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Evolution

Vertebrate characters and the Cambrian vertebrates

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Abstract

The question of the developmental characters which conventionally define the vertebrates, neural crests and epidermal placodes, and their indirect identification in the fossil material is briefly discussed. Comments are made upon some presumed Cambrian vertebrate or vertebrate-related taxa, with particular reference to the most likely Cambrian vertebrates, *Haikouichthys* and *Myllokunmingia*. ***To cite this article: Ph. Janvier, C. R. Palevol 2 (2003).***

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Résumé

Les caractères des Vertébrés et les Vertébrés cambriens. La question des caractères développementaux conventionnellement utilisés pour définir les Vertébrés, les crêtes neurales et les placodes épidermiques, est brièvement discutée, en particulier dans les cas où leur identification sur le matériel fossile est nécessairement indirecte. Quelques taxons cambriens considérés comme appartenant ou comme étant étroitement apparentés aux Vertébrés sont évoqués et quelques remarques sont apportées à l'interprétation des deux Vertébrés cambriens les plus probables, *Haikouichthys* et *Myllokunmingia*. ***Pour citer cet article: Ph. Janvier, C. R. Palevol 2 (2003).***

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Keywords: Vertebrates; Cambrian; anatomy; phylogeny; neural crest; epidermal placodes

Mots clés : Vertébrés ; Cambrien ; anatomie ; phylogénie ; crêtes neurales ; placodes épidermiques

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Les plus anciens Vertébrés certains sont des fragments de cuirasse dermique provenant de l'Ordovicien inférieur (Arenig) d'Australie [46]. Ces fragments sont clairement atribuables à des Arandaspides (Fig. 1), Vertébrés sans mâchoires par ailleurs connus par des spécimens complets dans des niveaux plus récents de l'Ordovicien d'Australie et de Bolivie [15,33]. Tous les restes plus anciens attribués à des Vertébrés sont plus ou moins débattus [3,25,43], à l'exception, pour le moment, de *Myllokunmingia* et *Haikouichthys*, récemment découverts dans le Cambrien inférieur de Chengjiang (Chine) [21,36,38].

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Les débats sur la nature des restes présumés de Vertébrés datant du Cambrien illustrent bien la difficulté à reconnaître sur des fossiles les caractères diagnostiques de ce groupe. Actuellement, il existe un consensus pour définir les Vertébrés sur la base de deux caractères de leur développement: les crêtes neurales et les placodes épidermiques, inconnues chez les autres Métazoaires [2,29,45], mis à part un possible tissu précurseur des crêtes neurales chez les Céphalochordés [19,20]. Les crêtes neurales sont notamment la source de cellules impliquées dans la formation des tissus ondotogènes de l'exosquelette et dans l'endosquelette de l'appareil branchial. Les placodes sont à l'origine d'organes sensoriels comme l'organe olfactif, le cristallin, la capsule otique et le système latéral. Ces deux structures embryonnaires peuvent néanmoins être inférées sur des fossiles à partir de leurs dérivés. Un simple fragment de cuirasse dermique d'un Vertébré ordovicien, par exemple, peut présenter des tubercules de tissus dentineux produits par des cellules dérivées des crêtes neurales, ainsi que des sillons pour les organes du système latéral, dérivé des placodes. Cette déduction est cependant impossible, ou très douteuse, dans le cas de fossiles, comme les Euconodontes ou les Lamproies et Myxines fossiles, où l'homologie des tissus durs avec ceux des Vertébrés est incertaine et où les organes dérivés de la crête neurale et des placodes ne sont plus conservés qu'à l'état d'empreintes.

La découverte d'Euconodontes complets semblait avoir résolu la question des affinités de ce groupe resté longtemps énigmatique [1,5,14]. Leurs yeux pairs, leurs myomères en chevrons et leurs rayons endosquelettiques de la nageoire caudale les plaçaient soit au sein des Vertébrés « apicaux » (tout descendant de l'ancêtre commun le plus récent des Vertébrés actuels; Fig. 1), soit comme Vertébrés basaux (groupe-frère des Vertébrés « apicaux »; Fig.1) [1,11,23], soit encore comme le groupe-frère des Céphalochordés [27,28]. Si les homologies suggérées entre les tissus durs de leurs denticules oraux (les « conodontes ») et ceux des Vertébrés restent débattues [1,3,10,11,12,27,28,35], les quelques caractères observés sur les tissus mous conservés (capsule optique, myomères, radiaux) s'accordent assez bien avec l'anatomie des Vertébrés [11,23–25]. Toutefois, la position des Euconodontes comme groupe-frère de l'ensemble des autres Gnathostomes (*sensu lato*: « Ostracodermes + Placodermes + Gnathostomes « apicaux » ; Fig. 1), proposée par plusieurs phylogénies récentes [11,12,23,43], repose sur l'interprétation de structures non minéralisées qui restent conjecturales. Par leur répartition stratigraphique, du Cambrien supérieur au Trias, les Euconodontes ont donc été considérés par certains comme les premiers Vertébrés cambriens connus.

