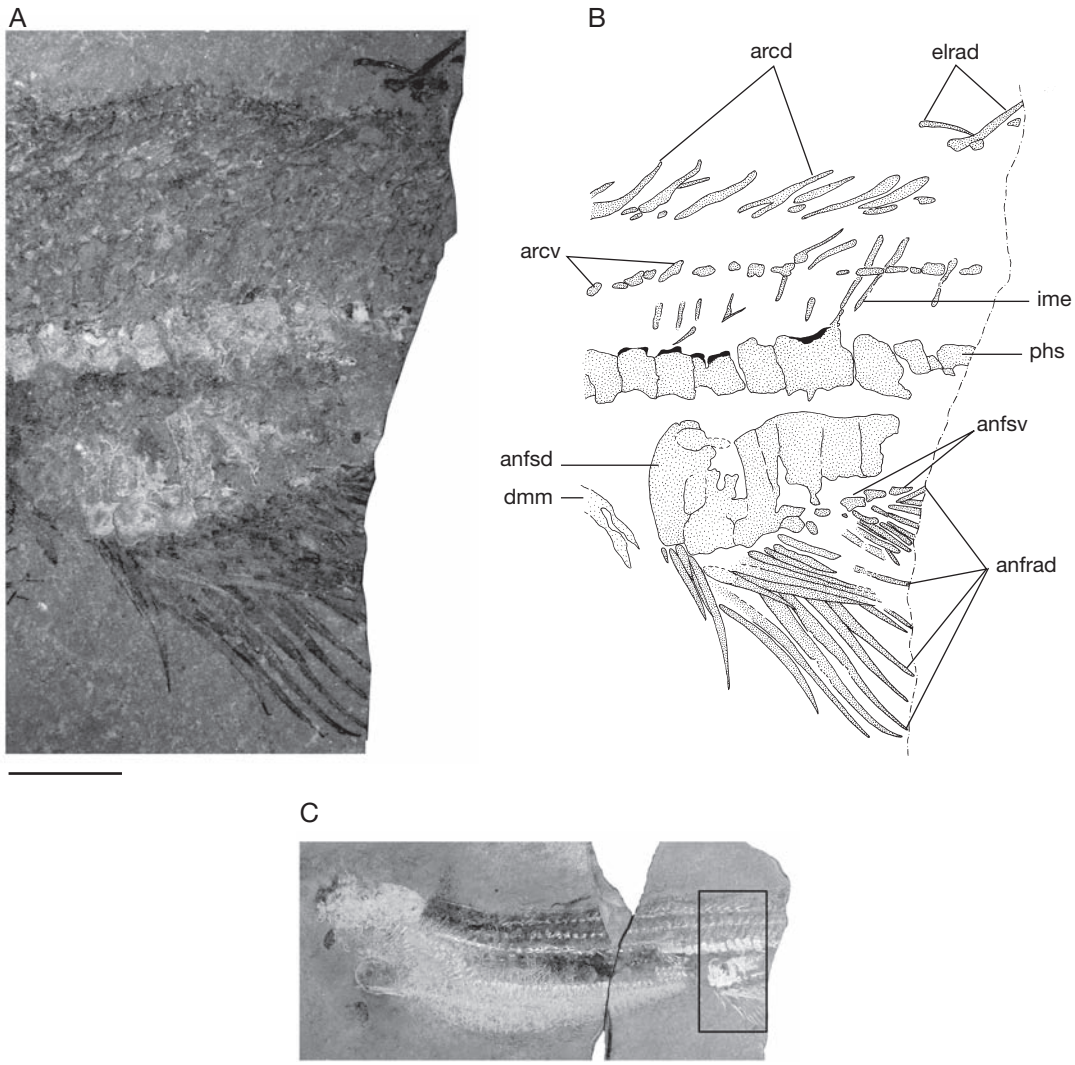


FIG. 28. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: photograph in immersion in water (**A**) and camera lucida drawing (**B**) of the mineralized skeletal elements of MHNM 01-123 at the level of the anal fin (area framed in **C**); black areas in the "posterior haemal series" indicate the extent of the more compact mineralized layer. Scale bar: 10 mm.

function of this structure, except that it may have served in maintaining open the entrance to the branchial apparatus.

AXIAL SKELETON

We refer to as the axial skeleton of *Euphanerops longaevus* three longitudinal series of elements which extend from shortly behind the braincase to the posterior limit of MHNM 01-123. These series include two series of arcualia and a more ventrally placed series of elements referred to below as the "haemal series" (arc, arcd, arcv, ahs, phs, Figs 16; 17; 21; 23; 28; 30; 40). We assume here that all these elements, even if mineralized *post-mortem*, are

skeletal elements, and not incidental accumulations of segmentally arranged mineralized soft tissues.

Arcualia

These elements are organised in two parallel series, and are rather irregular in shape. It remains uncertain as to whether these two series are dorsal and ventral series, or the right and left halves of the same series that became juxtaposed by a more or less transverse collapse of the carcass. The only argument for considering them as dorsal and ventral series, respectively, lies in the fact that their components are quite different in shape.

The elements of the dorsal series (arcd, Figs 16; 21; 23; 28; 40) are generally elongated, posterodorsally tilted, and display a slender dorsal process, as well as a frequently bifid ventral end, which recalls the shape of the basidorsals of lampreys (Marinelli & Strenger 1954: fig. 64). The elements of the ventral series are smaller and irregular in shape (arcv, Figs 16; 21; 28). We assume here that these elements are dorsal and ventral arcualia, respectively (i.e. basidorsals, interdorsals, basiventrals, and interventrals), separated by the notochord which occupied the broad gap between the two series of arcualia (nch, Figs 16; 40). However, it is impossible to clearly differentiate the basidorsals from the interdorsals (much as in lampreys) and the basiventrals from the interventrals. A longitudinal series of smaller elements (yet larger in the caudal region) is situated further below (ahs, phs, Figs 16; 21; 23; 28; 30; 40). These are referred to here as the "haemal series", but could in fact be readily interpreted as the series of ventral arcualia. However, we discard here this interpretation, because this would leave us with an extra series of elements dorsally (the dorsal arculia in the present interpretation), which could hardly be interpreted as fin supports, as there is no dorsal fin in *E. longaevus* (*contra* Arsenault & Janvier 1991: fig. 4), apart from the epichordal lobe of the tail.

If the present interpretation of the axial skeleton of *E. longaevus* is correct, this would be the first evidence for ventral arcualia in the axial skeleton of a jawless vertebrate (Donoghue & Sansom 2002), notwithstanding the recent interpretation of serially arranged imprints as a "vertebral column" in the Lower Cambrian myllokunmingiid *Haikouichthys* (Shu *et al*. 2003), which remains somewhat conjectural, as these imprints never extend posteriorly to the level of the branchial apparatus.

The broad notochordal gap between the two series of arcualia in MHNM 01-123 suggests that the notochord of *E. longaevus* was very large (nch, Figs 16; 40), and comparable in relative size to that of the living hagfishes and lampreys, and probably also osteostracans in the posteriormost part of their occipital region (Janvier 1977: 20, fig. 10B-D).

Anterior and posterior haemal series

The series of relatively small, elongated elements which extend dorsally and ventrally to the "white line" (wl, Figs 16; 39); see Enigmatic structures, p. 193) in MHNM 01-123 are referred here to as the "anterior haemal series" (ahs, Figs 16; 39; 40). As discussed above, this series of mineralized elements are situated too far ventrally to be regarded as the ventral arcualia proper, and, as it will be explained below, the "white line" is unlikely to be the notochord. We suggest here that they may have surrounded the dorsal aorta. Admittedly, the term "haemal" used here for these cartilage series may be misleading, as it suggests a homology with the haemal arches of the jawed vertebrates. Yet we justify its use by the assumption that the "white line" may be a trace of the (possibly *post-mortem*) mineralized wall of the dorsal aorta.

It is unclear whether this "anterior haemal series" is connected to the basiventrals and basidorsals, but some of the ventral arcualia seem to be united ventrally to elements of the "haemal series" by means of elongated structures that are more or less similar to those we refer to here as the "intermuscular elements" (ime, Fig. 28; see Enigmatic structures, p. 193). The "anterior haemal series" can be followed from the anterior end of the "white line" (wl, Figs 16; 17) to its ultimate, posterior traces (wl, Fig. 39B). Here, they seem to be prolonged posteriorly by a series of much larger, roughly rectangular elements, termed here the "posterior haemal series" (phs, Figs 16; 28; 30; 39; 40), and which begins dorsally to the posterior end of the visceral cavity.

The foremost elements of the "posterior haemal series" display a very compact superficial structure,

with a brownish surface which recalls the compact mineralized layer found locally in the "braincase" (Fig. 10). The series certainly extended posteriorly to the broken margin of the specimen MHNM 01-123 (Fig. 16); that is, posteriorly to the level of the posterior limit of the anal fin, but the caudal region, and thus the more posterior elements of the series, is not preserved in any of the specimens which display a mineralized skeleton. Scattered mineralized rods, referred to here as the "intermuscular elements" (ime, Figs 16; 21; 23; 28; 39; 40; see Enigmatic structures, p. 193) occur between the "posterior haemal series" and the ventral arcualia, but, as in the case of the "anterior haemal series", there is no unambiguous connection with the ventral arcualia.

"Anal fin supports" and anal fin

The anal fin of *E. longaevus* has been described by Woodward (1900: fig. 1a; although interpreted as a dorsal fin), Arsenault & Janvier (1991: fig. 4A) and Janvier (1996a: fig. 1). In MHNM 01-02, for example, it is composed of a dozen radials, apparently radiating from a small, prominent basal lobe (anfrad, Fig. 3B2). The large specimen MHNM 01-123 displays part of the anal fin, which is armed with large and distally pointed mineralized radials (anfrad, Figs 16; 28; 30; 40). However, the anal fin of this specimen strangely looks as if being composed of a paired series of radials, one of which overlaps the other and shows more closely-set and posteriorly directed radials (Figs 28; 30). This is particularly difficult to interpret, all the more so that it is unclear whether the series of the most posteriorly directed radials belongs to the same series as the more expanded ones, or lies on a different plane than the latter.

None of the other specimens of *E. longaevus* shows paired series of anal radials, although they are far less mineralized and distinct than in 01-123. It is possible that, in smaller specimens, what we interpret as radials in the anal and caudal fins are essentially alignments of small black grains, which may be centres of incipient mineralization at the surface of the cartilaginous radials. In the radials of the epichordal lobe, there are sometimes two or three such longitudinal series of black grains, which make the count of the radials extremely difficult (Fig. 29A). However, one may assume that this artefact of preservation may be misleading only as to the number of radials, but not the number of radial series.

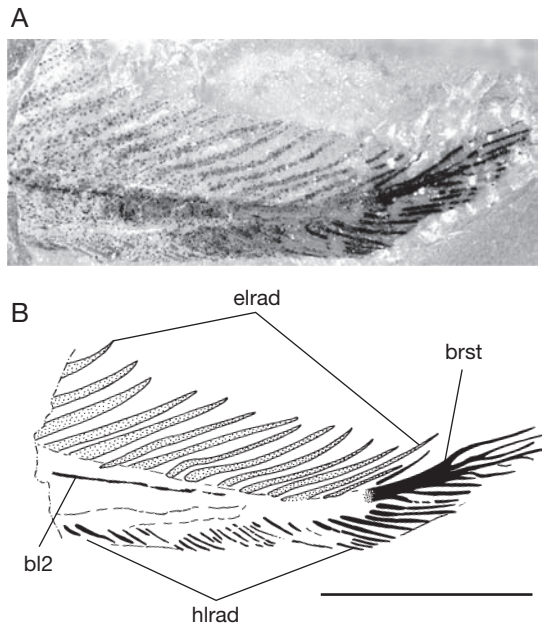


Fig. 29. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: posterior extremity of the caudal fin of MHNM 01-79B, photographed in immersion in water (**A**), and camera lucida drawing of the same specimen (**B**). Scale bar: 10 mm.

Moreover, no vertebrate shows paired radials in any of the median fins. It is also unlikely that the anal fin of *E. longaevus* is in fact a paired, pelvic fin, as it seems to be clearly situated posteriorly to the anus, and MHNM 01-123 shows no evidence for the gut passing dorsally to the endoskeletal supports of this fin (the "anal fin supports"; Fig. 16). One interpretation for this peculiar arrangement of the radials is that part of them (about seven radials; Fig. 28), from the posterior half of the fin, have been displaced forwards, over the foremost one. This seems to agree with the fact that, when considering the length gradient of the 10, or so, undisplaced radials, the length of the seven radials in the more oblique (and presumably displaced)

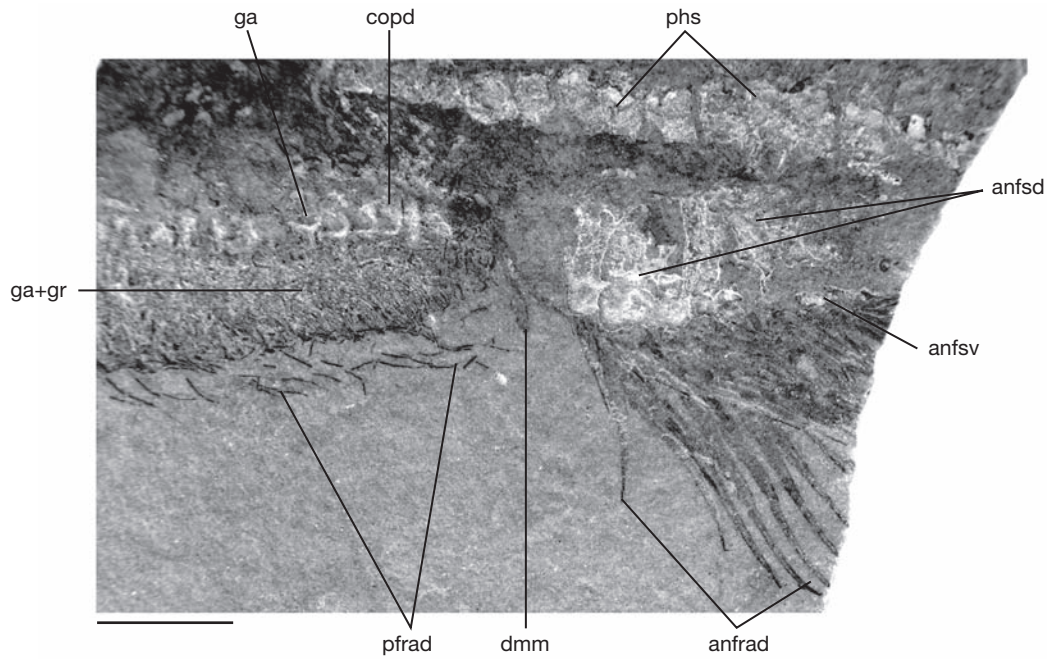


FIG. 30. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; posterior part of the branchial apparatus, posterior paired fin radials and anal fin of MHNM 01-123, photographed in immersion in water. Scale bar: 10 mm.

series matches that of the apparently missing radials of the posterior part of the fin (anfrad, Fig. 28). In sum, we are left with four possible interpretations, the first of which is preferred here, as it requires fewer ancillary assumptions than the others: 1) there is a single series of radials, but some radials of the posterior part of the anal fin have been displaced forwards; 2) there are two series of radials, but the fin is nevertheless an unpaired anal fin; 3) the position of the anus inferred here is wrong, and this fin actually is a pre-anal pelvic; and 4) the fin is a true anal fin but is actually paired. The latter condition is unknown in any other vertebrate, and this suggestion may sound absurd, but one should keep in mind that the peculiar "horizontal ventral lobe" (possibly a modified anal fin) of the osteostracan tail has a median axis, bordered laterally by a paired, narrow "fin web" (Heintz 1967). Although this problem is crucial to understanding of the distribution of paired and unpaired fin characters in vertebrates, it can only be resolved by the discovery of more, extensively mineralized, specimens of *E. longaevus*.

The radials of the anal fin are in contact with an ensemble of generally very large mineralized plates, which are situated ventral to the "posterior haemal series", and referred to here as dorsal and ventral "anal fin supports". There are about four or five large "dorsal anal fin supports" (anfsd, Figs 16; 28; 30; 40) and, in addition, a series of smaller "ventral anal fin supports", which extends between the dorsal ones and the proximal extremity of the posterior anal radials (anfsv, Figs 16; 28; 30; 40). Interestingly, the series of the posteriormost ventral "anal fin supports" and the posteriormost anal fin radials display a somewhat branching pattern, which recalls the structure of the metapterygium of the paired fin of jawed vertebrates.

CAUDAL FIN

The caudal fin of *Euphanerops longaevus* has been described in detail by Arsenault & Janvier (1991:

fig. 4B) and Janvier (1996a: fig. 4B), and the new material considered here only provides some additional information. Unfortunately, the caudal fin is not preserved in any of the specimens which have the most extensively mineralized skeleton. Only MHNM 01-123, shows some of the foremost radials of the epichordal lobe (elrad, Figs 16; 28). The caudal fin is, however, well preserved, though not mineralized, in MHNM 01-98, where the very fine-grained sediment shows the imprint of the skin web extending between the radials (Fig. 12A). The tip of the caudal fin of MHNM 01-79A (Fig. 29) is also exquisitely preserved and provides information about the posteriormost radials. The latter arise from a branching structure that prolongs the posterior tip of the notochord (brst, Fig. 29B), much as in the tail of lampreys or hagfishes (Marinelli & Strenger 1954: fig. 46; 1956: fig. 109). It also confirms that the radials of the hypochordal lobe (hlrad, Fig. 29B) are thinner and more closely-set than those of the epichordal lobe (elrad, Fig. 29B), as described by Arsenault & Janvier (1991). This tail also shows what may be the "black line" 2 (see Enigmatic structures, p. 193), which extends here almost to the posterior tip of the chordal lobe (bl2, Fig. 29B).

