

An experimental morphological investigation into the hydrodynamics and locomotion of the Palaeozoic jawless vertebrates *Poraspis*, *Errivaspis* and *Ateleaspis*

Benjamin Evan Davies

Ostracoderms represent a crucial phase of vertebrate evolution during which many of the characters that are now taken as typical vertebrate features appeared for the first time. While recent work has gone a long way to clarifying relationships and patterns of character acquisition, understanding of the ecology and biomechanics of these early fishes has lagged behind. Very little is known, for example, about how they swam. This thesis consists of two investigations, a new reconstruction of the caudal fin of *Errivaspis waynensis*, and an experimental investigation into the hydrodynamic characteristics of three ostracoderm species, *Poraspis polaris*, *Errivaspis waynensis* and *Ateleaspis tessellata* using models mounted in a wind tunnel.

Errivaspis waynensis has previously been reconstructed with an elongate ventral tail lobe or “hypocercal” tail, based on a number of mouldic specimens held at the Natural History Museum London. These specimens were examined and it was concluded that traditional reconstructions of an extended ventral lobe are not upheld by the material and that the previously interpreted extreme hypocercal morphology is an artefact of missing material in the specimens. A new reconstruction for the caudal fin of *Errivaspis* is proposed with the ventral margin slightly longer than the dorsal margin.

The experimental data from the wind tunnel tests suggested that *Ateleaspis* was more suited to a benthic lifestyle than *Poraspis* or *Errivaspis*, being able to utilize ground effect to swim very economically while close to the bottom and having a morphology that would permit it to turn rapidly in the vertical plane. *Poraspis* was found to have a morphology adapted to minimising drag for greater hydrodynamic efficiency and executing rapid manoeuvres in mid water column. *Errivaspis* was found to have a morphology with adaptations for both benthic and mid water swimming suggesting that it was a generalist.

Contents

Chapter 1,	
Introduction to the project	7
Ostracoderms as a group, importance and unanswered questions	7
Morphological anomalies in ostracoderms	7
Ecological role	8
Choice of genera for investigation	9
Morphological characteristics of Heterostraci and questions raised	10
Morphological characteristics of Osteostraci and questions raised	12
Methods of research	15
Thesis structure	20
Chapter 2,	
A new reconstruction of the caudal fin of the Devonian jawless vertebrate, <i>Errivaspis waynensis</i> , Pteraspidiformes Heterostraci	21
Abstract	21

Introduction	22
Caudal fin morphologies observed in extant fish and implications for swimming	22
Previous interpretations of the caudal fin in <i>Errivaspis</i> and other ostracoderms	26
Inherent uncertainties surrounding postcranial morphology in ostracoderms	31
Materials and methods	32
Method of measurement	33
P17477 part and P17478 counterpart	34
P17485 part and P17486 counterpart	37
P17521 part and 17522 counterpart	38
P16789-90	41
P 17527 part and P17528 counterpart	41
Analysis of postcranial measurements	43
Conclusions	47

Chapter 3,
A wind tunnel based investigation into the hydrodynamic
characteristics of three Palaeozoic jawless vertebrates, *Poraspis*,
Errivaspis and *Ateleaspis*. 50

Abstract 50

Introduction 51

Anatomical and hydrodynamic questions about ostracoderms 56

Anatomical questions about ostracoderms 56

Hydrodynamic considerations 59

Ecological questions raised 61

Previous research 64

Comparisons with extant species 64

Previous experimental interpretations of hydrodynamic characteristics
65

Materials and methods 66

Use of wind tunnels to interpret hydrodynamic behaviour of
ostracoderms 66

Dynamic similitude 68

Modifications to models reflecting latest research	63
Setup and experimental procedure	72
Setup of ground effect experiments	73
Limitations and assumptions	76
Summary of potential sources of error and their effects	77
Results	80
Effect of variation in angle of attack on <i>Poraspis</i> , <i>Errivaspis</i> and <i>Ateleaspis</i> (fixed velocity test)	80
Effect of variation in velocity on <i>Poraspis</i> , <i>Errivaspis</i> and <i>Ateleaspis</i> (fixed angle tests)	83
Impact of ground effect on <i>Ateleaspis</i> and <i>Errivaspis</i> (fixed angle tests)	87
Discussion	93
<i>Ateleaspis</i>	93
<i>Poraspis</i>	94
<i>Errivaspis</i>	95