Anatolepis, connu par de minuscules fragments phosphatés du Cambrien supérieur et de l'Ordovicien inférieur, a été attribué aux Vertébrés en raison de son histologie qui rappelle celle de la dentine [4,42–44]. En revanche, aucun spécimen d'*Anatolepis* ne présente de sillons ou canaux du système latéral, ni n'évoque la forme générale des plaques dermiques des « Ostracodermes » ou des Gnathostomes plus dérivés.

Les phylogénies des Vertébrés actuels et fossiles publiées au cours de ces dernières années montrent toutes une divergence basale des Cyclostomes (Myxines et Lamproies; Fig.1), ces derniers formant soit un clade (phylogénies moléculaires) [9,18,31], soit un grade (phylogénies morphologiques) [11,16,23,24]. Dans ce dernier cas, les Myxines sont toujours le groupe-frère de tous les autres Vertébrés. La paraphylie des Cyclostomes impliquerait donc que le squelette calcifié soit apparu tardivement dans l'histoire des Vertébrés (chez les Gnathostomes *s.l.*) et que la connaissance des Vertébrés fossiles plus basaux exige des conditions de fossilisation exceptionnelles, permettant la conservation de l'empreinte des tissus mous [23,25]. Au Cambrien, ces conditions se rencontrent principalement dans deux gisements, Burgess Pass (Cambrien moyen, Canada) et Chengjiang (Cambrien inférieur, Chine).

Plusieurs fossiles attribués aux Euchordés (Fig.1) ou aux Vertébrés ont été décrits dans les Schistes Burgess, dont *Pikaia gracilens*. Cette espèce a été considérée comme, soit un Céphalochordé, soit un « précurseur » des Vertébrés [8,17], bien qu'il ne présente aucun caractère non ambigu de l'un ou l'autre de ces deux groupes. Ses myomères ne présentent pas clairement la forme en chevron de ceux des Euchordés ; ses tentacules présentent un étrange renflement basal et son pharynx semble être en position dorsale. Un autre fossile des Schistes de Burgess, non nommé, a été rapporté à un Vertébré [22,39,43]. Là encore, il ne présente aucun caractère diagnostique de ce groupe, sinon de vagues myomères en chevrons, mais apparemment orientés vers l'arrière, contrairement à ceux des Euchordés.

Les gisements de la région de Chengjiang ont livré plusieurs taxons rapportés, soit à des Vertébrés basaux, soit à des Vertébrés « apicaux ». *Yunnanozoon* et *Haikouella* présentent un appareil branchial qui évoque celui des Vertébrés [6,7,13,19,30,40], mais peu d'autres caractères, notamment la forme de leurs myomères, s'accordent clairement avec l'anatomie des Euchordés en général. Ces deux formes ont été récemment considérées aussi comme des Deutérostomes basaux [37], mais la réinterprétation récente de *Haikouella* apporterait des arguments en faveur de sa position de Vertébré basal [30]. En revanche, *Myllokunmingia* et *Haikouichthys* (qui sont peut-être synonymes [21]) présentent des myomères en chevrons et une région céphalique comprenant six branchies filamenteuses, qui évoquent celles des lamproies larvaires [21,26,36,38] (Fig. 2D–F). La découverte récente d'environ 500 exemplaires attribués à *Haikouichthys* a permis d'en décrire en détail la tête (Fig. 2A–C), qui présente des capsules olfactives, optiques et peut-être otiques, ainsi que des éléments endosquelettiques métamériques interprétés comme des *arcualia* [36], mais qui évoquent aussi des arcs branchiaux sinueux, comparables à ceux des lamproies. *Haikouichthys* et *Myllokunmingia* ne présentent pas de nageoires paires certaines, mais probablement un repli préanal médian [21,36]. Bien qu'*Haikouichthys* évoque la morphologie générale d'une lamproie larvaire (Fig. 1F), quelques caractères restent discordants avec cette interprétation, tels les rayons endosquelettiques de la nageoire dorsale inclinés vers l'avant ou l' énigmatique série d'éléments sub-branchiaux [21,36,38] (Fig. 2D et E). La présence présumée de gonades métamériques chez *Haikouichthys* et *Myllokunmingia* [21,38] reste à confirmer. Si tel est le cas, ces taxons devront être considérés comme des Vertébrés basaux, groupes frères de tous les autres Vertébrés connus, dans la mesure où les gonades métamériques seraient un caractère général des Euchordés, perdu chez les Vertébrés « apicaux » (Fig.1).