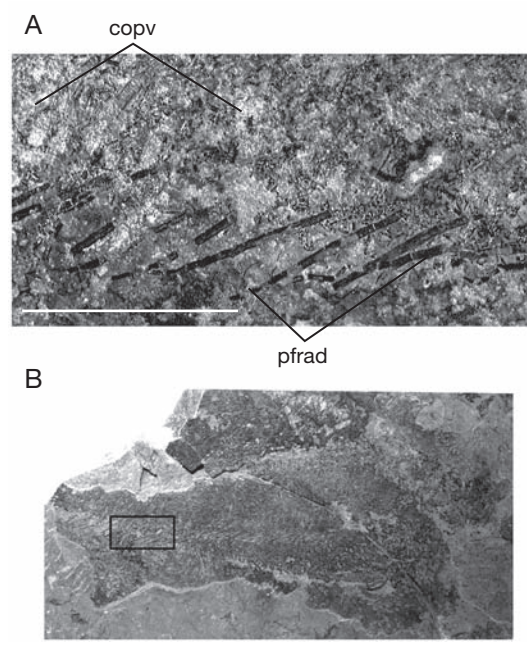


FIG. 31. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: **A**, detail of the paired fin radials in MHNM 01-135A (area framed in **B**). Photographed in immersion in alcohol. Scale bar: 10 mm.

PAIRED FINS

Neither the holotype of *Euphanerops longaevus* nor MHNM 01-02 (Figs 1-3) show any evidence for paired fin radials, and Arsenault & Janvier (1991) concluded that this species did not possess paired fins, contrary to anaspids, such as *Pharyngolepis* or *Rhyncholepis* (Ritchie 1964, 1984). Now, some of the larger specimens described here clearly show a series of mineralized rods arising from the ventral margin of the body, from slightly behind the "annular cartilage" back to the anal region (Fig. 5; pfrad, Figs 16; 22; 23; 30; 31; 32; 33C; 40). We regard it as very unlikely that these roughly parallel, mineralized rods might be either displaced portions of the gill arches or "gill rods", and rather interpret them as ventrolaterally placed paired fin radials. However, only MHNM 01-125 (Figs 32; 33C) provides some indication for these radials being arranged in paired series. The latter specimen is obliquely, almost dorsoventrally collapsed, and its branchial region is exposed in a more or less ventral aspect. The radials, which are quite distinct from the underlying gill arches and "gill rods" in being somewhat darker in colour and more compactly mineralized, are arranged into pairs along the posterior part of the branchial apparatus, and the two series diverge slightly anteriorly (pfrad1, pfrad2, Fig. 32B). This suggests that the paired, ribbon-shaped fins were situated far ventrally, close to the ventral midline posteriorly, and were more widely spaced anteriorly, exactly as reconstructed by Ritchie (1964: fig. 1B) in *Pharyngolepis oblongus* Kiaer, 1924.

HEART AND PERICARDIAC CARTILAGE

Among the questions raised by the odd morphology of *Euphanerops longaevus*, a particularly perplexing one is that of the position of heart, already alluded to by Arsenault & Janvier (1991) and Janvier (1996a). In all living, piscine vertebrates, as well as in some fossil taxa where it can be confidently located (e.g., osteostracans, Janvier 1981b), the heart is situated at the rear of the gill series. By comparison

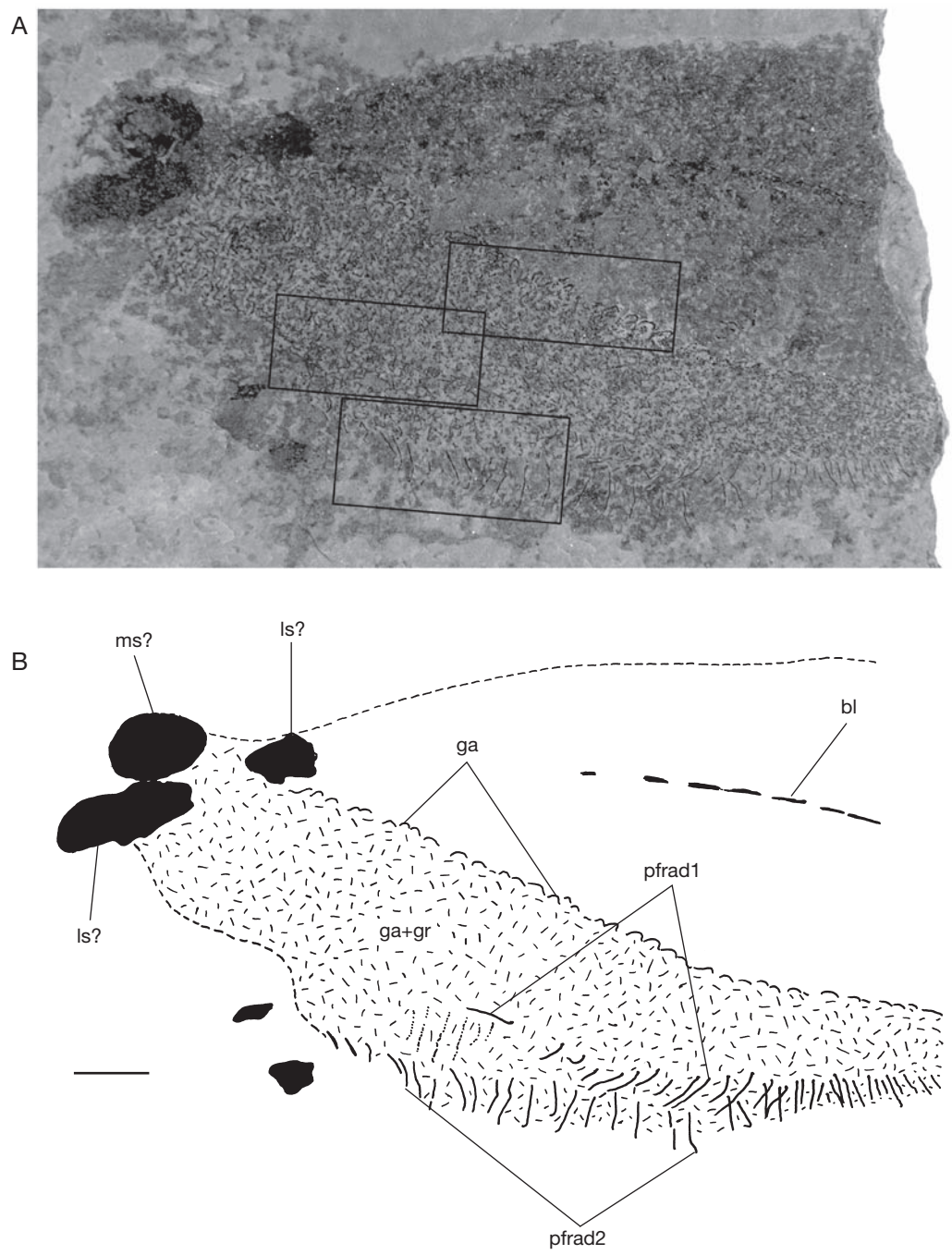


FIG. 32. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada: **A**, incomplete ventrolaterally collapsed specimen (MHNM 01-125A) photographed in immersion in water, and showing the series of paired fin radials overprinted on the branchial apparatus; framed areas are shown in detail in Figure 33; **B**, explanatory sketch. Scale bar: 5 mm.

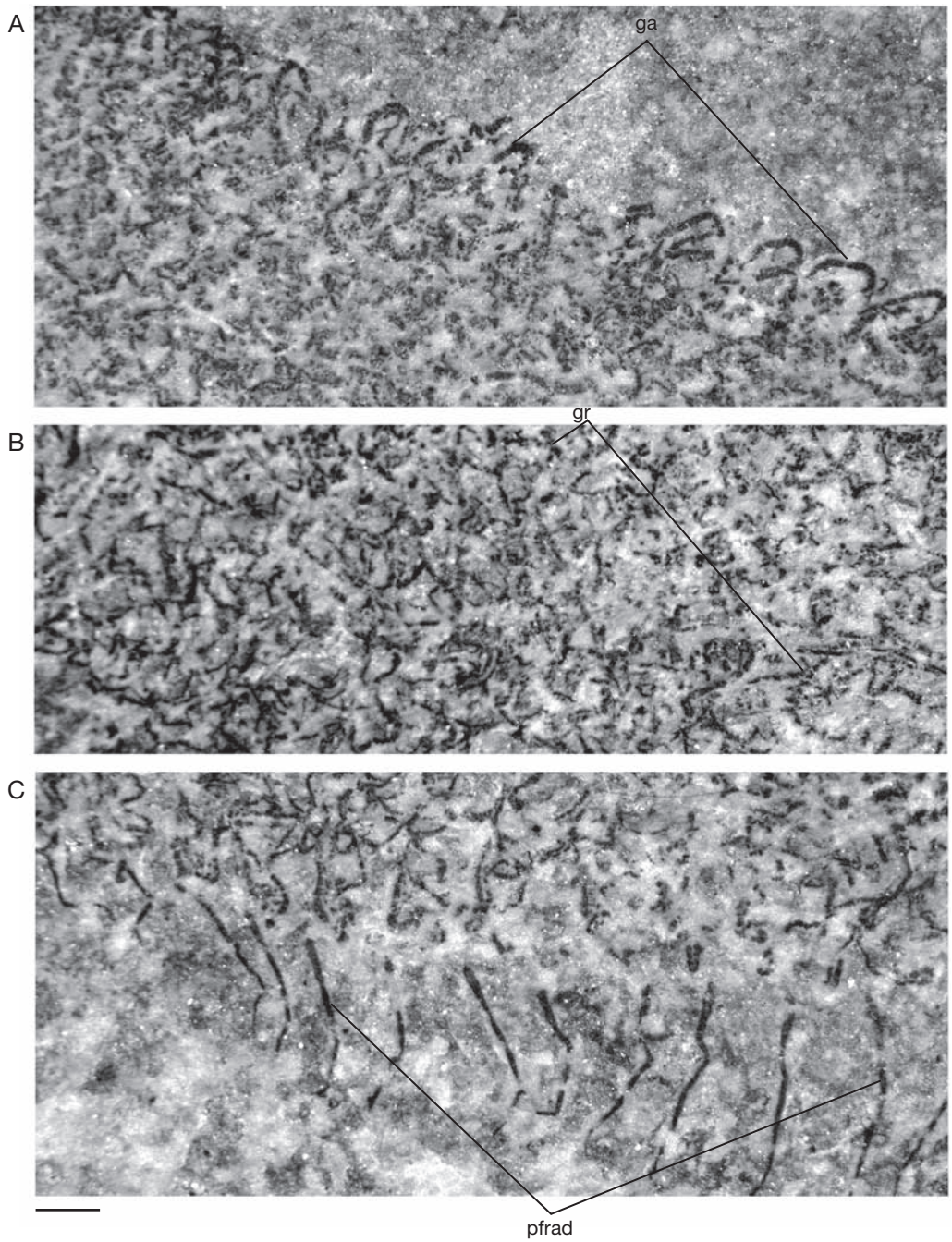


FIG. 33. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; detail views of the branchial apparatus and paired fin radials of MHNM 01-125A (areas framed in Figure 32A): **A**, dorsal boundary of the branchial apparatus, showing the loop-shaped structures assumed to be parts of the sinuous portion of the gill arches; **B**, assemblage of gill arch fragments and "gill rods"; **C**, ventral margin of the body, showing some gill arches and "gill rods", and a series of paired fin radials. Photographed in immersion in water. Scale bar: 1 mm.

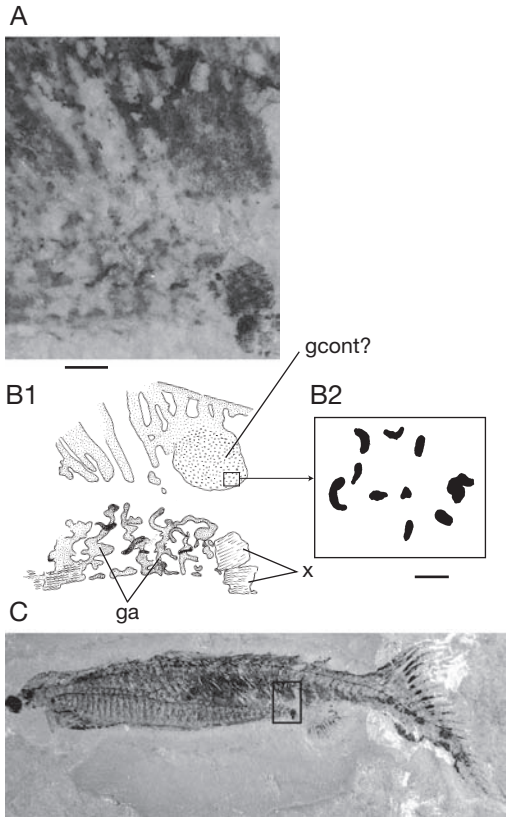


FIG. 34. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; specimen MHNM 01-02A: photograph in immersion in alcohol (**A**) and camera lucida drawing (**B1**) of the posterior part of the branchial apparatus and the overlying structure (framed in **C**), regarded by Arsenault & Janvier (1991) as the possible imprint of the heart; **B2**, detail drawing of the elongated black grains, which suggest that this structure may rather be either gut contents, or "diffuse mineralized matter". Scale bars: A, B1, 1 mm; B2, 0.1 mm.

to lampreys, which we have considered here as a living proxy for the interpretation of *E. longaevus*, the heart in this species should have been located at the posterior extremity of the branchial apparatus; that is, immediately anterior to the gap which is assumed to indicate the position of the anus (a, Fig. 3B2). However, nothing in this area clearly suggests a pericardiac cartilage. Arsenault & Janvier (1991: fig. 4C, "c?") suggested that the imprint of the heart in MHNM 01-02 might have been a patch of greyish matter that is situated dorsally to the posterior extremity of the branchial apparatus. However, the re-examination of the specimen showed that the patch in question contains numerous scattered, sausage-shaped, grains, and may rather be either gut contents (gcont?, Fig. 34B), or a small mass of "diffuse mineralized cartilage".

In MHNM 01-02, the rearmost gill arches progressively diminish in depth, until they reach two square-shaped, carbonaceous imprints, which display a peculiar, parallel-fibred structure (x, Figs 3; 34; 35). Arsenault & Janvier (1991: fig. 4C, "x") regarded these imprints as possible plant fragments, incidentally placed here. This was nevertheless surprising, since no other plant fragment, however small they may be, occur around this particular specimen, although plant remains do occur in the same laminite beds. We have tried to follow the posterior prolongation of the last posterior visible gill arch, by removing a small portion of the ventralmost part of one of these fibrous, carbonaceous imprints, and uncovered a small mass of pinkish, slightly mineralized matter, which may represent the pericardiac cartilage (pcard?, Fig. 35B), and seems to be in continuity with both carbonaceous imprints. Although this is not a definite evidence, these two "x" imprints seem in fact to be part of the animal, and closely associated with the underlying possible pericardiac cartilage. Strangely, no such fibrous imprints occur in other specimens of *E. longaevus*, however well preserved they may be. It should be pointed out here that, about 5 mm anterior to these "x" imprints, the branchial apparatus shows vague traces of longitudinal rods, which may be imprints of barely mineralized "gill rods" (gr?, Fig. 35A2), and this suggests that the "x" imprints could also be imprints of the rearmost gills or "gill rods".

Another possibility is that the heart was situated dorsal to the branchial apparatus, in the area termed here the "visceral cavity", although this would also imply an odd blood circulation, namely that the afferent arterial trunk would first have to run backwardly, and then turn around the posterior end of the branchial apparatus in order to reach the gill arches at the level of their ventral end.

VISCERAL CAVITY

Owing to the considerable posterior extension of the branchial apparatus, the stomach, intestine,

liver, kidneys and gonads of *Euphanerops longaevus* were necessarily housed dorsally to the latter. Their position is presumably indicated by the spindle-shaped, darker area, which extends dorsally to approximately the posterior half of the branchial apparatus, and is best visible in MHNM 01-02, 01-98, 01-69A, 01-123, and 01-130 (vsc, Figs 3; 4; 12; 16; 36).

In MHNM 01-98 and, to a lesser extent, MHNM 01-02, the imprint of the visceral cavity is partly filled with an oblong mass of fine-grained whitish or greyish matter, and it is assumed that this area of the visceral cavity corresponds to either the stomach, or the intestine (stc, Figs 3; 36; 37). A similar oblong patch of fine-grained matter is conspicuous in practically all the specimens of *Endeiolepis aneri* (Stensiö 1939: fig. 3, "int"; Janvier 1996a: fig. 5), and strikingly recalls the fine-grained stomach contents described by Wilson & Caldwell (1998) and Donoghue & Smith (2001) in furcacaudiform thelodonts and *Turinia*, respectively. In these two specimens of *E. longaevus* the presumed stomach contents shows, in its centre, one or two rounded dark stains that suggests the presence of larger food particles (stc, Figs 3B2; 36). However, the examination of the stomach contents of a large number of specimens of *Endeiolepis aneri* failed to reveal any large prey or particle. It is thus possible that these stains are artefacts due to the overprinting of the fine-grained stomach contents and other, skeletal or soft-tissue structures.