Implications for related taxa	96
Station holding	101
How this work relates to previous interpretations	102
Conclusions	103
Further work	105
Appendix	107
Analysis of trouble shooting data	107
Detailed clarification of wind tunnel equations	112
Moment	112
Pressure	112
Mode of manufacture of the models	114
References	115

Chapter 1

Introduction to the project

Ostracoderms as a group, importance and unanswered questions

Ostracoderms, are a series of radiations of extinct jawless fishes, often characterised by a covering of plates or scales which allows their external anatomy to be reconstructed in detail. They represent a crucial phase of vertebrate evolution during which many of the characters that are now taken as diagnostic vertebrate features are appeared for the first time. They also formed a large and successful radiation of early vertebrates which lasted for 100 million years showing considerable diversity of body form and adaptive potential (Mark-Kurik 1992). While recent work has gone a long way to clarifying phylogeny and patterns of character acquisition of these early fish, little is known about their biomechanics, ecology or niche differentiation.

Morphological anomalies in ostracoderms

There are a number of morphological characteristics observed in ostracoderms for which there are no analogues in extant fish. These raise serious questions over their mode of locomotion.

Extant fish and cetaceans use pectoral fins to manoeuvre, maintain trajectory against moment forces acting upon them and in some cases to hold station on the bottom. Pectoral fins are completely absent in many ostracoderms, notably heterostracans. The lack of pectoral fins raises questions about how they maintained control over their trajectory while swimming in mid-water column. A major objective of this project was to identify forces likely to be acting upon ostracoderms that lacked pectoral fins and the likely consequences of their apparent inability to correct for them.

Ostracoderms have evolved a diverse array of head shield morphologies, some bizarre and seemingly extreme. Very little is known about the hydrodynamic effect of these morphologies or whether their evolution was driven by pressure to produce the optimum morphology for hydrodynamic performance. There is also the question of whether adaptations relating to hydrodynamic performance would promote stability, manoeuvrability, or hydrodynamic efficiency.

While well preserved ostracoderm head shields are commonplace, articulated postcranial material indicating morphology prior to death is rare, particularly with respect of the caudal fin. Morphology of the caudal fin in marine animals has extensive implications for their hydrodynamic behaviour. Where there were uncertainties about the morphology of any of the genera selected for the hydrodynamic tests it was necessary to address them. This led to the production of a new reconstruction of the caudal fin of *Errivaspis waynensis* based on examination of the material described by White (1935).

Ecological role

While most major ostracoderm bearing faunas have been identified as fresh water or marginal marine little has been done to identify their role within these ecosystems. Dollo (1910) drew comparisons between osteostracans and extant benthic rays, arguing that they probably had a similar lifestyle due to their similar cross section and upward facing eyes. On the other hand experimental testing has suggested that Osteostraci were capable of swimming in mid water column (Bunker & Machin 1991). *Errivaspis* has been identified in the past as both being benthic (Dollo 1910) and free swimming (Kermack 1943, Belles-Isles 1987). To date no clear consensus has emerged on the lifestyle of these early fishes.

Choice of genera for investigation

The principal objective of this project was to investigate the hydrodynamic characteristics of representative members of the major ostracoderm groups, and likely implications for their ecology. The choice of subjects for this investigation was restricted by ability to reliably determine their external morphology. This made it necessary to select forms with head shields and extensive dermal scales, specifically those genera where articulated postcranial remains were available. Genera were also selected on the basis that they embodied many of the morphological anomalies that raise questions about ostracoderm locomotion. The genera selected for the project to focus upon were the two heterostracans *Poraspis polaris* and *Errivaspis waynensis* and the osteostracan *Ateleaspis tesselata*. The inclusion of *Poraspis* and *Errivaspis* meant that the investigation would compare representatives of the cyathaspids and Pteraspidiformes respectively. This was considered important because it would provide a comparison between examples of both of the major groups of Heterostraci. It would have been desirable to include a galeaspid genus in the study but no detailed description of postcranial material was available at the outset of the project.

It is thought the pteraspidiformes filled many of the niches vacated by the cyathaspids as the latter declined by the early Devonian, except in Siberia where the Amphiaspida remained abundant until the Pragian (Janvier 1996). Novitskaya (2007) concluded that cyathaspids appeared in the Silurian and achieved the peak of diversity in the first half of the Early Devonian as did Pteraspids. Cyathaspids are absent from later beds. Pteraspids persisted to the end of the Early Devonian, although they sharply decreased in number in the second half of the Early Devonian. Novitskaya (2007) further proposed that both major heterostracan groups became extinct due to archaic locomotor adaptations and insufficient protection from predators.