Aucun Vertébré « apical » n'est donc connu de manière indiscutable avant l'Ordovicien inférieur. Quelques fossiles cambriens, comme les Euconodontes ou *Anatolepis*, considérés par certains comme inclus dans ce clade, font encore l'objet de débats. A ce jour, les Vertébrés cambriens les mieux documentés et les plus probables sont *Myllokunmingia* et *Haikouichthys*, du Cambrien inférieur de Chengjiang (Chine). Cependant, même ces deux formes présentent des caractères inconnus chez les Vertébrés « apicaux ». Bien que leur organe olfactif, leurs yeux, leur éventuelle capsule otique et leurs arcs branchiaux suggèrent la présence de placodes épidermiques et de crêtes neurales, sceau des Vertébrés, la structure apparemment métamérique de leurs gonades pourrait les exclure des Vertébrés « apicaux ». Dans ce cas, ils combleraient la lacune morphologique qui existe entre les Céphalochordés et les Vertébrés. Ces taxons du Cambrien inférieur suggèrent donc une divergence entre Céphalochordés et Vertébrés antérieure au Cambrien, plus en accord avec des données récentes de l'horloge moléculaires [18,32], en dépit des biais inhérents à cette méthode [34,41].

1. Introduction

The earliest undisputed vertebrate remains are represented by isolated dermal bone fragments from the base of the Horn Valley Siltstone, and probably also from the top of the Pacoota Sandstone, of the Amadeus Basin in central Australia [46]. They are dated as Early Ordovician (Arenig) and referred to a group of armoured jawless vertebrates, the Arandaspida, known from articulated specimens in younger (Caradoc) formations of Australia and Bolivia [15,33]. All other earlier fossils referred to the vertebrates remain more or less heatedly debated [see review in 3,25,43], with the exception – to date – of the recently discovered *Myllokunmingia* and *Haikouichthys*, from the Lower Cambrian of Chengjiang, China, which have not yet been met with reservations to date [21,36,38]. The present article is a brief review of the most likely Cambrian vertebrates – at any rate, those which have not been demonstrated to be anything else –, with special reference to the anatomy of *Myllokunmingia* and *Haikouichthys*.

2. Vertebrate characters

The debates about the nature of many of the Early Palaeozoic isolated remains occasionally referred to vertebrates illustrate the difficulty of recognizing vertebrate characters in fragmentary fossil material. Currently, there is no better diagnose of the vertebrates

than that based on two developmental characters; namely, the presence of neural crests and epidermal placodes, which are unique among metazoans [2,29,45], although putative, non-migrating, neural crest cell precursors may be present in cephalochordates [19,20]. Neural crest cells are the source for many unique vertebrate characters, such as odontogenic tissues of the dermal skeleton and the branchial skeleton, and play a major role in the development of the skull. Epidermal placodes are involved in the formation of the major vertebrate sensory organs, such as the olfactory, optic and otic capsules, and the lateral line system. Although these embryonic structures cannot be directly observed in fossils, their adult derivatives can be regarded as good evidence for their presence. Even a small dermal bone fragment from the Ordovician, may display dentinous tubercles, which are evidence for neural crest cells, and lateral line grooves, which are evidence for placodes. This inference is nevertheless difficult to make in certain fossils, such as euconodonts or fossil lampreys and hagfish, when there are doubts as to their hard tissue homology, or when the neural crest and placodal derivative are only preserved as carbonaceous imprints.