Direct observation, in immersion, of the surface of the whitish area of the stomach contents in MHNM 01-98 shows minute black grains arranged into sinuous, branching lines (blv?, Fig. 37), much like the thinnest of the blood vessel imprints described by Arsenault *et al.* (2004) in the antiarch *Bothriolepis canadensis* from Miguasha. It is not ruled out that this pattern is fortuitous, but it may also be, like in *Bothriolepis*, the trace of the blood vessels from the wall of either the digestive tract, or the visceral cavity.

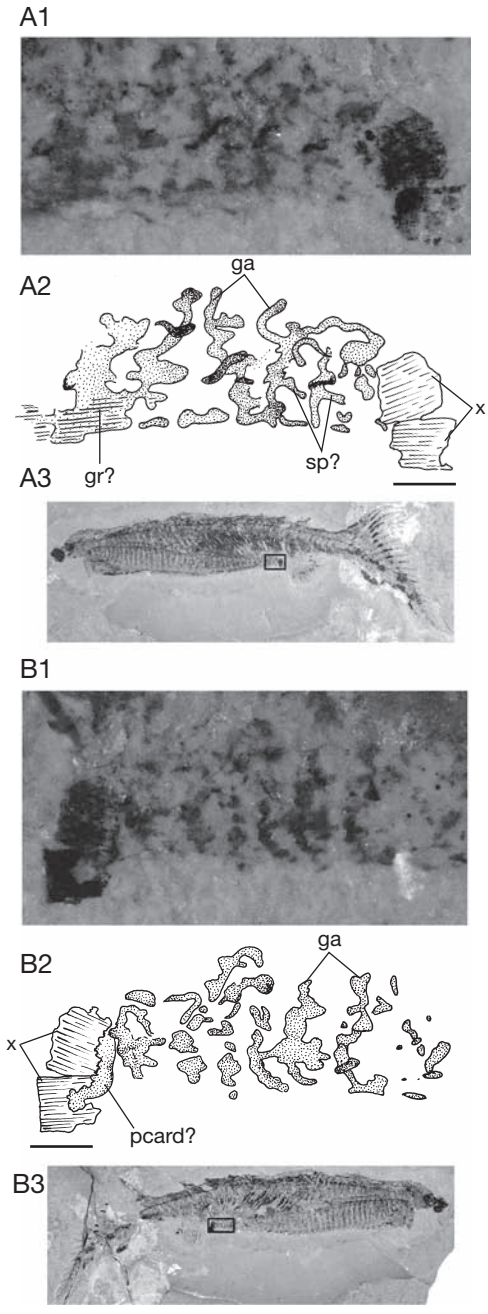


FIG. 35. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian Upper Devonian), Miguasha, Quebec, Canada: photograph in immersion in alcohol (**A1**, **B1**) and camera lucida drawings (**A2**, **B2**) of the posterior extremity of the branchial apparatus of MHNM 01-02A, B (areas framed in **A3** and **B3**, respectively). Scale bars: 1 mm.

ENIGMATIC STRUCTURES

We describe below a number of structures, which are observed to various extents in *Euphanerops longaevus*, and either have no clear homologue in other fossil

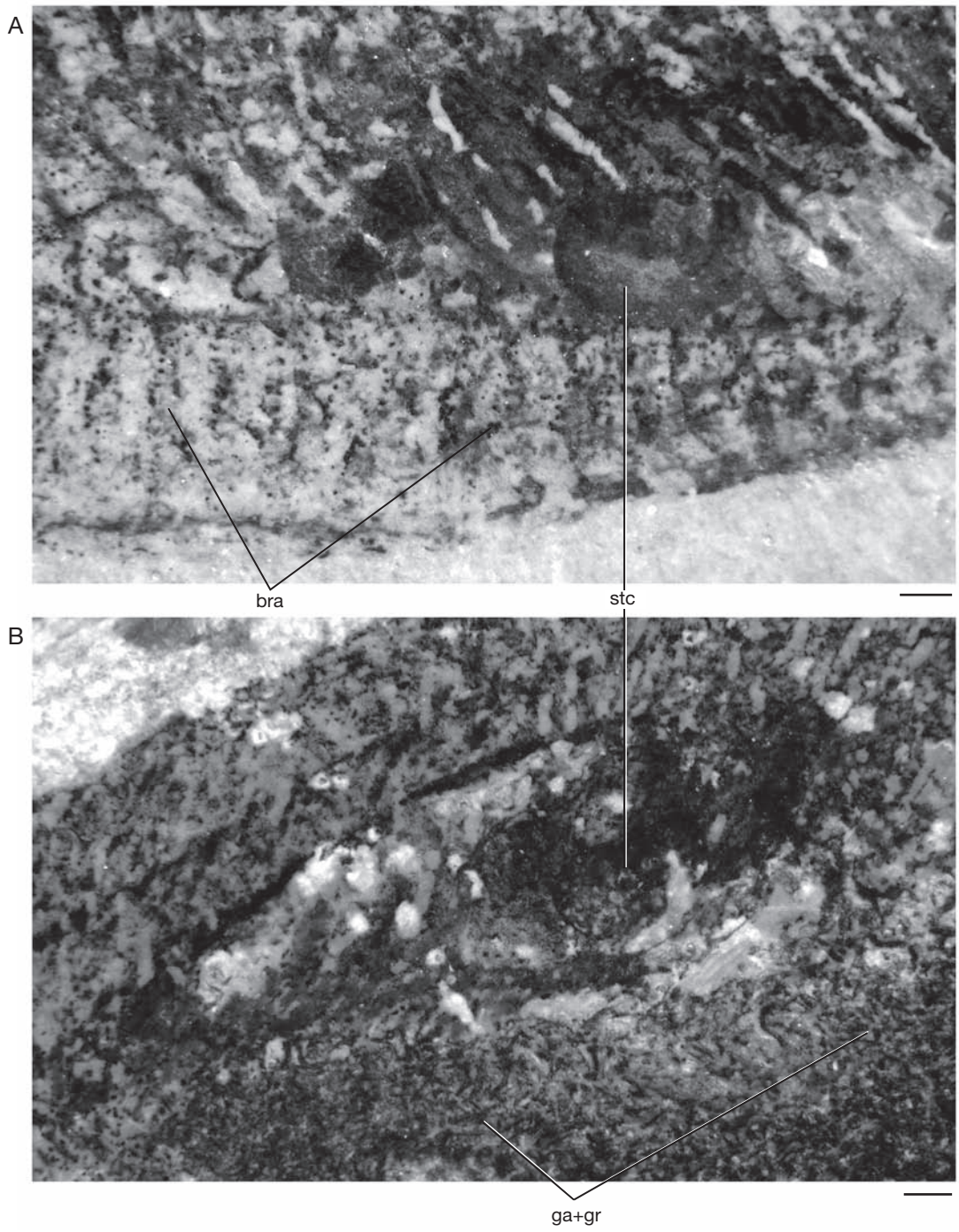


Fig. 36. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada, imprint of the visceral cavity in MHNM 01-02B (**A**) and 01-98 (**B**). Photographed in immersion in alcohol. Scale bars: 1 mm.

and living vertebrates in general, or are preserved in a way that does not allow any unambiguous interpretation. Some may be cartilages, as they are mineralized in the same way as, e.g., the arcualia and radials. Others are either mere carbonaceous imprints, or mineralized parts, though showing a structure that differs notably from the widespread spongiose structure of the majority of the mineralized elements described above.

"Doughnut-shaped structures"

We refer here to as the "doughnut-shaped structures", peculiar, thick, rounded imprints, which display a roughly torus-like shape. It is best exemplified in MHNM 01-69A (Fig. 38), where such a structure lies on the presumably internal surface of one of the "head stains" (dss, Fig. 38D, E). When Arsenault & Janvier (1991) first mentioned this structure in the same specimen, they compared it to the ring-shaped carbonaceous imprint at the anterior end of the holotype (Fig. 2C), and regarded both as a trace of the annular cartilage (Arsenault & janvier 1991: fig. 3, "cart.an?"; Janvier 1996a: fig. 6 "ac"). It is now quite clear that the apparently ring-shaped imprint at the anterior end of the holotype is in fact the "median stain", the central part of which has been eroded (ms, Fig. 2C). Although the "head stains" of MHNM 01-69A are poorly preserved and probably distorted (hs, Fig. 38B), the "doughnut-shaped structure" is clearly situated in a different plane (dss, Fig. 38D-E) and significantly thicker than the "median stain". Its surface is made up by a thin tarry layer, which seems to line a lumen filled with a whitish matter (possibly calcite or clay mineral). It shows no evidence of spongiose structure. In its central area are some black, tarry outgrowth (otg, Fig. 38E), which do not show any particular organization.

These "doughnut-shaped structures" could possibly be imprints of the collapsed eyeballs, but their shape is strangely irregular, and they do not seem to be paired. They could readily be regarded as artefactual deposits of organic matter, if they did not occur in at least two specimens, and in nearly the same position. A somewhat similar structure is also observed in some specimens of the long-enigmatic fossil *Achanarella trewini* Newman, 2002 (Newman 2002: pl. 2:1), from the Middle Devonian (upper Eifelian) Achanarras fish bed of Scotland, which displays a striking resemblance to young individuals of *Euphanerops* (e.g., Fig. 13B). In *Achanarella*, this ring-shaped structure always rests over (or beneath) the stain which is probably the homologue of what we refer here to as the "median stain" in *Euphanerops*. It is certainly not the same structure as the element referred to here as the "annular cartilage", because

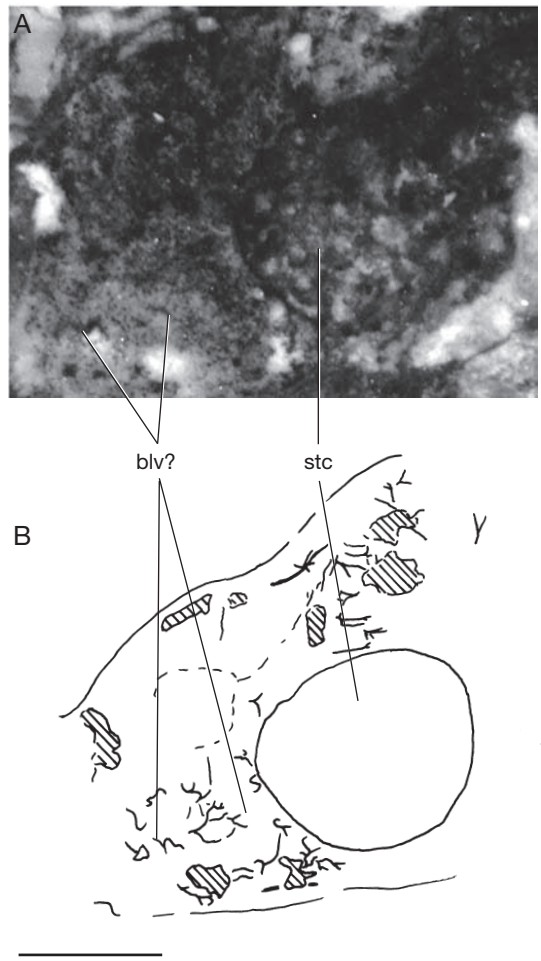


FIG. 37. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; photograph in immersion in alcohol (**A**) and camera lucida drawing (**B**) of the central part of the visceral cavity and stomach contents of MHNM 01-98A, showing some imprints interpreted as possible blood vessel imprints. Scale bar: 1 mm.

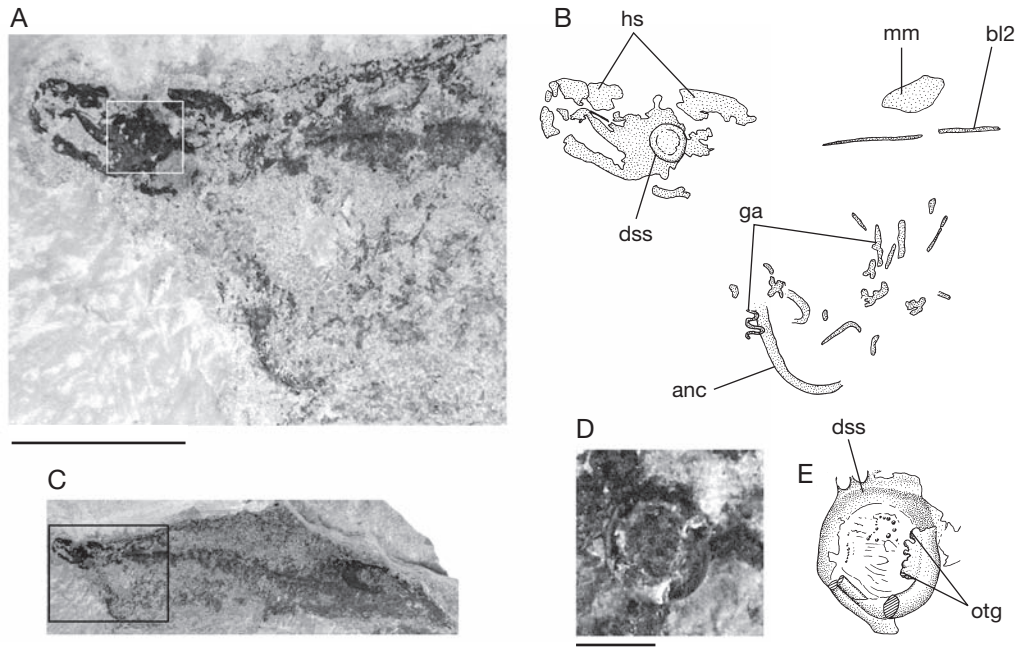


FIG. 38. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; specimen MHNM 01-69A: photograph in immersion in water (**A**) and camera lucida drawing (**B**) of the anterior part of the head of MHNM 01-69A (area framed in **C**; same specimen as in Figure 4A); **D**, **E**, detail photograph (**D**) and camera lucida drawing (**E**) of the "doughnut-shaped structure" (area framed in **A**). Scale bars: A, B, 5 mm; D, E, 1 mm.

a portion of the latter is also present in MHNM 01-69A, alongside a "doughnut-shaped structure" (anc, Fig. 38B). If the "doughnut-shaped structure" is associated with the mouth, such as an annular cartilage, then the mineralized "annular cartilage" would be a more posteriorly placed endoskeletal structure.

"White line"

One of the most peculiar features seen in MHNM 01-123 is what we refer to here as the "white line" (wl, Figs 16; 17; 21; 39). The "white line" is an apparently continuous, regularly constricted strand of whitish matter, which displays a dense, fibrous structure, and shows a markedly brownish stain at its surface. It is thus quite different from the pinkish, spongiose mineralized matter found elsewhere in the presumed endoskeletal elements. In radiographs, it appears as the most opaque structure in the specimen. Minute fragments sampled from this white line show, in thin sections, an amorphous mass of mineralized tissue, traversed by thin, longitudinal canals (Fig. 11; see Structure and nature of the mineralized tissues, p. 154).

Anteriorly, the "white line" begins at the level of the posterior end of the "braincase" (wl, Fig. 17) and ends posteriorly well in front of the anal region, somewhat anteriorly to the foremost elements of the "posterior haemal series" (wl, phs, Fig. 39). It runs between the series of small elements referred to here as the "anterior haemal series" (ahs, Figs 16; 21; 39; 40).

The structure of the mineralized tissue of the "white line" is entirely different from that of the other mineralized elements in the large, extensively mineralized, specimens of *E. longaevus* (Fig. 10; see Structure and nature of the mineralized tissues, p. 154).

Regarding the "white line" as an authigenic phosphatization of the notochord is tempting, but would not agree with our present interpretation of the axial skeleton. As mentioned above, this would leave us

with an extra series of elements (the dorsal arcualia in the present interpretation) in the axial skeleton. Moreover, it is too narrow, relatively to the size of MHNM 01-123, and does not seem to continue posteriorly to the anal region. It is not observed in any other specimen of *E. longaevus*, unless it corresponds to one of the "black lines" described below in other specimens.

Considering its position, the "white line" could possibly be a large blood vessel, such as the dorsal aorta, the walls of which became phosphatized either in old age, or *post-mortem*. Yet another possibility is that it has to do with the kidneys and may be the ureter. In adult lampreys the kidneys and adjoining ureters are situated on either sides of the dorsal aorta, beneath the notochord, approximately in the same position as the "white line" in *E. longaevus*. Yet, the histology of the "white line" does not show any particular resemblance to that of the kidney and ureters of lampreys, which lack a fibrous structure (PJ pers. obs.). In either cases, this mineralized structure would probably represent the best argument in favour of a *post-mortem* mineralization of soft tissues of *E. longaevus*.

"Black lines"

We term here "black lines" a number of black, longitudinal lines which are best visible in MHNM 01-02 and 01-150 (bl, Figs 3; 18-20), but also in some other specimens, such as MHNM 01-98, 01-69B, 01-125, and possibly 01-130 (bl, Figs 4C; 12; 32; 38). Homologizing these "black lines" between two specimens is virtually impossible, all the more so that the carcasses have been collapsed in various ways. In addition, some of the "black lines" may well be paired and overprinted in the fossil.