In summary, little is known about the ecological interrelationships and niche differentiation between cyathaspids, pterapidiformes and osteostracans, despite the fact

that they occur across many of the same horizons. The objective of the investigation was to conduct experiments that would produce constraining data on the hydrodynamic behaviour of a representative of each group. It was hoped that the results might provide some indicators about the hydrodynamic and ecological differences between the major ostracoderm groups.

Morphological characteristics of Heterostraci and questions raised

Heterostracans are characterised by a pair of common external branchial openings on either side of the head armour. The dermal plates are made of dentine and aspidine and display a peculiar honeycomb like structure (White & Tombs 1983). The two major groups are the cyathaspidiforms, of which *Poraspis polaris* is a member, and the Pteraspidiformes, to which *Errivaspis waynensis* belongs. They were chosen to provide a generalised representative of each group.

An elongate streamlined head shield is found in many cyathaspids like *Torpedaspis* (Broad & Dineley 1973) and *Anglaspis* (Blieck & Heintz 1983) as well as the species that was used in these experiments, *Poraspis polaris*. This body form would be expected to be optimal for minimising drag, rather than producing lift based on the hydrodynamic principles outlined by Hertel (1966) and later Videller (1993). *Poraspis polaris* was selected as a species that epitomised this “fusiform” morphology. Conversely, in some cyathaspids the head shield forms a delta shape as in *Eglonaspis* (Novitskaya 1986). It is streamlined and dorsoventrally compressed, and appears to have a morphology optimised for lift generation.

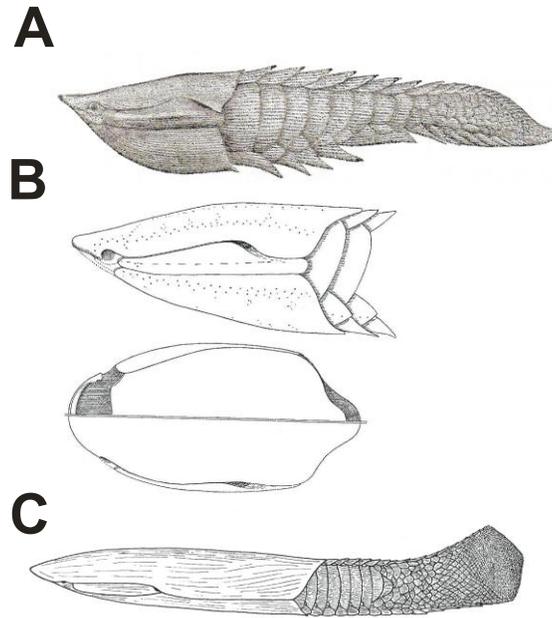


Fig. 1 A comparison of morphologies in cyathaspid genera □A. *Anglaspis* from Kiaer (1932), □ B. *Poraspis* from Kiaer & Heintz (1935), □C. *Torpedaspis* from Broad & Dineley (1973).

Pteraspids such as *Errivaspis waynensis* typically have a head shield of oval cross-section that is wider laterally than it is dorsoventrally. This morphology is neither optimal for minimising drag nor generating lift but might combine both characteristics to some extent. *Errivaspis waynensis* was chosen for this study in part because it had this cross-section of unknown functional significance. For contrast psammosteid heterostracans have a much more dorsoventrally flattened morphology that could be interpreted as lift inducing. The head shield of *Drepanaspis* appears to be flattened dorsoventrally and well streamlined (Gross 1963, Tarlo 1964). The wing-like lateral structures on the head shield of *Pycnosteus* point downwards, effectively creating an anedral wing (Mark 1961). This morphology reduces stability while producing lift and is therefore favoured for fighter aircraft which are designed for manoeuvrability. The fact that the head shield has evolved in this way implies that dynamic instability may have been a factor in these fish manoeuvring.