3. The euconodonts

Since the discovery of articulated specimens of the euconodonts *Clydagnathus* in the Carboniferous of Scotland and *Promissum* from the Ordovician of South Africa [5,14], the affinities of this long-enigmatic taxon has been regarded as settled by many authors. The large, paired eyes, chevron-shaped myomeres, and caudal fin radials, suggested that euconodonts are either crown-group vertebrates (i.e. any descendant of the youngest common ancestor of all extant vertebrates; Fig. 1) [1,11,12,23,43], sister-group to the crown-group vertebrates, or more closely related to cephalochordates than to any other taxon [27,28]. Yet attempts at homologizing the hard tissues of the euconodont denticles with typical vertebrate hard tissues (enamel, dentine, bone) [10–12] have failed to convince the entire community of vertebrate palaeontologists [27,35]. Nevertheless, the few other characters that can be observed as soft tissue imprints in the head and body of the two, best preserved articulated euconodonts rather accord with vertebrate anatomy [11,24].

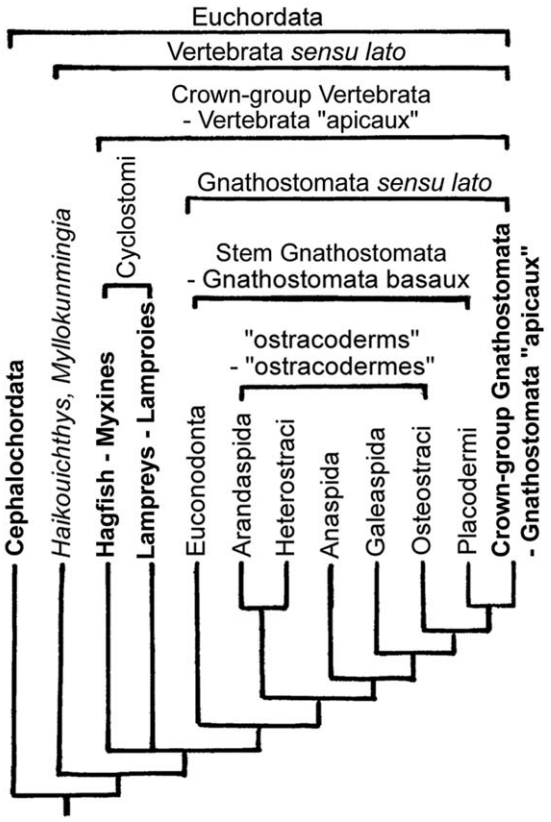

Fig. 1. One of the currently considered euchordate phylogenies, with *Haikouichthys* and *Myllokunmingia* added as stem vertebrates (i.e, the fossil sister-group to crown-group vertebrates). Terminal taxa in bold have extant representatives. Higher taxa (grades and clades) mentioned in the text are indicated above the brackets.
Fig. 1. L'une des phylogénies récentes des Euchordés, avec *Haikouichthys* et *Myllokunmingia* ajoutés en position de Vertébrés basaux (groupe-frère fossile des Vertébrés « apicaux »). Les taxons terminaux en gras ont des représentants actuels. Les taxons de rang supérieur (grades et clades) mentionnés dans le texte sont indiqués au-dessus des accolades.

The position of euconodonts as the sister-group to 'ostracoderms' and gnathostomes (i.e. gnathostomes *sensu lato*, or 'total group gnathostomes'; Fig. 1) in most current phylogenies is largely imposed by assumptions about the presence of certain characters such as extinsic eye muscles or gills [11]. Since euconodonts are known from the Late Cambrian to the Triassic, they are thus regarded – yet not unanimously so – as the most likely representatives of the Cambrian vertebrates [43].

4. Anatolepis

Anatolepis is represented by minute, three-layered phosphatic fragments from the Late Cambrian and Early Ordovician of North America and Greenland, which were first tentatively referred to the vertebrates [4]. This assigment has been debated, but recent histological studies of this taxon apparently support its vertebrate affinity to some extent. In particular, the tubercles of its ornamentation are made up by a canalicula-bearing hard tissue that agrees somewhat with the structure of vertebrate dentinous tissues [42–44]. In contrast, none of the *Anatolepis* fragments recorded to date shows any trace of a sensory-line system, nor do they show any morphological feature which would agree with the dermal plates of 'ostracoderms' and gnathostomes in general. Tube-shaped *Anatolepis* fragments have also been compared to gill denticles of certain living sharks [43]. The question of the affinity of *Anatolepis* may only be settled by the discovery of articulated specimens.