The numbering of the "black lines" proposed here is thus based on a single specimen, MHNM 01-02 (Figs 3; 18), and tentatively extrapolated to some other specimens. "Black line" 1 is the dorsalmost one, visible in 01-02B (bl1, Figs 3B2; 18); it only extends from the "head stains" to the level of the middle of the branchial apparatus. Contrary to the other "black lines", it is sinuous and its section seems tube-shaped. "Black line" 2 (bl2, Fig. 3B2) may be the continuation of the latter and extends to the tail. It is also probably present in MHNM 01-79A,

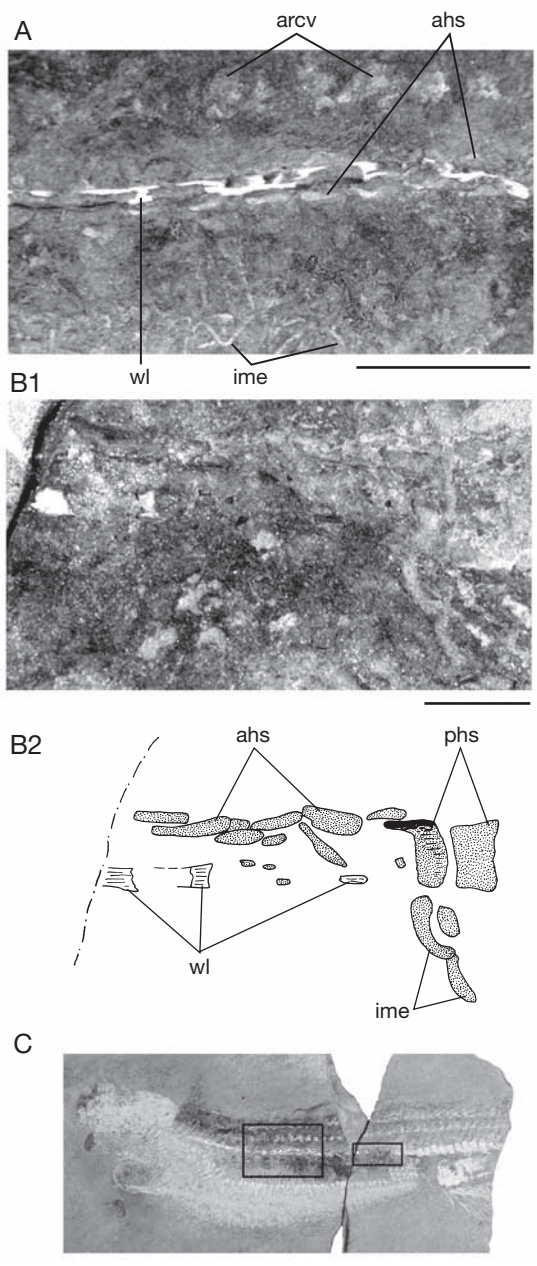


FIG. 39. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; specimen MHNM 01-123: **A**, detail view of the middle part of the "white line" (left framed area in **C**); **B**, photograph (**B1**) and camera lucida drawing (**B2**) of the posterior extremity of the "white line" and the transition between the anterior and posterior "haemal series" (right framed area in **C**). Scale bars: A, 10 mm; B, 5 mm.

where it continues almost to the posterior tip of the chordal lobe (bl2, Fig. 29B). Further ventrally, in MHNM 01-02A, a third "black line" runs along the dorsal margin of the branchial apparatus (bl3, Figs 3B2; 18B), from its anterior limit (anteriorly to the "annular cartilage") to the anterior tip of the imprint of the visceral cavity. Here it seems to bend dorsally and follows the dorsal margin of the imprint of the visceral cavity, until the level of the anal fin, where it seems to send off some ventral branches. This particular "black line" may correspond to the "white line" of MHNM 01-123 (wl, Fig. 16).

We have no interpretation to offer for these "black lines". We assume that most of them are probably major blood vessels. The more or less dorsoventrally collapsed specimen MHNM 01-150 (Figs 19; 20), in which the "black lines" are particularly conspicuous, nevertheless provides some interesting information in this respect. Although the arrangement of these "black lines" is difficult to compare to that in, e.g., MHNM 01-02, because of the different ways in which these specimens have collapsed during decay, those of the anterior part of the body seem to display side branches which would rather support their interpretation as blood vessels (bl, sbr, Fig. 20B). These side branches are clearly not gill arches, since they are not sinuous and are sometimes overprinted on the latter. However, their number and spacing seems to match that of the gill arches (ga, Fig. 20B). In addition, they are made up by the same amorphous tarry matter as the main, longitudinal "black lines", which differs from the brownish colour of the unmineralized (or barely mineralized) gill arches. They may thus be imprints of either the afferent or the efferent branchial arteries, or the efferent branchial veins. This interpretation would agree with Grogan & Lund's (1997, 2002) observation that, among the soft tissue imprints preserved in numerous fishes from the Carboniferous Konservat-Lagerstätte of Bear Gulch (Montana, USA), blood vessels seem to be among the best preserved. In addition, blood vessel imprints are also preserved in some fishes from Miguasha, notably the placoderm *Bothriolepis canadensis* (Arsenault *et al*. 2004). The same specimen also shows a somewhat different type of "black line", which extends from immediately behind the "head stains" to the posterior preserved end of the specimen (bl?, Fig. 20B, D), probably beyond the level of the anal fin, indicated by traces of the dorsal series of "anal fin supports" (anfsd?, Fig. 19A). Instead of being made up by dense tarry matter, this line is only marked by sparsely distributed black dots and seems to end with a peculiar series of densely mineralized vertical lamellae (z, Fig. 20D). Yet this may be a mere preservational artefact.

"Myomeres", "scales" and skin imprints

Multiple series of oblique, dark bands are visible all over the body in some specimens of *Euphanerops longaevus*, in particular the holotype (my?, Fig. 2B), but also MHNM 01-02, 01-98 (my?, Fig. 3B2) and 01-130 (Fig. 4C). They were first regarded by Woodward (1900: 417), Kiaer (1924) and Stensiö (1939, 1958, 1964), as very thin scales. Later, Arsenault & Janvier (1991) and Janvier (1996a) considered that some of these imprints may actually be scales, whereas others could be traces of the body muscle blocks, or myomeres, or of the intervening myocommata. This question is not settled to date but, strangely, these imprints never occur in large specimens, such as MHNM 01-123, 01-125, or 01-135, where the surface of the body imprint that is not occupied by the branchial apparatus is only covered with a continuous, dark layer (Figs 5; 16). Again, we have no explanation to offer for this difference, except that, after all, these oblique imprints may well be those of barely mineralized scales, present only in younger individuals, as it sometimes happens in certain modern actinopterygians. This interpretation could also be supported by the fact that these imprints sometimes look as if overlapping or crossing each other (Fig. 3A; Arsenault & Janvier 1991: fig. 3B), and that their margins are generally very distinct.

Impressions of the skin are rare in the specimens of *E. longaevus* known to date. It may be the case for the caudal fin web and area surroundings of the head stains in MHNM 01-98 (sk?, Fig. 12B), as well as for the very distinct anterior margin of the branchial region in MHNM 01-02 (sk?, Fig. 18B).

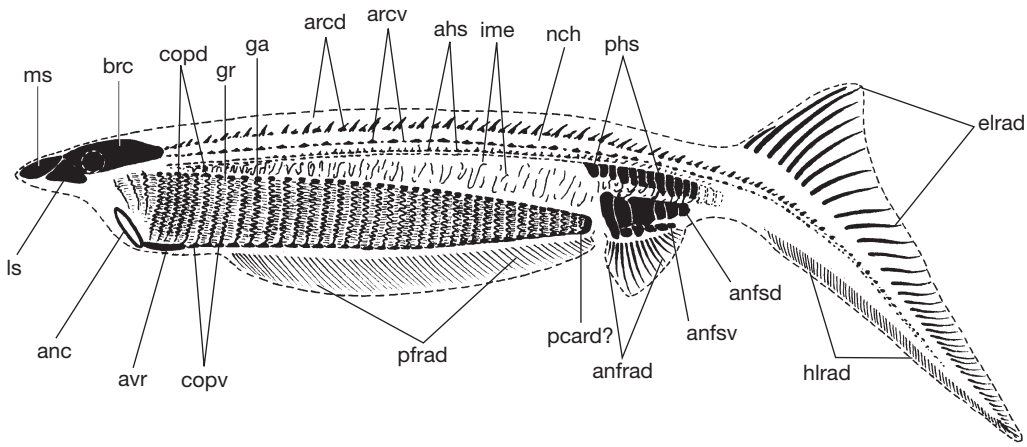


FIG. 40. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; attempted reconstruction of the mineralized elements (black) based on MHNM 01-123 and 135A, in lateral view (axial endoskeleton of the tail and eye outline are hypothetical, caudal fin radials based on MHNM 01-02 and 01-79B; "diffuse mineralized matter" and "white line" omitted). Not to scale.

"Intermuscular elements"

Here we refer to as "intermuscular elements" a number of sinuous or V-shaped, mineralized elements, which occur outside the branchial apparatus. They are unlikely to be displaced gill arches, because they occur also in the post-anal region, where no such typically branchial elements as the "gill rods" occur. They are particularly visible in the largest two specimens (MHNM 01-123 and 01-135; ime, Figs 16; 17; 21; 23; 40). Their structure is the same as that of the gill arches or radials described above; that is, a garland-like, mineralized cylinder (Figs 8; 9). We suggest, with great reservation, that these elements were situated between the muscle blocks of the body musculature, much in the same way (and, of course, by analogy) as the living gnathostome ribs or the intermuscular bones of acanthomorph teleosts. We are aware that there is no clear evidence for this interpretation, but we cannot offer any better one at the moment. These "intermuscular elements" occur, for example, dorsal to the "white line", behind the braincase (ime, Fig. 17), ventral to the "white line" further back (ime, Fig. 21), in particular between the plates of the "posterior haemal series" and the ventral arcualia (ime, Fig. 28), and within the black imprint of the visceral cavity (ime, Figs 16; 21). Again, the interpretation of these elements as cartilages becomes irrelevant if one assumes a massive *post-mortem* mineralization of widely different tissues.

RECONSTRUCTION OF *EUPHANEROPS LONGAEVUS*

The reconstruction of *Euphanerops longaevus* raises a number of questions, partly because of its unusual morphology (e.g., a very large number of gill arches), but chiefly because of the uncertainty as to the way the specimens have collapsed during decay, and the biogenic or diagenetic nature of the mineralized structures we observe in the large specimens.

E. longaevus can be readily compared to anaspids, with which it shares a markedly hypocercal tail and elongated, ventrolaterally placed paired fins, although the latter are only known from their dermal skeletal covering in anaspids. Conversely, *E. longaevus* shows no unambiguous element of the dermal skeleton that would allow more detailed comparison with the anaspids (except perhaps for the presumed elongated lateral scales). Comparisons with other major vertebrate taxa for which there is good information about the internal anatomy, namely hagfishes, lampreys, galeaspids, osteostracans,

placoderms, and crown-group gnathostomes, leaves us with very few uniquely shared characters, except perhaps when considering lampreys, with which *E. longaevus* shares sinuous gill arches forming a "branchial basket". By its very elongated branchial apparatus, *E. longaevus* also closely resembles other Devonian soft-bodied jawless vertebrates, namely *Endeiolepis*, *Achanarella*, *Cornovichthys*, and possibly *Jamoytius* (Stensiö 1939; Ritchie 1984; Arsenault & Janvier 1991; Janvier 1996a; Newman & Trewin 2001; Newman 2002; Janvier *et al.* 2006; see below). Certain galeaspids have a very large number of gills (up to about 45), but, contrary to the condition in *E. longaevus*, they never reach the anal region, which, by comparison to the anatomy of osteostracans, can be located further back, where the series of ventrolateral ridge scales meet along the midline (Janvier 2004).

In detail, the reconstruction of the branchial apparatus of *E. longaevus* remains difficult. Here, we have assumed that the gill arches were united dorsally and ventrally to a paired series of relatively large copular elements (ga, copd, copv, Figs 26A; 40). As for the "gill rods" (gr, Fig. 26B), new data on the three-dimensionally preserved branchial apparatus of *Endeiolepis aneri* provide information that enlighten the structure of *E. longaevus*, all the more so that the two taxa are probably synonyms (Janvier *et al*. 2006). The "gill rods" were possibly situated in the interbranchial septa that separated adjacent gill pouches or supported the anterior and posterior hemibranchs of the same arch. Morever, the fact that the "gill rods" of *E. longaevus* are generally not spread around the body suggests that they were enclosed in the branchial apparatus and did not extend into gill covers, as in chondrichthyans.

The position and the role of the "annular cartilage" remains uncertain. In all specimens where it is preserved, it lies at the entrance of the branchial apparatus, and seems more or less obliquely oriented (anc, Fig. 40). One may imagine that it served in maintaining open the incurrent opening of the branchial apparatus, or surrounded the oral opening. Although such a ring-shaped cartilage is only known elsewhere in lampreys, in the form of the annular cartilage, the position of the latter is different, and much more anteriorly placed. There is thus no certainty about the homology of these two ring-shaped structures.

The "braincase" and snout (possibly strengthened by cartilaginous plates, if the "head stains" actually are cartilages) were slightly overhanging the presumed incurrent opening at the anterior limit of the branchial apparatus, as suggested by the aspect of most laterally collapsed specimens (e.g., Figs 3; 4; 18; 40), but the main question raised by this peculiar anatomy is that of the position and organization of the mouth and oral cavity. The anatomy of the branchial apparatus is suggestive of particulate suspension feeding and ram-ventilation (Mallatt 1984). Such a mode of life in a jawless vertebrate is not unlikely, but would imply that the oral cavity was continued posteriorly by the pharynx, much as in larval lampreys and living gnathostomes. Assuming that the mineralization of the skeleton is biogenic, this would perhaps explain the fact that the gill arches could become extensively mineralized and thus partly lose their flexibility, without posing any functional problem. However, the new data provided by *Endeiolepis aneri*, which displays exactly the same type of elongated branchial apparatus as *E. longaevus*, suggest that the gills were enclosed in numerous, crowded pouches (Janvier *et al*. 2006). This, in turn, implies that respiration was effected through passive inspiration, as in lampreys (Mallatt 1996), and thus that the gill arches retained some flexibility throughout life.

There is unfortunately no indication as to the anatomical relationships between the mouth and the pharynx, and between the posterior end of the pharynx and the digestive tract. All we know is that the latter comprised a relatively large stomach filled with very fine-grained sediment. The anterior limit of the branchial apparatus, seems to coincide with the anteroventral limit of the head. The "annular cartilage" was also probably situated at this level (Fig. 40).

Inferences based on lamprey anatomy must take into consideration two possible models: the larval condition, in which the oral cavity, the pharynx (branchial apparatus) and the digestive tract are in direct continuity, and the adult model, in which the branchial apparatus is a cul-de-sac, connected to the oral cavity by an oesophagobranchial duct,

and thus does not convey the food particles to the digestive tract. The larval lamprey model would be consistent with what we can infer from the structure of the pharynx in *E. longaevus*; that is, the mouth would be a large opening, more or less posteroventral to the "head stains", possibly strengthened by the "annular cartilage", and continued posteriorly by a very elongated pharynx that extends back to the anal region. However, this model implies that the pharynx is, in turn, continued posteriorly by the oesophagus, stomach and intestine, which, based on the imprints of the visceral cavity, must have lain dorsally to the branchial apparatus. Therefore, assuming that the food passed through the entire pharynx (or was filtered by the pharynx) implies that the oesophagus formed an anterodorsally directed loop to meet the stomach, and that the posterior intestine formed a posterodorsally (or posterolaterally) directed loop to reach the anus (Fig. 41A). Such a condition in unknown in living jawless vertebrates, but is frequently met with in a wide range of living jawed vertebrates, notably chondrichthyans, where the loops of the posterior intestine are generally either lateral or ventral to the stomach (Pernkopf & Lehner 1937). The adult lamprey model would be more consistent with the posterior extension of the branchial apparatus. The food would enter the oral cavity, situated somewhere beneath the level of the "head stains" or behind the "annular cartilage", and then conveyed to the stomach by the oesophagus that passed dorsally to the branchial apparatus (Fig. 41B). The intake of the respiratory water could have been effected through the mouth and oral cavity, but then conveyed to the branchial apparatus by a median pharyngobranchial duct extending between the paired series of gill pouches, and connected to the latter by a series of individual branchial ducts (or branchial pores). This reconstruction is admittedly more consistent with the unusual size of the branchial apparatus and dorsal position of the stomach in *E. longaevus*, but also raises some questions. The fact that we cannot see any imprint of what could be an oesophagobranchial duct is perhaps not surprising, but the fact that the anterior limit the branchial apparatus coincides with the presumed position of the mouth leaves little space for such a duct. In addition, the adult lamprey model entails

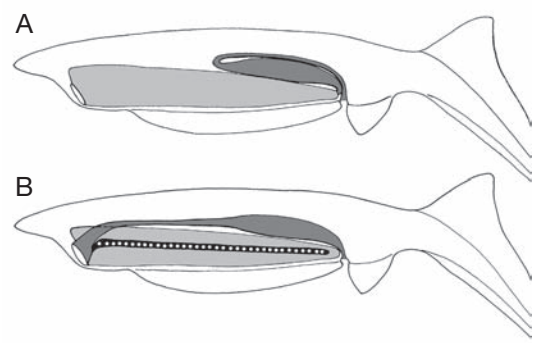


FIG. 41. — *Euphanerops longaevus* Woodward, 1900; Escuminac Formation, lower Frasnian (Upper Devonian), Miguasha, Quebec, Canada; two possible interpretations of the digestive tract in the visceral cavity: **A**, interpretation based on the larval lamprey, hagfish or even gnathostome models, assuming that the entrance to the oesophagus is situated at the posterior end of the branchial apparatus, and that the stomach and posterior intestine form loops inside the abdominal cavity; **B**, interpretation based on the adult lamprey model, assuming that the oesophagus, stomach and intestine (dark grey) are dorsal to the pharynx (light grey), and that the respiratory water was conveyed to the gill pouches through a median oesophagobranchial duct (black), passing between the right and left series of gill pouches, and numerous individual branchial ducts (white dots). Not to scale.

an active mode of feeding, thus a relatively complex feeding apparatus, for which we have no evidence in *E. longaevus*. The hagfish model would resolve the problem of the food transmission through the pharynx, assuming that the mouth served both the water and food intake (there is no indication of a separate nasopharyngeal duct of hagfish type), but the question of the position and path of the oesophagus, posteriorly to the branchial apparatus, would remain the same and inevitably entail a loop of the digestive tract.