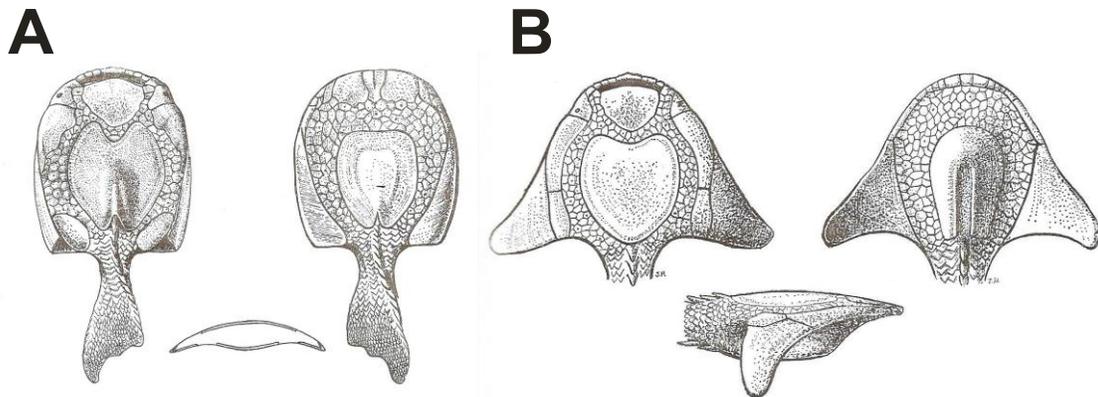


Fig. 2. Wing-like morphologies found in psammosteoid heterostracans, □A. *Drepanaspis* from Tarlo (1964). □B. *Pycnosteus* from Tarlo (1964).

Morphological characteristics of Osteostraci and questions raised

The osteostracans have a perichondrally ossified endoskeleton and an exoskeleton of cellular bone (Ritchie 1967). The dorsal surface of the head shield is covered with median and lateral depressions which are covered with free polygonal dermal platelets of bone (Janvier 1996). They are characterised by a triangular cross-section with a broad flat ventral surface. The head shield of Osteostraci is typically of a semi-circular morphology as in *Hemicyclaspis* (Stensio 1932), *Hemiteleaspis* (Westoll 1945), *Ateleaspis* (Ritchie 1967), *Hirella* (Heintz 1969) and *Aceraspis* (Janvier 1981). There are cornuate forms with a very large caudal span of the head shield, some of which display well preserved pectoral fins.

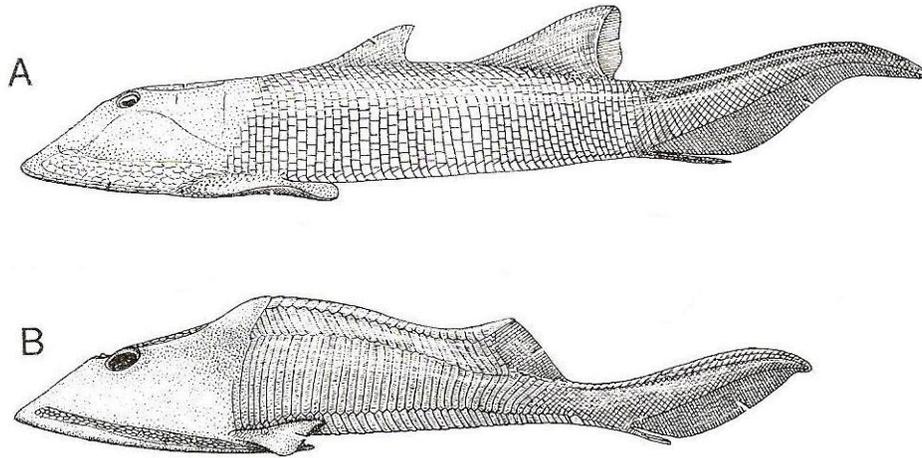


Fig. 3. Morphologies of osteostracans, □A. *Ateleaspis*, from Janvier (1996). □B. *Zenaspis*, from Janvier (1996).

While the morphological characteristics of osteostracans have been interpreted in the past as adaptations for a benthic lifestyle, no experimental data currently supports this. It was decided to research *Ateleaspis tessellata*, an osteostracan thought to be plesiomorphic, to differentiate it functionally from the two heterostracan genera. It was hoped that by doing so to identify the functional significance of the osteostracan body plan and identify hydrodynamic variables that might have driven their evolution.