5. The implications of vertebrate phylogeny

During the past ten years, a number of phylogenetic analyses of the major living and fossil vertebrate groups have been carried out, and all of them resulted in a tree where the living hagfish and lampreys show a more basal divergence than the 'ostracoderms' (a grade of fossil, armoured jawless vertebrates, currently included in the gnathostomes *sensu lato*; Fig. 1) [11,12,16,23–25,36,38,41,43]. Contrary to recent molecular sequence-based trees, which show a strong support for the cyclostome clade (hagfish + lampreys) [9,18,31], morphology-based trees always support a closer relationship of lampreys to the gnathostomes, than to hagfish (paraphyletic cyclostomes) [11,23,24,41]. Since there is no evidence that hagfish and lampreys have ever possessed an extensively calcified skeleton, the implication of cyclostome paraphyly is that the common ancestor to all vertebrates had no calcified skeleton, which thus appeared after the divergence of lampreys [12]. This suggests that the pre-Ordovician vertebrate fossil record of the vertebrates would essentially occur under exceptional conditions of fossilisation, which allow soft-tissue preservation, such as in the Burgess Shale or the Chengjiang area (see below). However, this, alone, cannot explain the scarcity of the typical, undisputable calcified vertebrate remains before the mid-Ordovician and their absence from the Cambrian. There are probably other, biogeographical or environmental reasons for this lack of record [41].

6. The Burgess Shale euchordates and 'vertebrates'

Presumed euchordates (i.e. cephalochordates + vertebrates; Fig. 1), or even vertebrates, all preserved as imprints, have been recorded from the Middle Cambrian Konservat-Lagerstätte of the Burgess Shale in Canada. The most often-cited of them is *Pikaia gracilens*, which has been widely popularized as either a cephalochordate, or some kind of vertebrate 'precursor' [8,17]. However, *Pikaia* shows no unambiguous character of either vertebrates or even euchordates. Its overall body shape recalls that of the cephalochordates, but its myomeres are not clearly chevron-shaped and may have looked more like those of the yunnanozoans [30]; its paired tentacles vaguely recall those of hagfish [25], but hagfish tentacles show no basal swelling, contrary to those of *Pikaia*. In addition, there is no evidence for any gill-like structure, and the presumed, oval-shaped pharyngeal cavity seems to be dorsal in position. Another, unnamed Burgess Shale fossil has been tentatively referred to the vertebrates and compared to a larval lamprey [22,39,43], but the examination of this single specimen also provides no clear evidence for its euchordate affinity, except perhaps for its chevron-shaped myomeres, which, however, seem to point backwards.

7. The Chengjiang euchordates and vertebrates

The Lower Cambrian Konservat-Lagerstätte of Chengjiang, China, yields a number of well-preserved fossils which have been regarded as either crown-group vertebrates (*Haikouichthys, Myllokunmingia*) [21,26,36,38], or possible stem-vertebrates, stem-euchordates, and even stem-chordates (*Yunnanozoon, Haikouella*) [6,7,13,19,30,40]. The yunnanozoans *Yunnanozoon* and *Haikouella* are very similar in aspect and have recently been regarded as 'naked', close rela-

tives of vetulicolans, and stem deuterostomes [37]. Both *Yunnanozoon* and *Haikouella* possess a large, laterally compressed body, an elongate branchial region with six gill arches, and possibly sensory capsules. However, their myomeres are not chevron-shaped, and the structures referred to as gill arches and 'gill rays' display an unusual, segmented structure [6,30]. Morever, the 'gill rays' are lateral to the gill arches, and possibly external [30,37]; that is, surprizingly gnathostome-like. The recent, detailed re-examination of *Haikouella* nevertheless provides convincing arguments in favour of its position as a basal vertebrate [30].

Haikouichthys ercaicunensis and *Myllokunmingia fengjiaoa* were initially described on the basis of two specimens which only differ by a few, ambiguous characters [38]. These two, monospecific genera have recently been synonymized as *Myllokunmingia* [21], but this is not unanimously accepted [36]. Both species display an elongate body, which shows imprints of chevron-shaped myomeres, and a head, with a relatively short branchial region composed of six filamentous gills (Fig. 2D–F). The recent discovery of about 500 specimens referred to *Haikouichthys* provided additional evidence for vertebrate characters [36]. Several of these specimens are dorsoventrally compressed and show the head in dorsal view (Fig. 2A–C). It distinctly shows paired eyes and a dorsomedially placed, probably paired, olfactory organ. The presence of otic capsules is still unclear, but probable. The anterior margin of the head displays paired lobes which recall the endoskeleton of the upper lip of larval lampreys. The surroundings of the sensory capsules form a smooth surface, which suggests the presence of some kind of either cartilaginous or fibrous braincase, like that of hagfish, and show a conspicuous constriction behind the optic capsules. Behind the sensory capsules, and dorsally to the gill impressions, there is a series of irregularly-shaped, often sinuous stains which have been interpreted as possible arcualia of the axial