There is no clear indication of the position of the eyes, unless the "lateral stains" or the "doughnut-shaped structures" are actually collapsed scleral capsules. If such is the case, assuming that the elongation of the snout is exagerated by the dorsoventral flattening of the carcasses and that the "head stains" have lain in a more frontal position, the overhanging snout and almost frontally placed eyes of *E. longaevus*, bear some resemblance to some other fossil vertebrates, which display various types of rostralization, notably euconodonts and arandaspids (Gagnier 1993a; Donoghue *et al.* 2000).

Although the aspect of the "head stains" is similar to that of the three stains described in other soft-bodied jawless vertebrates (notably *Achanarella* and *Jamoytius*) and classically regarded as imprints of the median olfactory organ (or the annular cartilage) and the eyes, the presence of mineralized matter in the "head stains" of the large specimens of *E. longaevus* raises questions about this interpretation, at any rate if this mineralization is either *pre-mortem*, or, if a substrate microfabric preserves the actual structure of the cartilage. If these "head stains" are in fact cartilages, the "median stain" somewhat compares in position and shape to the large, posterior median tectal cartilage of adult lampreys (ms, Fig. 40). In contrast, the "lateral stains" do not compare to any of the cartilages in the adult lamprey snout, except possibly the small paired spinose cartilages (ls, Fig. 40). There is, however, some resemblance between the "head stains" of *E. longaevus* and the distribution of the mucocartilage in the snout of larval lampreys, which is distributed into a large median plate and smaller, paired lateral plates (Damas 1935, 1944; Johnels 1944; Mallatt 1996).

The question of whether the anal fin radials are paired or unpaired remains unanswered, until more significant material turns up, but we have chosen here the most parsimonious interpretation; that is, there is a single, median series of radials, but part of them have been shifted forwards in MHNM 01-123.

The fin radials that extend along the ventral margin of the body, underneath the branchial apparatus, seem to be paired, on account of MHNM 01-125 (pfrad1, pfrad2, Fig. 32). This distribution of the paired fin radials strikingly recalls the position of the paired fins of the anaspid *Pharyngolepis oblongus*, as reconstructed by Ritchie (1964: fig. 1B), and assumed to be also present in *Jamoytius kerwoodi* (Ritchie 1960, 1968; Freedman 1996, 1998). Such ribbon-shaped, elongated ventrolateral paired fins have been regarded by Arsenault & Janvier (1991) and Janvier (1996a, c) as a general character of a clade including anaspids, lampreys, *Euphanerops*, *Endeiolepis* and *Jamoytius*. These paired fins were thus assumed to have been lost in lampreys and much reduced or lost in most anaspids. *E. longaevus* raises the question of the homology of these paired fins. Clearly, they possessed radials and were thus not a mere skin fold, but they strangely extended ventral to the branchial apparatus (Fig. 40). This is a unique condition among vertebrates, with the possible exception of certain acanthodians (Hanke & Wilson 2006). The paired fin endoskeleton and musculature of living gnathostomes is derived from the lateral plate mesoderm and its development is constrained posteriorly to the branchial apparatus and anteriorly to the anus (Coates & Cohn 1998; Coates 2003). The extension of paired fins all along the body, behind the branchial appartus, in *Pharyngolepis* was thus already a problem *per se*, but the presence of such paired fins ventral to the branchial apparatus in *E. longaevus* further complicates this problem and somehow defies the current rules of fin development. We suggest here that the paired fins of anaspids may be the homologue of the pelvic fins of the jawed vertebrates, as once suggested by Mark Wilson (unpublished communication at meeting, London 1999; see also Hanke & Wilson 2006; Wilson *et al*. in press), and extended forward along a narrow, median ventral anterior prolongation of the postbranchial trunk musculature, comparable to the hypobranchial musculature of lampreys. This does not necessarily imply serial homolgy of pectoral and pelvic fins, as once suggested by Tabin & Laufer (1993), but only that pelvic fins may be a more general character than previously believed, and were lost in a number of benthic stem gnathostomes.

COMPARISONS

The question of the relationships of *Euphanerops longaevus* depends on the confidence one may (or may not) have in the homology of the various structures that have been described above, be they mineralized or not. The interpretation of elements that are preserved as mere imprints or collapsed structures, whatever the taxon, is almost always ambiguous, except for some of them, which have unambiguous homologues either in living taxa, or in mineralized fossils, as in the case of the anal and caudal fin radials, and possibly the branchial apparatus of *E. longaevus*. Moreover, the homology

of most of the mineralized elements in *E. longaevus* remains ambiguous, because of the uncertainty as to the nature of the mineralization. If these elements are actually made up by calcified cartilage, then they are a potential source of characters that can be compared to endoskeletal structure of living and fossil taxa. Conversely, if they are an assemblage of various authigenically phosphatised tissues (some of which could be cartilage), then any conclusion as to the homology of these structures becomes tenuous. Here, we opt for a compromise, assuming that all the mineralized elements that display the characteristic "chondrocyte spaces" are actually cartilages, although the origin of their mineralization (i.e. either biomineralization or authigenic phosphatization) remains undecided.

Remarks on *Endeiolepis*, *Achanarella*, *Cornovichthys*, *Jamoytius,* and *Lasanius*

Before considering the various characters that may be shared between *Euphanerops longaevus* and other, more informative, vertebrate taxa, we shall discuss its possible resemblance to other Palaeozoic fossils that are conventionally regarded as soft-bodied jawless vertebrates.

The case of *Endeiolepis aneri*, the second anaspid-like form from Miguasha, has been alluded to above in connection with the question of the structure of the branchial apparatus, and deserves particular attention. *E. aneri* had been regarded by Stensiö (1939, 1958, 1964) as differing from *E. longaevus*, because of its distinctive ventrolateral series of prominent "scales", forming a festooned blade, and assumed to be a kind of modified ventrolateral fin fold. Apart from this character, *E. aneri* only differs from *E. longaevus* by the relative position of its anal fin, the posterior limit of which is situated at the level of the foremost radials of the epichordal lobe (Arsenault & janvier 1991: fig. 1B), whereas it seems slightly more anteriorly placed in *Euphanerops longaevus*. It is, however, uncertain how much this difference may be due to either individual variation or collapse of the carcass during decay; at any rate the available material of *E. longaevus* does not allow any statement about individual variation in this species and, if real, such a difference would be regarded as merely specific. The head of *E. aneri* is practically unknown and the specimens found to date only show a faint stain that marks the position of the snout (Janvier 1996a: fig. 1C). Again, this stain is generally regarded as an eye stain (Arsenault & janvier 1991; Janvier 1996a), but might correspond to the "head stains" of *E. longaevus*. In most specimens of *E. aneri*, the mid-part of the body shows a conspicuous, oblong, dark grey stain that is partly occupied by a patch of fine-grained sediment (Stensiö 1939: pl. 1; Arsenault & janvier 1991: fig. 1a). This stain most probably corresponds in position to the imprint of the visceral cavity of *E. longaevus*, and extends along the posterodorsal margin of the presumed ventrolateral scale series. In sum, the latter lies in exactly the same position as the branchial apparatus in *E. longaevus*, relative to the imprint of the visceral cavity. Now, a number of specimens of *E. aneri*, show that this "ventrolateral scale series" is a three-dimensionally preserved, elongated cone-shaped or sleeve-shaped structure, and is in fact the natural cast of the branchial apparatus, somewhat displaced ventrally during decay in some specimens (e.g., that used by Stensiö [1939: pl. 1] for his reconstruction). In several specimens, this natural cast, which displays evidence for numerous, closely-set gill pouches, shows impressions of either the gill filaments proper, the "gill rods", or the afferent branchial arteries (Janvier *et al*. 2006). We assume that this reflects the structure of the branchial apparatus in *E. longaevus*, when not collapsed in a single plane. In addition, all the specimens of *E. aneri* known to date are preserved in a relatively coarse, green sandstone of Unit VI of the Escuminac Formation (Parent & Cloutier 1996), which has also yielded three-dimensional specimens of other fishes, and soft-tissue imprints (e.g., the gill rays and gill filament imprints in the specimen NHRM P.222 of *Eusthenopteron foordi* Whiteaves, 1889 (Jarvik 1980: fig. 114B). Therefore, we assume that *E. aneri* and *E. longaevus* are most likely to be, if not the same species, two, closely similar ones, preserved in different sediments and under different taphonomic conditions.

There is a striking resemblance between the smallest specimens of *E. longaevus* (e.g., MHNM 01-89, 01-126; Fig. 13) and certain specimens of *Achanarella trewini*, from the upper Eifelian Achanarras fish

bed of Scotland (Newman 2002). The latter are presumably also preserved in either dorsal or ventral aspect and display the same three dark "head stains", sometimes fused into a arrowhead-shaped stain, which Newman (2002: pl. 2: 1, 4, 6) referred to the eyes and mouth, respectively. Interestingly, as pointed out above, some specimens of *A. trewini* show, at some distance behind the "head stains", a pair of spots (Newman 2002: pl. 2: 4, 5), which seem to correspond in position to the small paired masses of mineralized matter that occurs in some small to medium-sized specimens of *E. longaevus* (mm, Figs 2C; 3B; 13B; 14B; 18A), presumably at the level of the otic region.

Cornovichthys blaauweni Newman & Trewin, 2001, from the same locality and horizon as *A. trewini*, shows a single, large anterior "head stain", which overhangs the anterior limit of the branchial apparatus in exactly the same way as in most specimens of *E. longaevus* and may well be the "median stain" (Newman & Trewin 2001: fig. 1). In addition, the oblong stain of the abdominal cavity imprint in *C. blaauweni* lies exactly in the same posterior position as that of *E. longaevus*, dorsally to the vague imprint of an elongated branchial apparatus. It is thus likely that, as suggested by Newman & Trewin (2001), *Cornovichthys* and *Achanarella* are close relatives of *Euphanerops* and should be gathered in the family Euphaneropidae Woodward, 1900.

Jamoytius kerwoodi, from the Lower Silurian of the Lesmahagow Inlier (Scotland), was initially gathered with *Euphanerops* in the Jamoytiiformes by White (1946). It shows the same three "head stains" as *Euphanerops*, and an imprint of a probably elongated branchial apparatus, but its overall body shape seems different from that of *Euphanerops* and *Endeiolepis*. This may be due to the fact that the best preserved specimens described to date are more or less dorsoventrally collapsed and provide little information about the shape of the tail (e.g., Ritchie 1968: pls 3:2, 5:1-3; 1984: pl. 1). At any rate, *J. kerwoodi* is certainly more slender than *Euphanerops*. In addition, it displays a long series of rod-shaped structures that have no equivalent in *Euphanerops* and have been regarded as either imprints of the myomeres, or poorly mineralized scales (White 1946; Forey & Gardiner 1981; Ritchie 1960, 1968, 1984; Freedman 1996, 1998). The "lateral stains" of *J. kerwoodi* do not readily compare with the subtriangular lateral stains of *E. longaevus*. They look somewhat doughnut-shaped and more convincingly suggestive of eye imprints (Ritchie 1968; Freedman 1998). The "median stain" is a rounded imprint, as in *Euphanerops*. In only one specimen (Ritchie 1960, 1968: pl. 5:1), this median stain compares somewhat in relative size to the "median stain" of *E. longaevus*, but in all other specimens described to date, this stain is somewhat smaller and sometimes displays a central lumen (e.g., Ritchie 1968: pl. 5:2, "ac"), hence its interpretation by Ritchie (1968) and Freedman (1996, 1998) as the imprint of an annular cartilage.

Although a re-consideration of *J. kerwoodi* is beyond the scope of the present work, we can briefly mention here that the presumed central lumen of the anterior median stain of this form (Ritchie's "annular cartilage") may be an artefact of preservation. At any rate, it is clearly lacking in BMNH P.47786 (Ritchie 1968: pl. 5:1; and PJ, pers. obs.). As pointed out above, a similar median gap sometimes also occurs in the "median stain" of *E. longaevus* (e.g., Figs 2C; 20), due to the fact that it is slightly bowl-shaped, and that its central part is thinner than its margins, thus more easily eroded or broken off. Finally, the "scales" of *J. kerwoodi* have a complex structure (Ritchie 1968: 31), in which there are distinct branching canals (regarded by Ritchie as minute cracks) that arise from a larger longitudinal canal. These canals seem to open at the surface of the scales by pores, the internal natural casts of which give the impression of being small tubercles. Curiously, these "scales" never extend over the anterior part of the head, nor beyond the level of the anus (indicated by the posterior extremity of the imprint of the digestive tract in BMNH P.47784). In sum, the structure and distribution of the scales of *J. kerwoodi* is at odds with that of, e.g., anaspids, and one may wonder if they could not be in fact more complex elements of a very elongated branchial apparatus, more or less similar to that of *Euphanerops* and *Endeiolepis*. In contrast, the boomerang-shaped structures described by Janvier & Busch (1984) in

a "*Jamoytius*-like" fossil from the Lower Devonian of USA are more convincingly scale-like. Yet the affinities of this fossil remain uncertain.

The specimen MHNM 01-02 of *E. longaevus* (Fig. 3) seems to show a "ladder-shaped" imprint, extending along the dorsal limit of the branchial apparatus, but which has no equivalent in the extensively mineralized specimens. Quite a similar ladder-shaped imprint is visible in *Cornovichthys* in exactly the same position (Newman & Trewin 2001: fig. 2, "br"). Arsenault & Janvier (1991: fig. 4B, "o.br") and Janvier (1996a: fig. 6A, "bro"; 2004) compared this imprint to the series of ring-shaped imprints decribed in *Jamoytius* by Ritchie (1968: pl. 5:1, 3, "b.b."), and regarded both as possible evidence for trematic rings surrounding the gill openings, as in lampreys (*annulus trematicus*, Marinelli & Strenger 1954: fig. 64). Janvier (2004) also compared it to the dark, ladder-shaped imprint seen in some thelodonts (Traquair 1905; Turner 1991; Wilson & Caldwell 1998; Märss & Ritchie 1998) at the level of the series of gill openings. However, it is not ruled out that the ladder-shaped imprint in MHNM 01-02 is an artifact, due to the overprinting of either the gill arches or blood vessels ("black lines") of the left and right sides. In contrast, the series of ring-shaped imprints regarded by Ritchie (1968) as the trace of an elongated branchial apparatus are visible in several specimens of *J. kerwoodi* and seem to be paired (Ritchie 1984: pl. 1). Assuming that the "scales" of *J. kerwoodi* are in fact components of the branchial apparatus, these imprints could actually be a series of trematic rings.

In sum, it is not ruled out that the anatomy of *J. kerwoodi* was quite similar to that of *E. longaevus* and that this form, alongside the Euphaneropidae, represent a particular group of jawless vertebrates whose range extends at least from the Early Silurian to the Late Devonian.

Lasanius problematicus Traquair, 1899, from the Lower Silurian of Lanarkshire (Scotland), is unanimously regarded as an anaspid, because of its large median dorsal scales and postbranchial spines ("post-cephalic rods"). However, the rest of the head and body of *Lasanius* is naked, and this is generally regarded as a derived condition, relative to the extensive dermal skeleton of other anaspids. Whatever the interpretation of the limited extension of its dermal skeleton, *Lasanius* is interesting in the framework of the debate about the nature of the "head stains" in *Euphanerops*. Most specimens of *Lasanius problematicus* are preserved as imprints in a fine-grained sediment, but display no conspicuous soft-tissue imprints, apart from two rounded stains that are interpreted as traces of the eyes (Parrington 1958). The specimens are generally preserved in lateral aspect, yet some of them are dorsoventrally collapsed, but in either cases their eye imprints are always rounded to oval in shape and somewhat doughnut-shaped, as in euconodonts (Briggs *et al*. 1983; Aldridge & Theron 1993; Gabbott *et al*. 1995) but do not resemble the triangular "lateral stains" of *Euphanerops*. In all specimens of *Lasanius* described to date, there is no clear evidence of a third, "median stain" comparable to that of *Euphanerops* or *Jamoytius*. Only a few dorsoventrally collapsed specimens, which have been pointed out to us by W. Van der Brugghen (pers. comm. 2006), seem to show a small stain anterior to the pair of eye stains, but its size is far smaller than the "median stain" of *Euphanerops* or *Jamoytius*. Since *Euphanerops* has long been regarded as an anaspid, and actually displays an anaspid-like overall morphology, this difference between *Euphanerops* and *Lasanius* in the number, aspect and relative size of the "head stains" is rather surprising, and one would have expected an anaspid with a "naked" head to display the same "head stains" as *Euphanerops*.