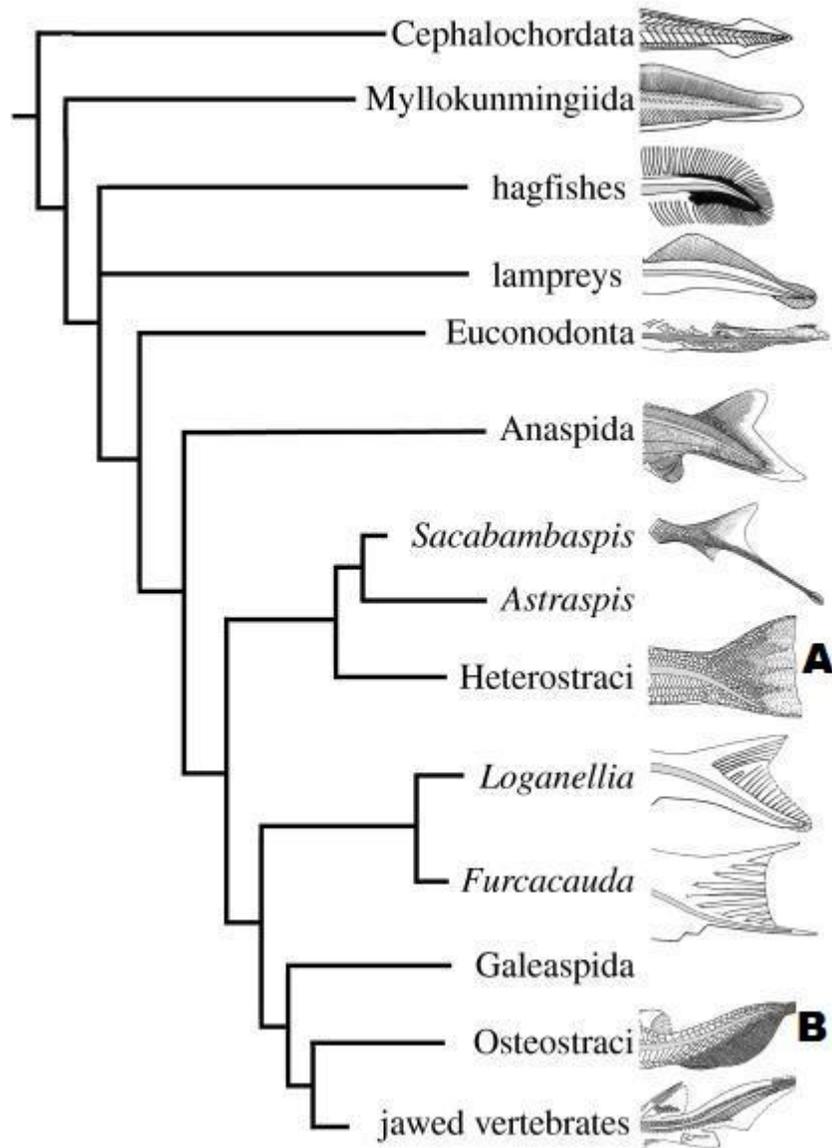


Fig. 4, The taxa selected for this project: *Poraspis polaris*, *Errivaspis waynensis* and *Ateleaspis tessellata* are all stem gnathostomes. □A. *Poraspis polaris* and *Errivaspis waynensis* are heterostracans. □B. *Ateleaspis tessellata* is a plesiomorphic osteostracan. Both groups represent highly diverse and adaptive radiations that have no extant representatives. After Pradel *et al.* (2007).