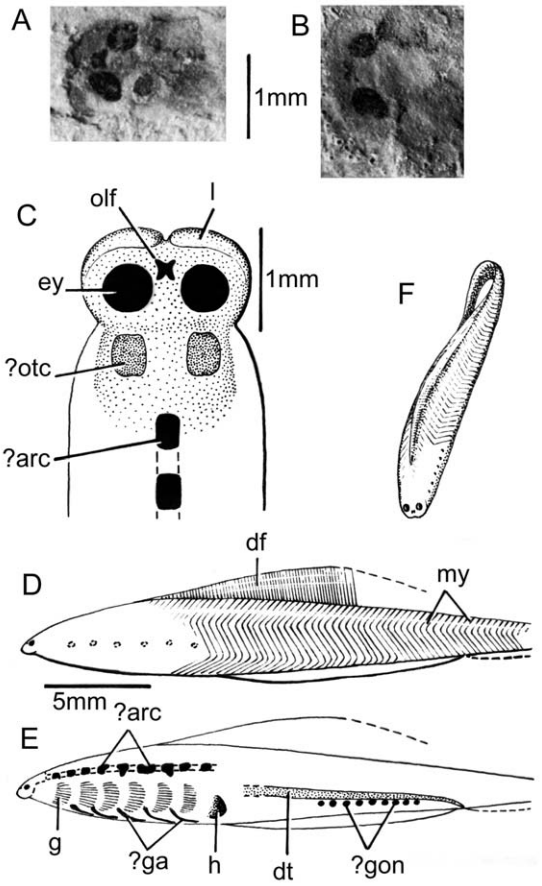

Fig. 2. *Haikouichthys ercaicunensis* Luo, Hu & Shu, 1999, Qiongzhusi Formation, Lower Cambrian, Haikou, Chengjiang area,Yunnan, China. A, B, heads in dorsal view; Early Life Institute, Xi'an, China (reproduced with the permission of Degan Shu, Xi'an, and Nature Publishing Group for A). C, attempted reconstruction of the imprints of the head in dorsal view (stippled: smooth area suggesting a fibrous braincase); D, attempted reconstruction of the body in lateral view (position of gill openings hypothetical); E, attempted reconstruction of some internal structures preserved as imprints, in lateral view; F, probable aspect in life. A, from [36]; C–F, based on data in [21, 36, 38]

?arc, presumed arcualia; **df**, dorsal fin; **dt**, digestive tract; **ey**, optic capsules; **g**, gills; **?ga**, presumed gill-arch elements; **?gon**, presumed gonads; **h**, imprint of the heart or pericardic cartilage; **l**, lobed upper lip; **my**, myomeres; **olf**, olfactory organ; **?otc**, presumed otic capsule.

Fig. 2. *Haikouichthys ercaicunensis* Luo, Hu & Shu, 1999, Formation de Qiongzhusi, Cambrien inférieur, Haïkou, région de Chengjiang,Yunnan, Chine. A, B, têtes en vue dorsale; Early Life Institute, Xi'an, China (reproduit avec l'autorisation de Degan Shu, Xi'an et de Nature Publishing Group pour A). C, essai de reconstitution des empreintes visibles dans la région céphalique, en vue dorsale (en grisé: surface lisse suggérant la présence d'un neurocrâne fibreux); D, essai de reconstitution du corps en vue latérale (la position des orifices branchiaux est hypothétique); E, essai de reconstitution de quelques structures internes conservées sous forme d'empreintes, en vue latérale; F, aspect probable de l'animal. A, tiré de [36]; C–F, fondé sur les données de [21, 36, 38].