It is also worth pointing out here a detail recently described by Van der Brugghen (2005) in certain thelodonts from the Silurian of Scotland. Notwithstanding an extensive dermal skeleton composed of minute scales, specimens of *Lanarkia horrida* Traquair, 1899, sometimes display tarry imprints of presumed soft tissues within the snout, notably a paired stain, regarded by Van der Brugghen (2005) as imprints of the olfactory organs (they actually lie anteriorly to the orbits), and a peculiar, distinctly rectangular, median stain, that is sometimes displaced anteriorly to the snout margin. This stain could be the imprint of a median cartilage, and possibly the homologue of the "median stain" of *Euphanerops*.

Shared characters of *Euphanerops longaevus* and other craniates

Despite our attempt at interpreting the structure of *Euphanerops longaevus*, we are conscious that most of the features described herein are doomed to be the subject of controversies, either because of the way they are supposed to have collapsed before fossilization, or because of the interpretation of their mineralization. As a result, we are left with very few characters for which plausible homologues are found in other living or fossil taxa. One might even raise the question whether *Euphanerops* is a vertebrate, or belongs to another chordate group. The peculiar structure of its branchial basket inevitably recalls cephalochordates, but we infer from *Endeiolepis* that it possessed gill filaments enclosed in gill pouches, and cephalochordates lack gill filaments (Janvier *et al*. 2006). Moreover, *Euphanerops* possesses fin radials, which are lacking in cephalochordates and such presumed stem vertebrates, as yunnanozoans and myllokunmingiids. This question can thus be regarded as settled.

Here we sum up the few primary homologies that we assume to be shared by *Euphanerops* (or *Endeiolepis*) and other vertebrates. For some of these characters, the homology can be regarded as reliable, whatever the nature of the mineralization that affects the specimens, because of the position of the elements and their relations to adjacent ones. For other characters, the homology statement is merely tentative. These homology statements are listed below in an order that we regard as their decreasing degree of reliability, however subjective it may be.

Anal fin

There is little doubt that *Euphanerops* possessed a median anal fin, despite its curious organization in MHNM 01-123 (see Anatomy, p. 169), which may indicate the presence of paired series of radials. Nevertheless, in all other specimens the anal fin accords with the morphology of that of the anaspid *Pharyngolepis*, only known by its dermal skeleton, and of crown-group gnathostomes. Hagfishes and lampreys have no anal fin, and the significance of the "atavistic" occurrence of anal fin radials in some lamprey individuals (Vladikof 1973) remains uncertain. Moreover, the alleged presence of an anal fin in the Carboniferous lamprey *Hardistiella* needs confirmation (Janvier & Lund 1983). Among jawed vertebrates, the anal fin is only known in crown-group gnathostomes, but with much variation. It is generally present in early osteichthyans and acanthodians, highly variable in chondrichthyans (lacking in most stem chondrichthyans). It is lacking in placoderms. In fossil jawless vertebrates, other than *Euphanerops*, *Endeiolepis*, *Cornovichthys*, and some anaspids, it is virtually unknown, unless it is represented by a small median ventral postanal fin fold of some thelodonts, or by the peculiar horizontal caudal lobe of osteostracans.

Anal fin supports

Assuming that the large mineralized elements referred to here as "anal fin supports" are actually calcified cartilages, the only comparable, and possibly homologous, structures are found in jawed vertebrates, where the anal fin, when present, is supported by a variable number of endoskeletal elements.

Hypocercal tail

The tail of *Euphanerops* shows the same, pronounced hypocercal condition as that of anaspids, and this is regarded as a shared derived condition. However the hypocercal structure of the tail is, as a whole, a more general condition. Lampreys show a slightly hypocercal tail, which is better marked in hatching larvae (Richardson & Wright 2003: fig. 3), and the posterior tip of the notochord in hagfishes clearly bends downwards (Janvier 1998: fig. 6D), although this detail is generally overlooked in illustrations of the hagfish tail. The tail is also hypocercal to various extents in certain thelodonts (Märss 1986b; Turner 1991), and possibly galeaspids (Liu 1975; Pan & Chen 1993), arandaspids (Pradel *et al*. 2006), euconodonts (Briggs *et al*. 1983; Aldridge *et al*. 1986) and even myllokunmingiids (Zhang & Hou 2004). It is also possible that the apparently isocercal tail of heterostracans and furcacaudiform thelodonts (Wilson & Caldwell 1998) is merely a particular case of hypocercal tail, in which the epichordal lobe becomes as large as the chordal lobe. Consequently, what one may regard as unique to *Euphanerops* and anaspids is the way in which the

chordal lobe abruptly bends downwardly posterior to the anal fin.

Large unpaired fin radials

The anal and dorsal caudal fin radials of *Euphanerops* are remarkably large and thick proximally. In this, they differ from the relatively thin caudal radials of hagfishes and lampreys, and rather resemble the large median fin radials of placoderms and chondrichthyans. Median fin radials are unknown in other fossil jawless vertebrates, except perhaps in the form of imprints in the posterior dorsal fin of a single specimen of *Escuminaspis laticeps* (MHNM 01-09) from Miguasha, where they appear as thin, closely-set rods (Janvier & Arsenault 1996), and in the caudal fin of euconodonts, where they seem to be relatively thin and closely-set as well (Briggs *et al.* 1983; Aldridge *et al.* 1986). In all other fossil jawless vertebrates, their size, position and spacing is merely inferred from the arrangement and size of the overlying scales, notably in anaspids, thelodonts, heterostracans, galeaspids, and osteostracans. These indirect data nevertheless suggest that large-sized unpaired fin radials, similar to those of *Euphanerops*, were also present in anaspids, thelodonts, heterostracans, and possibly galeaspids.

Spacing of the unpaired fin radials

Whether the unpaired fin radials are closely-set or not is a character that has often been used in phylogenetic analyses of the vertebrates (Janvier 1981a, 1996b; Donoghue *et al.* 2000; Donoghue & Smith 2001). The caudal radials of hagfishes are widely spaced, in contrast to those of lampreys, which are closely-set, and more so in the epichordal lobe than in the narrow hypochordal web (Marinelli & Strenger 1954, 1956). The condition in jawed vertebrates is barely comparable, as the tail is epicercal, but if one assumes that the posterior dorsal fin of osteostracans and jawed vertebrates is the homologue of the epichordal lobe, then the radials can be regarded as closely-set. In *Euphanerops*, the radials of the epichordal lobe are widely spaced, but those of the hypochordal web seem closely set. Those of the anal fin are closely set, at any rate proximally. Again, the comparison with other fossil jawless vertebrates is difficult, because of the lack of direct information about radials, except in euconodonts and osteostracans, but the organization of the scale-covered zonations in thelodonts, anaspids, heterostracans, and galeaspids suggests that the underlying radials (at any rate those of the epichordal lobe) were as widely spaced as in *Euphanerops*.

Arcualia

We have considered here that *E. longaevus* possessed dorsal and ventral series of arcualia, although there remains the possibility that these two series of elements of the axial skeleton are left and right series brought into the same plane by oblique collapse during decay. Dorsal arcualia are known in lampreys and jawed vertebrates, and have been inferred in heterostracans, galeaspids and osteostracans on the basis of indirect arguments (median series of impressions on the internal surface of the dorsal dermal skeleton, very elongated occipital component of the endoskeletal head shield; Janvier 1996c). Ventral arcualia are unique to gnathostomes among living vertebrates, and now known in *Euphanerops*. The condition in all other fossil jawless vertebrates is unknown. The presence of arcualia (whether dorsal or ventral) in the myllokunmingiid *Haikouichthys* (Shu *et al*. 2003) remains highly conjectural (Janvier 2003).

Large chondrocytes arranged in "cell nests"

Assuming that they actually reflect cellular structures, whatever the origin (*pre-* or *post-mortem*) of their mineralization, the "chondrocyte spaces" described here in the mineralized elements of *Euphanerops* strikingly resemble chondrocytes, and more particularly the very large chondrocytes of lampreys, which are characteristically grouped side-by-side into "cell nests". Moreover, the size of the chondrocytes in lampreys increases from the periphery to the centre of the cartilage elements, and their territorial extracellular matrix is more compact and abundant around the peripheral chondrocytes than around the more centrally placed ones (Langille & Hall 1993; McBurney & Wright 1996). The "chondrocyte spaces" of *Euphanerops* show much the same organization, being smaller and surrounded by more compact mineralized matter near the periphery of the elements. Again, and

notwithstanding the reservations one may express as to whether or not the structure of the mineralized endoskeletal elements of *E. longaevus* actually reflects a histological structure, the shape and organization of the "chondrocyte spaces" described herein resemble those of lamprey chondrocytes more than anything else.

Sinuous gill arches

Sinuous gill arches are known only in living lampreys. In *Euphanerops*, the vertical bars referred to as gill arches, be they mineralized or not, display a strongly sinuous shape that recalls the condition in lampreys. However, the presence of spinous processes branching off from these arches remains uncertain. No other fossil vertebrate shows such a gill arch morphology. Yet their presence has been invoked to explain certain sinuous impressions in the roof of the oralobranchial cavity of osteostracans (Janvier 1981b). Leaving aside this possible indirect evidence, sinuous gill arches seem, to date, unique to lampreys and *Euphanerops*.

Large number of gills

The definition of this character poses a problem, since one has to decide what should be regarded as a "large number". Among living vertebrates, lampreys always have seven gill-bearing arches, and jawed vertebrates have five or less, with the exception of hexanchiform sharks, which have up to seven gill arches. Hagfishes display from five to 15 gill pouches, with some cases of minor intraspecific variation and even variations by one or two pouches between the right and left pouches of the same individual (Martini *et al*. 1997). Most fossil jawless vertebrate taxa have more than seven gills, and their number is generally inferred from either the number of the gill openings, or the number of branchial fossae or gill impressions on the surface of the skeleton, but in some cases by the number of imprints of the actual gills or gill arches (e.g., myllokunmingiids, *Euphanerops* or *Endeiolepis*). Currently, the distribution of the gill number in these fossil taxa is as follows: Myllokunmingiida: 6; Arandaspida: 17 to 19 (inferred from the number of the branchial plates and some impressions on the dorsal and ventral head shields); Astraspida: at least 8; Heterostraci: at least 8 (based on gill impressions on the surface of the dorsal and ventral shield plates); Anaspida: 8 to 15; Galeaspida: 7 to about 45; Osteostraci: 8 to 10; Thelodonti: 5 to 8 (Janvier 2004). The number of gill arches in *Euphanerops* is estimated at 33, based on MHNM 01-02, yet this count may be biased by the overprinting of the arches of the left and right sides. However, counts based on the tree-dimensionally preserved branchial basket of *Endeiolepis* agree, as a whole, with this value, with a number of gill pouch impressions ranging from 28 to 30. The number of gills in *Jamoytius* depends on which structure their count is based on; nevertheless, when considering the rounded imprints that Ritchie (1968, 1984) regarded as the branchial apparatus, one may infer the presence of certainly more than 20 gill units. It would be far more if the presumed scales of *Jamoytius* are actually gill arches. In all the major taxa which display a wide range of difference in gill numbers, one notices that there is generally a gap between the species that have about 8-10 gills, and those that have far more gills (15 or more). Therefore, we suggest here that two states can be arbitrarily defined for this character; that is, 10 gills or less, and more than 10 gills. In this respect, the polybranchic condition would apply to eptatretid hagfishes, *Euphanerops*, *Endeiolepis*, *Pharyngolepis*, most Devonian galeaspids (except for eugaleaspidiforms), and probably *Jamoytius* and arandaspids. Although the polybranchic condition of these vertebrates vaguely recalls the large number of pharyngeal slits in cephalochordates, we are reluctant to apply this character state to the latter, which possesses neither true gill arches, nor gill filaments. Admittedly, this is also the case for hagfishes, but the little we know of hagfish development shows that the early formation of their pharyngeal pouches and branchiomeres is globally similar to that of other vertebrates, and quite different from the early development of the pharyngeal slits of cephalochordates (Holmgren 1946; Jefferies 1986).

Gill pouches

Gill pouches that enclose the gills are unique to hagfishes and lampreys, and were long regarded as one of the synapomorphies of the Cyclostomi,

despite important differences in gill shape and structure in these two groups, respectively. Notably, each afferent branchial artery irrigates the gills of two adjacent gill pouches in lampreys, but those of a single pouch in hagfishes. Moreover, hagfishes have no real gill filaments, but a folded respiratory tissue covering the inner surface of the gill pouches. The presence of gill pouches has been also inferred in other fossil jawless vertebrates (anaspids, pteraspidomorphs, galeaspids, osteostracans) on various grounds, but without any direct evidence (Stensiö 1927, 1964, 1968; Watson 1954). *Euphanerops* shows no direct evidence for gill pouches, but *Endeiolepis* now provides indications of their presence and, considering the virtually similar morphology of the two taxa, this character may be extrapolated to both of them, as well as to *Achanarella* and *Cornovichthys* (Janvier *et al*. 2006). Although far more numerous and crowded than those of lampreys, the natural cast of the gill pouches of and the gill filament impressions in *Endeiolepis* suggests quite a similar morphology.

Ribbon-shaped paired fins

Euphanerops possesses a ventrally placed series of numerous radials that we regard as paired on the basis of a single specimen. One may wonder if such a ribbon-shaped ventrolateral paired fin would have been reconstructed in the same way, without having in mind Ritchie's (1964, 1968, 1984) models of the similar-shaped paired fins of the anaspid *Pharyngolepis* and in *Jamoytius*. Although the radials of *Pharyngolepis* are not preserved, they are assumed to have been present, on the basis of the rows of minute scales that cover the fin web. Nevertheless, we provisionally regard here the paired fins of *Euphanerops*, *Pharyngolepis*, and probably *Rhyncholepis* (Ritchie 1980) and *Jamoytius*, as basically similar in position and shape.

"Braincase"

Among living vertebrates, only the gnathostomes possess a massive braincase that completely encloses the olfactory and otic capsules and the brain. Hagfishes have no braincase proper, and the so-called braincase of lampreys is a lightly built cartilaginous structure that is not closed dorsally. Among fossil vertebrate taxa, placoderms display much the same type of braincase as living gnathostomes, and the endoskeletal head shield of such stem gnathostomes as galeaspids, pituriaspids and osteostracans, is regarded as a massive braincase. Assuming that the large mass of mineralized matter referred to herein as the "braincase" in *Euphanerops* actually represents a poorly preserved braincase, its relatively large size and vague outline may be regarded as more suggestive of that of galeaspids, osteostracans, and jawed vertebrates (in particular the platybasic braincase of placoderms and chondrichthyans), than of that of lampreys.

"Gill rods" and gill rays

In the light of the recent data provided by *Endeiolepis* (Janvier *et al.* 2006), the structures referred to here as "gill rods" are likely to be endoskeletal supports of either the gill filaments or interbranchial septa. Among living vertebrates, only gnathostomes display endoskeletal gill filament supports, the gill rays, which are situated either in the interbranchial septa (elasmobranchs), or in the proximal part of adjacent gill filaments (acanthodians, osteichthyans). Placoderms show evidence for gill rays (notably in rhenanids), but their precise position is unclear. Gill ray-like structures are present in presumed stem vertebrates, yunnanozoans and myllokunmingiids (Mallatt & Chen 2003; Hou *et al.* 2002; Zhang & Hou 2004) and seem to extend laterally to the presumed gill arches, more or less as in jawed vertebrates. The position of the "gill rods" relative to the gill arches is unclear in *Euphanerops* and *Endeiolepis*, because no specimen of the former displays a three-dimensionally preserved branchial basket, and no specimen of the latter shows traces of the gill arches. Therefore, the only character that can be considered as possibly shared by myllokunmingiids, *Euphanerops*, *Endeiolepis* and jawed vertebrates is the presence of endoskeletal gill filament supports as a whole. Nevertheless, judging from the orientation of the natural casts of the gill pouches in *Endeiolepis*, there is a strong probablility that the "gill rods" were medial to the gill arches and oriented anteromedially toward the pharynx (Janvier *et al*. 2006).

"Annular cartilage" and "median ventral rod"
As pointed out above (see Anatomy, p. 169), the "annular cartilage" and "median ventral rod" of *Euphanerops* could be readily regarded as homologous to the annular and piston cartilages of lampreys. However, the position of these elements relative to the anterior end of the head, marked by the "head stains", is inconsistent with the much more anterior position of the annular and piston cartilage in lampreys. Coding these two structures as present in *Euphanerops* and lampreys in a data matrix is a matter of choice, but this would give much weight to a homology relationship that we consider as not being supported by unambiguous positional arguments.

"Head stains"
The three "head stains" of *Euphanerops* readily recall those of the Silurian and Devonian "naked" agnathans *Jamoytius* and *Achanarella*, classically interpreted as the median annular cartilage (or olfactory organ) and paired eye imprints. Here, we propose the rather counter-intuitive interpretation that these three stains correspond to large cartilage plates, homologous to the tectal cartilages of the lamprey snout. We are aware that this interpretation needs to be further tested, but if this interpretation holds, then, we may have a homology shared uniquely by lampreys and at least some of the fossil "naked" agnathans.