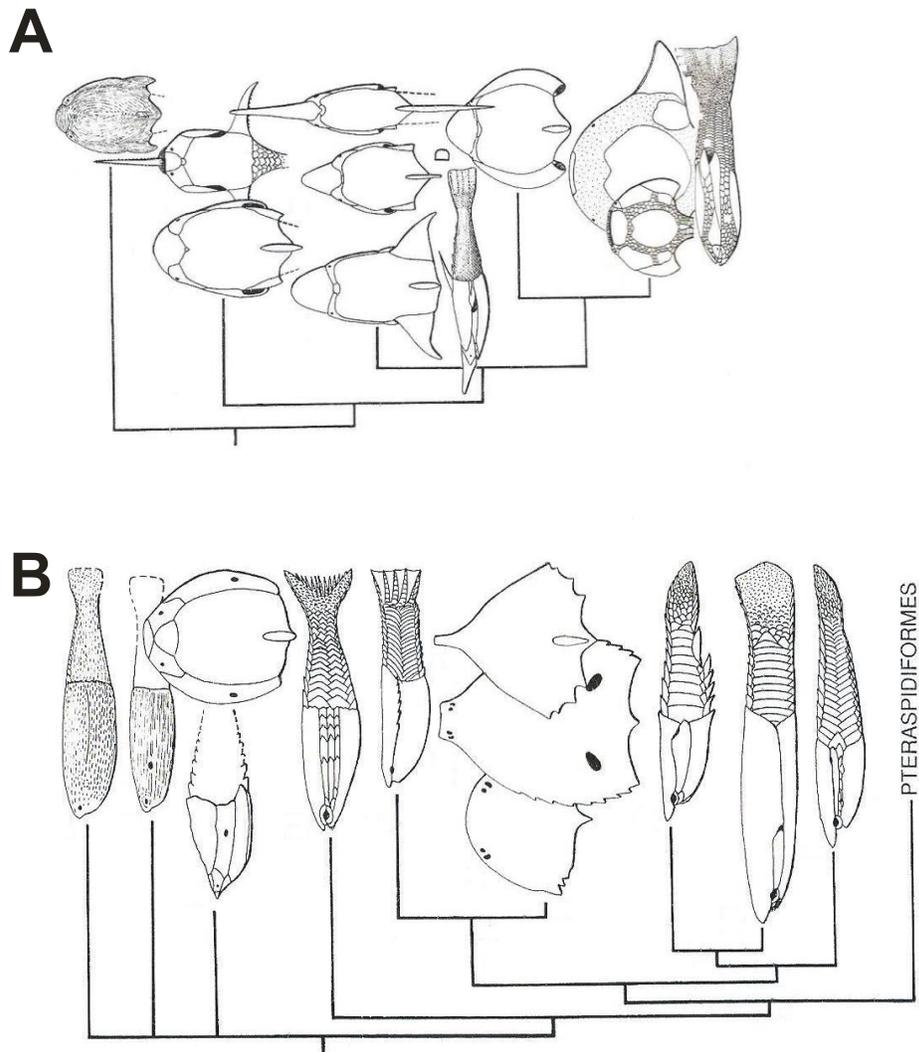


Fig. 5, The two major heterostracan groups are the cyathaspidiformes and pteraspidiformes. □A. *Poraspis polaris* is a cyathaspid. □B. *Errivaspis waynensis* is a pteraspidiform. After Janvier (1996).

Methods of research

The experimental aspects of this project necessitated extensive interdepartmental cooperation between the Geology Department and the Engineering Department to gain

access to experimental facilities and guidance upon experimental methods. Three undergraduate modules and one postgraduate module in fluid mechanics were attended in order to gain a greater understanding of the principles involved. The Engineering department co-operated at all stages of this project, providing supervision of use of their facilities and manufacturing components necessary for many of the experiments.

Beyond what can be undertaken using theoretical techniques such as formulae, there are two approaches or methods that can be used to solve problems in fluid mechanics, namely experimental and numerical methods. Experimental methods include the use of models in wind tunnels or flume tanks. Such techniques have been used extensively in palaeontology in the past, including in the study of ostracoderms (Kermack 1943, Bunker & Machin 1991, Bottela & Farina 2008). They are regarded in engineering circles as being the most reliable approach but there are difficulties associated with measuring the results. One of the most serious disadvantages of experimental techniques for large objects such as aircraft and ships is calculating the effects of scaling the model to the subject. The fact that the subjects of this study were of such a size that a life-size model could easily be used was seen to strengthen the case for such an approach.

Numerical methods involve the use of computer fluid dynamics. The application of numerical methods to extant fish is in its infancy, although there are precedents. The idea to apply such an approach to extinct vertebrate would bring the methodology into new territory. There are uncertainties inherent in the numerical approach, including truncation errors and boundary condition problems. The overwhelming advantages requiring that such an approach be considered were that such simulations are not restricted to linearity and that more complex physical processes can be treated. There is also a large reduction in cost which increases the number of simulations that can be run. The Engineering Department has access to the FLUENT software which is a finite volume package used extensively in aeronautics and industry. Many CFD problems can readily be tackled using two-dimensional simulations such as problems involving flow in pipes or aerofoil. This type of simulation is straightforward and not