?arc, arcualia présumés; **df**, nageoire dorsale; **dt**, tube digestif; **ey**, capsules optiques; **g**, branchies; **?ga**, éléments présumés d'arcs branchiaux; **?gon**, gonades présumées; **h**, empreinte du coeur ou du cartilage péricardique; **l**, lèvre supérieure lobée; **my**, myomères; **olf**, organe olfactif; **?otc**, capsule otique présumée.

skeleton [36] (Fig. 2C, E). These stains seem to be connected by a faint strand-shaped stain, which may be the trace of the notochord. Although cartilaginous arcualia (basidorsals and interdorsals) are present in lampreys, these stains in *Haikouichthys* are surprisingly large, widely spaced, and send off processes far ventrally, thereby recalling the cartilaginous branchial arches of lampreys. Moreover, these stains do not clearly extend into the posterior, myomere-bearing part of the body. Another, peculiar feature has been described in a specimen referred to *Myllokunmingia*, and consists of loop-shaped imprints extending from the branchial region into the body [21], which may be imprints of the segmental blood vessels within the myocommata. In both taxa, a large stain behind the gill series may be regarded as the trace of either the heart or a pericardic cartilage (Fig. 2E). As a whole, *Haikouichthys* (and probably *Myllokunmingia*) displays acceptable evidence for placodes in the form of optic (yet a lens is still unknown), olfactory, and possibly otic capsules, but less obvious evidence for neural crest tissues, except perhaps for a cartilaginous branchial skeleton. Three characters, however, may be at odds with what we know of crown-group vertebrates. The presence of serially arranged gonads has been suggested in both *Haikouichthys* and *Myllokunmingia* (Fig. 2E) [21,36], and in the yunnanozoans [6,30]. Although this might also be an artefact due to the compression of the digestive tract by the overlying myomeres, this retention of this cephalochordate-like condition, if confirmed by further discovery, would exclude these Chengjiang taxa from the crown-group vertebrates (assuming that serially arranged gonads are a general euchordate character, lost only once in the crown-group vertebrates). Ventrally to the gill series, there is a series of possibly calcified, oblique bars, the orientation of which recalls that of the ceratobranchials of the gnathostomes (Fig. 2E) [36,38]. These may be part of the branchial skeleton (but certainly not ceratobranchials) and have no clear homologue in the branchial skeleton of extant jawless vertebrates. Finally, the structure interpreted as a dorsal fin is at odds with that of the dorsal fin in all other known vertebrates, by its numerous, rostrally tilted radials (Fig. 2D) [36,38], that are seen in only a few specimens, but recently regarded as a possible fabric of the sediment [21]. The presence of other fins remains questionable. There is no clear evidence for paired fins, but a median ventral, preanal skin fold may be present (Fig. 2D), like in hagfish and larval lampreys. The tail is currently unknown.

As a whole, and provided that we are not misled by an extraordinary case of convergence, the overall aspect of *Haikouichthys* (and probably *Myllokunmingia*) may have been somewhat similar in aspect to that of a larval lamprey (Fig. 2F), yet many characters remain too uncertain to decide whether it is a stem vertebrate, or a crown-group vertebrate.

8. Conclusion

To date, undisputable crown-group vertebrates remain unknown before the Early Ordovician. However, some Cambrian taxa are more and more likely to be either actual crown-group vertebrates, or stem-vertebrates. During the past decade, new articulated euconodont material has provided acceptable evidence for the vertebrate affinities of this long-enigmatic group, although the homology of euconodont hard tissues and the conventional vertebrate hard tissues remains debated, as it is also the case for the hard tissues of the Late Cambrian–Early Ordovician skeleton fragments referred to *Anatolepis*. Currently, the best documented and most informative, putative Cambrian vertebrates are *Haikouichthys* and *Myllokunmingia*, from the Early Cambrian of Chengjiang, China, whose overall anatomy is quite suggestive of that of a larval lamprey, yet certain of their characters remain at odds with the structure of crown-group vertebrates. Although they show evidence for placode- and neural crest-derived organs (olfactory organ, eyes, ?otic capsules, branchial arches) which suggest vertebrate affinities, it is still uncertain whether these two taxa are stem-vertebrates or crown-group vertebrates. If their presumed, serially arranged gonads are confirmed, then would rather be stem-vertebrates and thus fill the morphological gap between the cephalochordates and vertebrates (Fig. 1). At any rate, these Early Cambrian forms strongly suggest that the divergence between cephalochordates and vertebrates occurred before the Cambrian; that is, in better agreement with recent molecular clock data (notwithstanding the numerous biases in molecular clock inferences [34,41]), which indicate a date of about 750 Myr for this divergence [18], and about 550 Myr for the cyclostome-gnathostome divergence [18,32].

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