Considering the poor quality of the homology statements that can be made about these characters, some of which may be mere artifacts of preservation or diagenesis, we prefer to avoid inserting them in any of the recently published vertebrate data matrices (e.g., Janvier 1996b; Donoghue *et al.* 2000; Donoghue & Smith 2001; Shu *et al.* 2003; Gess *et al.* 2006) and thereby generating perhaps one more vertebrate tree. At any rate, such characters, as the markedly hypocercal tail and possibly ribbon-shaped paired fins suggest affinities to anaspids. Anal fin, ventral arcualia and possibly gill rays (assuming that the "gill rods" actually are gill rays) would be shared at least by *Euphanerops*, and jawed vertebrates, but may appear as a general character for the total goup gnathostomes (except perhaps euconodonts). In contrast, assuming that the "head stains" are tectal cartilage, that the "annular cartilage" and "median ventral rod" actually are the homologues of the annular and piston cartilages of lampreys, and that the structure of the mineralized endoskeleton actually reflects that of a lamprey-like cartilage, would strongly support a closer relationship between *Euphanerops* and lampreys (and possibly anaspids), as formerly suggested and recently reiterated by Gess *et al*. (2006).

CONCLUSIONS

The anatomy of *Euphanerops longaevus* is reconstructed here on the basis of 17 specimens, 14 of which were hitherto undescribed. Most of the specimens of this species described to date were relatively small-sized, presumably juvenile or young adults, and did not show clear traces of mineralization. Significantly larger and presumably more aged individuals now display extensively mineralized internal structures thought to be the endoskeleton. Although this mineralized matter is made of calcium phosphate, with local traces of silicates, it remains undecided whether it is *in vivo* calcified cartilage, as suggested earlier by Janvier & Arsenault (2002), various tissues that became mineralized *post-mortem*, or a mixture of both. At any rate, the traces of silicates that could be evidenced in some elements are likely to be of diagenetic origin.

Practically all the mineralized elements that can be observed in the largest individuals of *E. longaevus* display the same structure, which strikingly recalls that of lamprey cartilage, despite the uncertainty as to the origin of its mineralization. It consists of comparatively large, ovoid shells of calcium phosphate surrounding generally paired spaces that are tentatively regarded as having housed large chondrocytes. Several such "chondrocyte spaces" may sometimes be grouped into a "cell nest", as characteristically seen in lamprey cartilage. These shells are more or less loosely cemented by an interstitial, finely spherulitic calcified or, at any rate, mineralized matrix. A more densely mineralized endoskeletal tissue occurs locally, in the "braincase" and the large elements of the "posterior haemal series". The only exception found among the mineralized structures that can

be observed in one of the large specimens of *E. longaevus* is the calcified "white line" (possibly a blood vessel), which shows no "chondrocyte spaces", but traces of thin longitudinal canals. The presence of such a calcified soft tissue structure would rather support *post-mortem* mineralization.

Thanks to this mineralization, and assuming that it mainly concerns endoskeletal elements, it is now possible to suggest that *E. longaevus* possessed a relatively complex skull, comprizing at least a very large branchial apparatus, possibly a large braincase, and a ring-shaped structure, or an annular cartilage, that armed the entrance to either the mouth of the pharynx. Three large stains, or "head stains" at the anterior end of the head could represent a median olfactory organ and eye imprints, but the fact that they show, in large individuals, the same spongiose mineralized structure as unequivocal endoskeletal elements also suggests that they are in fact cartilaginous plates that armed the snout as do the tectal cartilages of lampreys. These extensively mineralized specimens also provide the first hint for the presence of dorsal and ventral arcualia in the axial skeleton of a jawless vertebrate. Beneath the ventral arcualia extends a series of "haemal" elements, which, anteriorly to the anal region, surround a strongly calcified structure (the "white line"), assumed here to be possibly the calcified dorsal aorta.

The large individuals of *E. longaevus* also confirm the presence of a very elongated branchial skeleton, which consists of at least 30 sinuous gill arches that are associated with numerous gill ray-like structures, non-committally referred to here as "gill rods". The branchial skeleton ends posteriorly with a possible pericardiac cartilage. The gill arches are interpreted here as being united dorsally and ventrally to a paired series of closely-set (or even fused) median dorsal and median ventral element referred to as the dorsal and ventral "copular elements". The ventral series of "copular elements" is prolonged anteriorly by a thick median bar, the "anterior ventral rod". The latter contacts anteriorly the large, ring-shaped mineralized cartilage element, referred to as the "annular cartilage", but whose position does not support a homology with the annular cartilage of lampreys. The radials of the anal fin are supported by two median series of large, presumably cartilaginous plates referred to as the "anal fin supports". The most extensively mineralized specimens also show a number of elements which display the same vacuolar or spongiose structure as in presumed cartilages, but for which no satisfactory interpretation can be offered. It is notably the case for the "intermuscular elements", which seem to have been dispersed in the body musculature, and the "diffuse mineralized matter", made up by free mineralized "chondrocyte spaces" mainly scattered in the mid-dorsal region of the trunk.

The new material of *E. longaevus* described here provides strong support for the presence of ventrolateral, ribbon-shaped, paired fins armed with numerous parallel radials. These fins extend from the anus to the anterior part of the branchial apparatus anteriorly, and are the first instance of paired fins with radials, whose anteroposterior extension largely overlaps that of the branchial apparatus in a vertebrate.

The visceral cavity of *E. longaevus* shows evidence for a stomach, the contents of which consists of a very fine-grained sediment and suggests microphagous particulate feeding, but there is no information about the organization of the posterior digestive tract and its relations to the branchial basket.

A number of non-skeletal structures observed in the largest specimens of *E. longaevus* remain enigmatic. It is notably the case for the "doughnut-shaped structures" of the head of some specimens, which may either be the imprint of the eye sclera, or mere artefactual accumulation of carbonaceous matter. The structure referred to here as the "white line" may be a large blood vessel, possibly the dorsal aorta, which is calcified either pathologically, or through *post-mortem* microbially induced calcification. Similarly, the two or three longitudinal "black lines" observed in some non-mineralized specimens may also be imprints of major blood vessels, some of which seem associated to the branchial apparatus.

The structure of the mouth and pharynx, and their relationships to the overlying snout and, posteriorly, the oesophagus and stomach remains unclear. It is assumed here that the entrance to the pharynx was large, possibly strengthened by the "annular cartilage", and that the branchial

apparatus was more or less sleeve shaped, but it is unknown whether it was continued posteriorly by the oesophagus, or connected to the latter by an oesophagobranchial duct.

The organization of the three "head stains" and branchial apparatus of the Middle Devonian "naked" jawless vertebrates *Achanarella* and *Cornovichthys* and of the Late Devonian *Endeiolepis aneri* seems to be similar to that of *Euphanerops longaevus*, and it makes little doubt that these four taxa are most closely related and can be referred to the same family Euphaneropidae. It is also possible that much the same type of organization applies to the Silurian "naked" jawless vertebrate *Jamoytius*. However, the relationships of the Euphaneropidae remains a riddle. Any attempt at elucidating the phylogenetic position of the Euphaneropidae among the vertebrates is largely illusory at this stage, because assumptions about primary homology, by reference to other living or fossil taxa, for most of the characters described here in *E. longaevus* are subject to several possible interpretations. The characters that we regard as possibly shared only by *E. longaevus* (or euphaneropids) and other particular taxa are: 1) the cartilage structure with large chondrocytes grouped into "cell nests", and the sinuous gill arches, shared with lampreys; 2) the strongly hypocercal tail and ribbon-shaped paired fins, shared with anaspids; 3) the anal fin, shared with anaspids and crown-group gnathostomes; and 4) the ventral arcualia, anal fin and gill filament supports (gill rays or "gill rods") shared with jawed vertebrates. No acceptable conclusion as to the affinities of the Euphaneropidae can be reached until the structure of the "braincase", snout and oral region of *E. longaevus* is better elucidated.

Acknowledgements
The authors are endebted to the Sepaq (Quebec), the Director of the Parc de Miguasha, Rémi Plourde, and his staff, Sylvain Desbiens, Johanne Kerr, Norman Parent, and Jason Willett, for the access to the material and their assistance in the realization of this study. Peter Forey (London) is gratefully acknowledged for his help in consulting the collection of the Natural History Museum. Michael Newman (Kemnay, Scotland) is warmly thanked for his information and suggestions about the interpretation of *Achanarella*. The authors are very grateful to Louise Zylberberg (CNRS, Paris) for her attempts at finding organic matter in the "white line". The authors are also indebted to Philip Donoghue (Bristol) and Mark Purnell (Leicester), who reviewed twice the previous versions of this manuscript, as it was submitted to a different journal, and made crucial points regarding the question of the *pre-* or *post-mortem* origin of the mineralization of the specimens. Thanks are also due to David Martill (Portsmouth), Moya M. Smith (London) and B. Kremer (Warsaw) regarding this question. The thin sections have been made by Michel Lemoine (UMR 5143, Paris), and the photographs by Sylvain Desbiens (Miguasha) and Philippe Loubry (UMR 5143, Paris). We are also grateful to Didier Geffard (UMR 5143, Paris) for his assistance in the realization of the some figures, Christiane Chancogne (UMR 5143, Paris) for the SEM photographs, M. Fisalain (CAMPARIS, Paris 6 University), and M.-M. Blanc-Valleron (UMR 5143, Paris) for their assistance in the microprobe analyses.

REFERENCES

ALDRIDGE R. J. & THERON J. N. 1993. — Conodonts with preserved soft tissue from a new Ordovician Konservat-Lagerstätte. *Journal of Micropalaeontology* 12: 113-117.

ALDRIDGE R. J., BRIGGS D. E. G. & CLARKSON E. N. K. 1986. — The affinities of the conodonts – new evidence from the Carboniferous of Edinburgh, Scotland. *Lethaia* 19: 279-291.

ARSENAULT M. & JANVIER P. 1991. — The anaspid-like craniates of the Escuminac Formation (Upper Devonian) from Miguasha (Quebec, Canada) with remarks on anaspid-petromyzontid relationships, *in* CHANG M. M., LIU Y. H. & ZHANG G. R. (eds), *Early Vertebrates and Related Problems of Evolutionary Biology*. Science Press, Beijing: 19-44.

ARSENAULT M., DESBIENS S., JANVIER P. & KERR J. 2004. — New data on the soft tissues and external morphology of the antiarch *Bothriolepis canadensis* (Whiteaves, 1880) from the Upper Devonian of Miguasha, Québec, *in* ARRATIA G., CLOUTIER R. & WILSON M. V. H. (eds), *Recent Advances in the Origin and Early Radiation of Vertebrates*. Verlag Dr. Friedrich Pfeil, Munich: 439-454.

BARDACK D. & ZANGERL R. 1971. — Lampreys in the fossil record, *in* HARDISTY M. W. & POTTER I. C. (eds), *The Biology of Lampreys*, Volume 1. Academic Press, London: 67-84.

BÉLAND P. & ARSENAULT M. 1985. — Scauménellisation de l'Acanthodii *Triazeugacanthus affinis* (Whiteaves) de la Formation d'Escuminac (Dévonien supérieur de Miguasha, Québec) : révision de *Scaumenella mesacanthi* Graham-Smith. *Canadian Journal of Earth Sciences* 22: 514-524.

BLOM H., MÄRSS T. & MILLER C. G. 2001. — Silurian and earliest Devonian birkeniid anaspids from the Northern Hemisphere. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 92: 263-323.

BRIGGS D. E. G. 2003. — The role of decay and mineralization in the preservation of soft-bodied fossils. *Annual Review in Earth and Planetary Sciences* 31: 273-301.

BRIGGS D. E. G. & KEAR A. J. 1994. — Decay of the lancelet *Branchiostoma lanceolatum* (Cephalochordata): implication for the interpretation of soft-tissue preservation in conodonts and other primitive chordates. *Lethaia* 26: 275-287.

BRIGGS D. E. G., CLARKSON E. & ALDRIDGE R. J. 1983. — The conodont animal. *Lethaia* 20: 1-14.

BRIGGS D. E. G., MOORE R. A., SHULTZ J. W. & SCHWEIGERT G. 2005. — Mineralization of soft-part anatomy and invading microbes in the horseshoe crab *Mesolimulus* from the Upper Jurassic Lagerstätte of Nusplingen, Germany. *Proceedings of the Royal Society, London* B272: 627-632.

CLOUTIER R. & SCHULTZE H.-P. 1996. — Porolepiform fishes (Sarcopterygii), *in* SCHULTZE H.-P. & CLOUTIER R. (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Verlag Dr. Friedrich Pfeil, Munich: 248-270.

COATES M. I. 2003. — The evolution of paired fins. *Theory in Biosciences* 122: 266-287.

COATES M. I. & COHN M. 1998. — Fins, limbs, and tails: outgrowth and axial patterning in vertebrate evolution. *BioEssays* 20: 371-381.

DAMAS H. 1935. — Contribution à l'étude de la métamorphose de la tête de la lamproie. *Archives de Biologie* 46: 171-227.

DAMAS H. 1944. — Recherches sur le développement de *Lampetra fluviatilis* L. Contribution à l'étude de la céphalogenèse des vertébrés. *Archives de Biologie* 55: 1-284.

DENISON R. H. 1967. — Ordovician vertebrates from western United States. *Fieldiana: Gelology* 16: 269-288.

DONOGHUE P. C. J. & SANSOM I. J. 2002. — Origin and early evolution of vertebrate skeletonization. *Microscopy Research and Technique* 59: 352-372.

DONOGHUE P. C. J. & SMITH M. P. 2001. — The anatomy of *Turinia pagei* (Powrie) and the phylogenetic status of the Thelodonti. *Transactions of the Royal Society of Edinburgh (Earth Sciences)* 92: 15-37.

DONOGHUE P. C. J., FOREY P. L. & ALDRIDGE R. J. 2000. — Conodont affinity and chordate phylogeny. *Biological Reviews* 75: 191-251.

DONOGHUE P. C. J., SANSOM I. J. & DOWNS J. P. 2006. — Early evolution of vertebrate skeletal tissues and cellular interactions, and the canalization of skeletal development. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 306B: 278-294.

FOREY P. L. 1984. — Yet more reflections on agnathan-gnathostome relationships. *Journal of Vertebrate Paleontology* 4: 330-343.

FOREY P. L. & GARDINER B. G. 1981. — J. A. Moy-Thomas and his association with the British Museum (Natural History). *Bulletin of the British Museum (Natural History), Geology* 35: 131-144.

FOREY P. L. & JANVIER P. 1994. — Agnathans and the origin of jawed vertebrates. *Nature* 361: 129-134.

FREEDMAN K. A. 1996. — *Jamoytius kerwoodi* White: an unimaginative interpretation. *42nd Annual meeting of the Palaeontological Association*, Abstracts: 3.

FREEDMAN K. A. 1998. — An unimaginative interpretation of *Jamoytius kerwoodi* White. 58th Annual meeting of the Society of Vertebrate Paleontology, abstract 1100. *Journal of Vertebrate Paleontology* 18 (supplement to Number 3): 43A.

GABBOTT S., ALDRIDGE R. J. & THERON J. 1995. — A giant conodont with preserved muscle tissue from the Upper Ordovician of South Africa. *Nature* 374: 800-803.

GAGNIER P.-Y. 1993a. — *Sacabambaspis janvieri*, vertébré ordovicien de Bolivie. 1. Analyse morphologique. *Annales de Paléontologie* 79: 19-69.

GAGNIER P.-Y. 1993b. — *Sacabambaspis janvieri*, vertébré ordovicien de Bolivie. 2. Analyse phylogénétique. *Annales de Paléontologie* 79: 119-166.

GESS R. W., COATES M. I. & RUBIDGE R. S. 2006. — A lamprey from the Devonian period of South Africa. *Nature* 443: 981-984.

GROGAN E. D. & LUND R. 1997. — Soft tissue pigments of the Upper Mississippian chondrenchelyid, *Harpagofututor volsellorhinus* (Chondrichthyes, Holocephali) from the Bear Gulch limestone, Montana, USA. *Journal of Paleontology* 71: 337-342.

GROGAN E. D. & LUND R. 2002. — The geological and biological environment of the Bear Gulch limestone (Mississippian of Montana, USA) and a model for its deposition. *Geodiversitas* 24 (2): 295-315.

GROSS W. 1938. — Der histologische Aufbau der Anaspiden-Schuppen. *Norsk Geologisk Tidskrift* 17: 191-195.

GROSS W. 1958. — Anaspiden-Schuppen aus dem Ludlow des Ostseegebiets. *Paläontologische Zeischrift* 32: 24-37.

HANKE G. & WILSON M. V. H. 2006. — Anatomy of

the Early Devonian acanthodian *Brochoadmones milesi* based on nearly complete body fossils, with comments on the evolution and development of paired fins. *Journal of Vertebrate Palaeontology* 36: 526-537.

HEINTZ A. 1958. — The head of the anaspid *Birkenia elegans* Traq., *in* WESTOLL T. S. (ed.), *Studies on Fossil Vertebrates*. The Athlone Press, London: 71-85.

HEINTZ A. 1967. — Some remarks about the structure of the tail in cephalaspids, *in* LEHMAN J. P. (ed.), *Évolution des vertébrés*. Colloques internationaux du Centre national de la Recherche scientifique, 163. CNRS, Paris: 21-36.