particularly time consuming, permitting it to be used repeatedly. A computer package called GAMBIT is used to produce a two-dimensional outline of the subject. A box is created enclosing the outline and GAMBIT is used to create an inflow and an outflow at alternate ends. The area surrounding the fish model is meshed using a fine unstructured mesh. The simulation works in much the same way as a model suspended in a flume tank, but has the advantage of being cheaper, more easily manipulated and not requiring the facilities. Computer fluid dynamics packages have been used in the past to investigate the mechanical properties of the skulls of reptiles (Jasinoski *et al.* 2007) and the hydrodynamic properties of graptolites (Rigby & Tabor 2006). These simulations utilised larger models or specimens than those used in this investigation that can be mapped by low resolution scanners to produce a three-dimensional mesh. While simulations were conducted with two-dimensional meshes it ultimately proved impossible to gain access to the type of high resolution scanner necessary to produce an accurate three-dimensional mesh of a life size ostracoderm model. Various options for using industrial and medical scanners were examined but none that could be accessed in the UK within the practical budget for the project had a sufficiently fine resolution. This left the alternative of experimental methods for investigating the hydrodynamic properties of ostracoderms.

Models of three ostracoderm genera namely *Poraspis polaris*, *Errivaspis waynensis* and *Ateleaspis tessellata* were manufactured for use in flow experiments. The Engineering Department has extensive facilities for experimental hydrodynamic testing, including a number of flume tanks and wind tunnels.

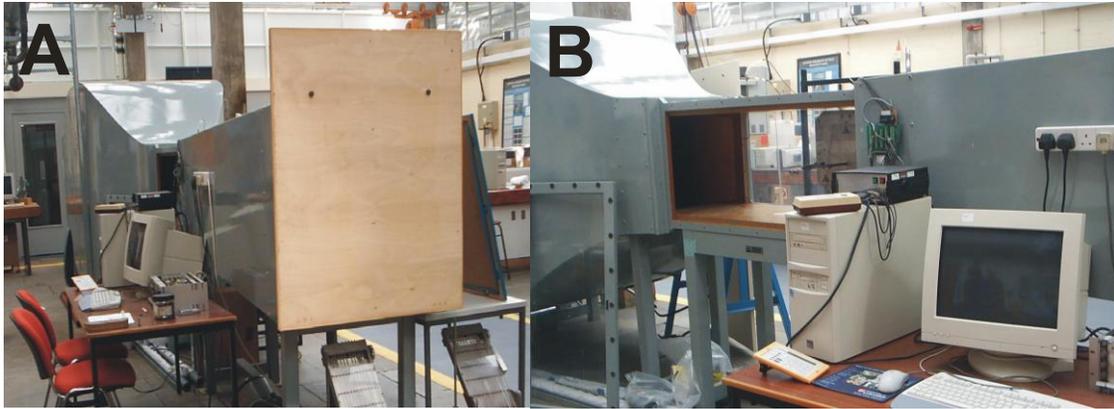


Fig. 6, The wind tunnel and apparatus used for the hydrodynamic studies, owned by the Engineering Department of the University of Leicester. □A. View of the wind tunnel. □B The computer used to run the LABVIEW software used to measure forces on the balance.

The fact that the subject of the study is an aquatic animal makes the use of a flume tank logical. Hydrodynamic tests can, however be carried out using wind tunnels if the velocity is adjusted to allow for the difference in viscosity between air and water. It was decided to use a wind tunnel because of the availability of the software package LabVIEW, which can be used to record forces acting on a balance, upon which the model is mounted. This made the matter of calculating the forces acting upon the model much easier. The LabVIEW software was used to measure the effects of lift, drag and moment upon the models in the pitching axis and yawing axis. Investigation into the hydrodynamic characteristics of the three chosen ostracoderm taxa ultimately led to questions about whether close proximity of the fish to the bottom would result in any ground effect induced forces. In order to investigate the effects of these forces a conveyer belt was constructed over which the models could be mounted in the wind tunnel. This was necessary in order to simulate the physical effects of movement between the fish and the bottom of the water column.

The investigation into the hydrodynamic characteristics of ostracoderms, involved a systematic approach to testing every physical variable that the software measured, or that could be varied in the experimental procedure. This resulted in a huge array of experiments many of which produced no data of any value other than to suggest future lines of investigation. The experimental procedures that form the basis of the third

chapter of this thesis are those that were found by practical application to produce the most informative data. By combining the conclusions of these procedures it was possible to build up a clear picture of the hydrodynamic characteristics of the three genera selected to form the focal point of this investigation.