HOLMGREN N. 1946. — On two embryos of *Myxine glutinosa*. *Acta Zoologica*, Stockholm 27: 1-90.

HOLMGREN N. & STENSIÖ E. A. 1936. — Kranium und Visceralskelett des Akranier, Cyclostomen und Fische, *in* BOLK L., GÖPPERT E., KALLIUS E. & LUBOSCH W. (eds), *Handbuch der vergleichenden Anatomie der Wirbeltiere*, Vol. 4. Urban & Schwartzenberg, Berlin; Vienna: 233-500.

HOU X. G., ALDRIDGE R. J., SIVETER D. J., SIVETER D. J. & FENG X. H. 2002. — New evidence on the anatomy and phylogeny of the earliest vertebrates. *Proceedings of the Royal Society of London* B269: 1865-1869.

JAEKEL O. 1911. — *Die Wirbeltiere. Eine Übersicht über die fossilen und lebenden Formen*. Borntraeger, Berlin, 252 p.

JANVIER P. 1977. — Contribution à la connaissance de la systématique et de l'anatomie du genre *Boreaspis* Stensiö (Agnatha, Cephalaspidomorphi, Osteostraci) du Dévonien inférieur du Spitsberg. *Annales de Paléontologie* 63: 1-32.

JANVIER P. 1981a. — The phylogeny of the Craniata, with particular reference to the significance of fossil "agnathans". *Journal of Vertebrate Paleontology* 1: 121-159.

JANVIER P. 1981b. — *Norselaspis glacialis* n.g., n.sp. et les relations phylogénétiques entre les kiaeraspidiens (Osteostraci) du Dévonien inférieur du Spitsberg. *Palaeovertebrata* 11: 19-131, pls 1-3.

JANVIER P. 1996a. — Anaspida, *in* SCHULTZE H.-P. & CLOUTIER R. (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada.* Verlag Dr. Friedrich Pfeil, Munich: 134-140.

JANVIER P. 1996b. —The dawn of the vertebrates: characters versus common ascent in the rise of current vertebrate phylogenies. *Palaeontology* 39: 259-287.

JANVIER P. 1996c. — *Early Vertebrates*. Oxford University Press, Oxford, xiii + 408 p.

JANVIER P. 1998. — Les vertébrés avant le Silurien. *Geobios* 30: 931-950.

JANVIER P. 2003. — Vertebrate characters and Cambrian vertebrates. *Comptes Rendus Palevol* 2: 523-531.

JANVIER P. 2004. — Early specializations of the branchial apparatus in jawless vertebrates: a consideration of gill number and size, *in* ARRATIA G., CLOUTIER R. & WILSON M. V. H. (eds), *Recent Advances in the Origin and Early Radiation of Vertebrates*. Verlag Dr. Friedrich Pfeil, Munich: 439-454.

JANVIER P. & ARSENAULT M. 1996. — Osteostraci, *in* SCHULTZE H.-P. & CLOUTIER R. (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada.* Verlag Dr. Friedrich Pfeil, Munich: 123-133.

JANVIER P. & ARSENAULT M. 2002. — Calcification of early vertebrate cartilage. *Nature* 417: 609.

JANVIER P. & BUSCH R. 1984. — *Jamoytius*-like vertebrates from the Lower Devonian Manlius Formation of New York State. *Journal of Vertebrate Paleontology* 4: 501-506.

JANVIER P. & LUND R. 1983. — *Hardistiella montanensis* n. gen. et sp. (Petromyzontida) from the Lower Carboniferous of Montana, with remarks on the affinities of the lampreys. *Journal of Vertebrate Paleontology* 2: 407-413.

JANVIER P., ARSENAULT M. & DESBIENS S. 2004. — Calcified cartilage in the paired fins of the osteostracan *Escuminaspis laticeps* (Traquair 1880), from the Late Devonian of Miguasha (Quebec, Canada), with a consideration of the early evolution of the pectoral fin endoskeleton in vertebrates. *Journal of Vertebrate Paleontology* 24: 773-779.

JANVIER P., DESBIENS S., WILLETT J. A. & ARSENAULT M. 2006. — Lamprey-like gills in a gnathostome-related Devonian jawless vertebrate. *Nature* 440: 1183-1185.

JARVIK E. 1980. — *Basic Structure and Evolution of Vertebrates*, Volume 1. Academic Press, London, xvi + 575 p.

JEFFERIES R. P. S. 1986. — *The Ancestry of the Vertebrates*. British Museum (Natural History), London, 376 p.

JOHNELS A. 1944. — On the cartilage and mucocartilage of the Petromyzon larva. *Acta Zoologica*, Stockholm 25: 67-73.

JOHNELS A. 1948. — On the development and morphology of the skeleton of the head of *Petromyzon*. *Acta Zoologica*, Stockholm 29: 140-279.

KIAER J. 1924. — The Downtonian fauna of Norway. 1. Anaspida. *Videnskapsselskapets Skrifter. 1. Matematiske-Naturvidenskapslige Klasse* 6: 1-139.

KREMER B. 2005. — Mazuelloids: product of *post-mortem* phosphatization of acanthomorphic acritarchs. *Palaios* 20: 27-36

LANGILLE R. M. & HALL B. K. 1993. — Calcification of cartilage from the lamprey *Petromyzon marinus* (L.) *in vitro*. *Acta Zoologica*, Stockholm 74: 31-41.

LIU Y. H. 1975. — [Lower Devonian agnathans of Yunnan and Sichuan]. *Vertebrata PalAsiatica* 13: 215-223 (in Chinese with English summary).

MAISEY J. G. 1986. — Heads and tails: a chordate phylogeny. *Cladistics* 2: 201-256.

MAISEY J. G. 1989. — Visceral skeleton and musculature of a Late Devonian shark. *Journal of Vertebrate*

Paleontology 9: 174-190.
MALLATT J. 1984. — Feeding ecology of the earliest vertebrates. *Zoological Journal of the Linnean Society* 82: 261-272.
MALLATT J. 1996. — Ventilation and the origin of jawed vertebrates: a new mouth. *Zoological Journal of the Linnean Society* 117: 329-404.
MALLATT J. & CHEN J. Y. 2003. — Fossil sister-group of craniates: predicted and found. *Journal of Morphology* 258: 1-31.
MARINELLI W. & STRENGER A. 1954. — *Lampetra fluviatilis* L., *in Vergleichende Anatomie und Morphologie der Wirbeltiere*. Franz Deuticke, Wien: 1-80.
MARINELLI W. & STRENGER A. 1956. — *Myxine glutinosa* L., *in Vergleichende Anatomie und Morphologie der Wirbeltiere*. Franz Deuticke, Wien: 81-172.
MÄRSS T. 1986a. — [Silurian vertebrates of Estonia and West Latvia]. *Fossilia Baltica*, Valgus, Tallinn 1: 1-104 (in Russian with English summary).
MÄRSS T. 1986b. — Squamation of the thelodont agnathan *Phlebolepis*. *Journal of Vertebrate Paleontology* 6: 1-11.
MÄRSS T. & RITCHIE A. 1998. — Silurian thelodonts (Agnatha) of Scotland. *Transaction of the Royal Society of Edinburgh* 88: 143-195.
MARTILL D. M. 1990. — Macromolecular resolution of fossilized muscle tissue from an elopomorph fish. *Nature* 346: 171-172.
MARTILL D. M. & WILBY P. R. 1994. — Lithified prokariotes associated with fossil soft tissues from the Santana Formation (Cretaceous) of Brazil. *Kaupia* 4: 71-77.
MARTINI F. H., HEISSER J. B. & LESSER M. P. 1997. — A population profile for hagfish, *Myxine glutinosa* L., in the Gulf of Maine: I. Morphometrics and reproductive state. *Fishery Bulletin* 95: 311-330.
MCBURNEY K. M. & WRIGHT G. M. 1996. — Chondrogenesis of a non-collagen-based cartilage in the sea lamprey, *Petromyzon marinus*. *Canadian Journal of Zoology* 74: 2118-2130.
MOY-THOMAS J. A. & MILES R. S. 1971. — *Palaeozoic Fishes*. 2nd edition, extensively revised by R. S. Miles. Chapman and Hall, London, xi + 259 p.
NEWMAN M. 2002. — A new naked jawless vertebrate from the Middle Devonian of Scotland. *Palaeontology* 45: 933-941.
NEWMAN M. & TREWIN N. 2001. — A new jawless vertebrate from the Middle Devonian of Scotland. *Palaeontology* 44: 43-51.
ØRVIG T. 1951. — Histologic studies of placoderms and fossil elasmobranchs. 1: The endoskeleton, with remarks on the hard tissues of lower vertebrates in general. *Arkiv för Zoologi* 2: 321-454.
ØRVIG T. 1967. — Phylogeny of tooth tissues: evolution of some calcified tissues in early vertebrates, *in* MILES A. E. W. (ed.), *Structural and Chemical Organization of Teeth*, Vol. 1. Academic Press, New York: 45-110.
ØRVIG T. 1968. — The dermal skeleton; general considerations, *in* ØRVIG T. (ed.), *Current Problems of Lower Vertebrate Phylogeny*. Almqvist & Wiksell, Stockholm: 373-397.
PAN J. & CHEN L. Z. 1993. — [Geraspididae, a new family of Polybranchiaspidida (Agnatha) from Silurian of Northern Anhui]. *Vertebrata PalAsiatica* 31: 225-230 (in Chinese with English summary).
PARENT N. & CLOUTIER R. 1996. — Distribution and preservation of fossils in the Escuminac Formation, *in* SCHULTZE H.-P. & CLOUTIER R. (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Verlag Dr. Friedrich Pfeil, Munich: 54-78.
PARRINGTON F. R. 1958. — On the nature of the Anaspida, *in* WESTOLL T. S. (ed.), *Studies on Fossil Vertebrates*. The Athlone Press, London: 108-128.
PERNKOPF E. & LEHNER J. 1937. — Vorderdarm, *in* BOLK L., GÖPPERT E., KALLIUS E. & LUBOSCH W. (eds), *Handbuch der vergleichenden Anatomie des Wirbeltiere*. Urban & Schwarzenberg, Berlin; Vienna: 349-476.
PRADEL A., SANSOM I. J., GAGNIER P.-Y., CESPEDES R. & JANVIER P. 2006. — The tail of the Ordovician fish *Sacabambaspis*. *Biology Letters* 3: 72-75.
PRICHONNET G., DI VERGILIO M. & CHIDIAC Y. 1996. — Stratigraphical, sedimentological and paleontological context of the Escuminac Formation: paleoenvironmental hypotheses, *in* SCHULTZE H.-P. & CLOUTIER R. (eds), *Devonian Fishes and Plants of Miguasha, Quebec, Canada*. Verlag Dr. Friedrich Pfeil, Munich: 23-36.
PURNELL M. A. & DONOGHUE P. C. J. 1999. — Flattened fossils, physical modelling and the restoration of collapsed skeletons, *in* SAVAZZI E. (ed.), *Functional Morphology of the Invertebrate Skeleton*. John Wiley, New York: 91-99.
RICHARDSON M. K. & WRIGHT G. M. 2003. — Developmental transformations on a normal series of embryos of the sea lamprey *Petromyzon marinus* (Linnaeus). *Journal of Morphology* 257: 348-363.
RITCHIE A. 1960. — A new interpretation of *Jamoytius kerwoodi* White. *Nature* 188: 647-649.
RITCHIE A. 1964. — New light on the morphology of the Norwegian Anaspida. *Skrifter utgitt av det Norske Videnskaps-Akademi, 1, Matematisk-Naturvidenskapslige Klasse* 14: 1-35, pls 1-4.
RITCHIE A. 1968. — New evidence on *Jamoytius kerwoodi* White, an important ostracoderm from the Silurian of Lanarshire, Scotland. *Palaeontology* 11: 21-39.
RITCHIE A. 1980. — The Silurian anaspid genus *Rhyncholepis* from Oesel, Estonia, and Ringerike, Norway. *American Museum Novitates* 2699: 21-36.
RITCHIE A. 1984. — Conflicting interpretations of the Silurian agnathan, *Jamoytius*. *Scottish Journal of Geology* 20: 249-256.
ROBSON P., WRIGHT G. M., YOUSON J. H. & KEELE F.

W. 1997. — A family of non-collagen-based cartilages in the skeleton of the sea lamprey, *Petromyzon marinus*. *Comparative Biochemistry and Physiology* 118B: 71-78.

SHU D. G., CONWAY MORRIS S., HAN J., ZHANG Z. F., YASUI K., JANVIER P., CHEN L., ZHANG X.-L., LIU J. N., LI Y. & LIU H. K. 2003. — Head and backbone of the early Cambrian vertebrate *Haikouichthys*. *Nature* 421: 526-529.

SIMPSON G. G. 1926. — New reconstruction of *Lasanius problematicus*. *Bulletin of the Geological Society of America* 37: 397-402.

SMITH I. C. 1956. — A note on the axial skeleton of the anaspid *Pharyngolepis* sp. *Arkiv för Zoologi* 9: 573-577.

STENSIÖ E. A. 1927. — The Devonian and Downtonian vertebrates of Spitsbergen. 1. Family Cephalaspidae. *Skrifter om Svalbard og Nordishavet* 12: 1-391.

STENSIÖ E. A. 1939. — A new anaspid from the Upper Devonian of Scaumenac Bay in Canada, with remarks on the other anaspids. *Kungliga Svenska Vetenskaps-Akademiens Handlingar* 18: 1-25.

STENSIÖ E. A. 1958. — Les cyclostomes fossiles ou ostracodermes, *in* GRASSÉ P. P. (ed.), *Traité de Zoologie*, vol. 13, *Agnathes et Poissons*. Masson, Paris: 173-423.

STENSIÖ E. A. 1964. — Les cyclostomes fossiles ou ostracodermes, *in* PIVETEAU J. (ed.), *Traité de Paléontologie*, vol. 4 (1). Masson, Paris: 96-382.

STENSIÖ E. A. 1968. — The cyclostomes with special reference to the diphyletic origin of the Petromyzontida and the Myxinoidea, *in* ØRVIG T. (ed.), *Current Problems in Lower Vertebrate Phylogeny*. Almqvist and Wiksell, Stockholm: 13-71.

STETSON E. A. 1928. — A restoration of the anaspid *Birkenia elegans* Traquair. *Journal of Geology* 34: 458-470.

TABIN C. J. & LAUFER E. 1993. — Hox genes and serial homology. *Nature* 361: 692-693.

TRAQUAIR R. H. 1899. — Report of fossil fishes collected by the Geological Survey of Scotland in the Silurian rocks of the South of Scotland. *Transactions of the Royal Society of Edinburgh* 39: 827-864.

TRAQUAIR R. H. 1905. — Supplementary report on fossil fishes collected by the Geological Survey of Scotland. *Transactions of the Royal Society of Edinburgh* 40: 879-888.

TURNER S. 1991. — Monophyly and interrelationships of the Thelodonti, *in* CHANG M. M., LIU Y. H. & ZHANG G. R. (eds), *Early Vertebrates and Related Problems of Evolutionary Biology*. Science Press, Beijing: 87-119.

VAN DER BRUGGHEN W. 2005. — Enige bijzondere kaaklose vissen (Agnatha) uit het Onder-Siluur van Lanakshire (Scotland). *Grondbor & Hamer* 2: 24-28.

VLADIKOV V. D. 1973. — A female sea lamprey (*Petromyzon marinus*) with a true anal fin, and the question of the presence of an anal fin in the Petromyzontidae. *Canadian Journal of Zoology* 51: 221-224.

WANG N. Z., DONOGHUE P. C. J., SMITH M. M. & SANSOM I. J. 2005. — Histology of the galeaspid dermoskeleton and endoskeleton, and the origin and early evolution of the vertebrate cranial endoskeleton. *Journal of Vertebrate Paleontology* 25 (4): 745-756.

WATSON D. M. S. 1954. — A consideration of ostracoderms. *Philosophical Transactions of the Royal Society, London* B238: 1-25.

WHITE E. I. 1946. — *Jamoytius kerwoodi*, a new chordate from the Silurian of Lanarkshire. *Geological Magazine* 83: 89-97.

WILSON M. V. H. & CALDWELL M. W. 1998. — The Furcacaudiformes: a new order of jawless vertebrates with thelodont scales, based on articulated Silurian and Devonian fossils from northern Canada. *Journal of Vertebrate Paleontology* 18: 10-29.

WILSON M. V. H., HANKE G. F. & MÄRSS T. in press. — Paired fins of jawless vertebrates and their homologies across the agnathan-gnathostome transitions, *in* SUES H.-D. & ANDERSON J. (eds), *Evolutionary Transitions*. Indiana University Press, Bloomington.

WOODWARD A. S. 1900. — On a new ostracoderm fish (*Euphanerops longaevus*) from the Upper Devonian of Scaumenac Bay, Quebec, Canada. *Magazine of Natural History* ser. 7, 5: 416-419.

WOODWARD A. S. 1902. — Fishes, *in* ZITTEL K. A. VON (ed.), *Text-book of Palaeontology*, Volume 2. MacMillan, London: 50-55.

ZHANG Y.-G. & HOU X.-G. 2004. — Evidence for a single median fin-fold in tail in the Lower cambrian vertebrate, *Haikouichthys ercaicunensis*. *Journal of Evolutionary Biology* 17: 1162-1166.

Submitted on 14 November 2006;
accepted on 30 January 2007.