Thesis structure

This thesis consists of three chapters including the introductory section. The second chapter is a new reconstruction of the caudal fin of *Errivaspis waynensis* which will ultimately be submitted to *Paleontologica Electronica*. The third chapter is an experimental investigation into the hydrodynamic characteristics of three ostracoderm species, *Poraspis polaris*, *Errivaspis waynensis* and, *Ateleaspis tessellata* using a wind tunnel which will ultimately be submitted to *Lethaia*. Some aspects of the second chapter have been written in *Lethaia* format to keep it consistent with the third chapter.

Chapter 2

A new reconstruction of the caudal fin of the Devonian jawless vertebrate, *Errivaspis waynensis*, Pteraspidiformes Heterostraci

Abstract

Errivaspis waynensis is an extinct jawless fish, belonging to the Heterostraci, a morphologically and geographically diverse group of early vertebrates characterised by a covering of plates and scales. It has previously been reconstructed with an elongate ventral tail lobe or “hypocercal” tail, based on a number of mouldic specimens held at the Natural History Museum London, which show details of articulated postcranial material. In recent years several well preserved heterostracan tail fins have been found that have a symmetrical, or “homocercal” morphology, bringing previous interpretations into question. The specimens from which the hypocercal anatomy was originally interpreted, described by White (1935), are examined and a detailed analysis of this material, critically assesses previous reconstructions of the caudal fin. It is concluded that traditional reconstructions of an extended ventral lobe are not upheld by the material and that the strongly hypocercal morphology inferred previously is an artefact of missing material in the specimens. A new reconstruction for the caudal fin of *Errivaspis* is proposed with the ventral margin slightly longer than the dorsal margin that would be functionally similar to a “homocercal” or symmetrical caudal fin.

Introduction

The Heterostraci are an extinct group of jawless fishes characterised by head shields and extensive dermal scales composed of dentine and aspidin. They represent one of the most successful and morphologically diverse radiations of stem gnathostomes. While well preserved head shields are commonplace, articulated postcranial material and in particular well preserved caudal fins are rare. *Errivaspis waynensis*, previously identified as a species of *Pteraspis* is a generalised pteraspidiform heterostracan. It is one of the most common vertebrate fossils found in the Lochkovian (Devonian), of the sequence formerly identified as “Lower Old Red Sandstone” of the United Kingdom. Owing to the availability of a number of mouldic specimens preserving detail of extensive articulated postcranial scales, it has become the genus that has defined general interpretations of pteraspid postcranial morphology. The material in question was described by White (1935) as possessing an elongate ventral lobe on the caudal fin, or “hypocercal” tail. Popular illustrations of *Errivaspis waynensis* and some scientific ones continue to portray it with this feature (e.g. Morrissey *et al* 2004, Botella & Farina 2008). Since White’s description, a number of well-preserved heterostracan tails have been described which have a symmetrical morphology, and clearly do not have an extended ventral lobe.

Caudal fin morphologies observed in extant fish and implications for swimming

A range of tail morphologies are found in the heterostracans which correlate morphologically and perhaps functionally to the caudal fins of extant fish. It is necessary to examine the observed relationship between morphology, hydrodynamic effect and ecological role in extant species to understand the implications of various reconstructions. A caudal fin with an elongate dorsal lobe is called an epicercal tail. This condition is found in some extant sharks and extinct ostracoderms such as cephalaspids. A hypocercal tail is defined as a caudal fin with an elongate ventral lobe, the condition previously attributed to *Errivaspis waynensis*. The only extant group that

exhibits a similar tail morphology are flying fish Exocoetidae, which have a lower lobe slightly longer than the upper lobe. This feature seems to have evolved to facilitate leaping clear of the water to evade predators. Looking at the three winged flying fish *Parexocoetus brachypterus*, Shadwick & Pitman (2007) found that the enlarged lower lobe allowed a leaping fish to continue to accelerate even when the rest of its body was clear of the water. While the caudal fin of flying fish have similar proportions to those of some anaspids (Hopson 1974) and psammosteid heterostracans (Tarlo 1964) the difference between the length of the dorsal and ventral lobes is much less pronounced than in White's (1935) reconstructions of *Errivaspis* and the general morphology is different (Fig. 2). Extant lampreys have a protocercal caudal fin with two keel like lobes dorsal and ventral of the vertebral axis, which can vary in size and shape. They do not however correlate functionally to the hypocercal caudal fin of the type found in anaspids and thelodonts. Outside of the reconstructions of *Errivaspis* being assessed and the extant species mentioned the anaspids and thelodonts are the only aquatic vertebrates that exhibit hypocercal morphology.

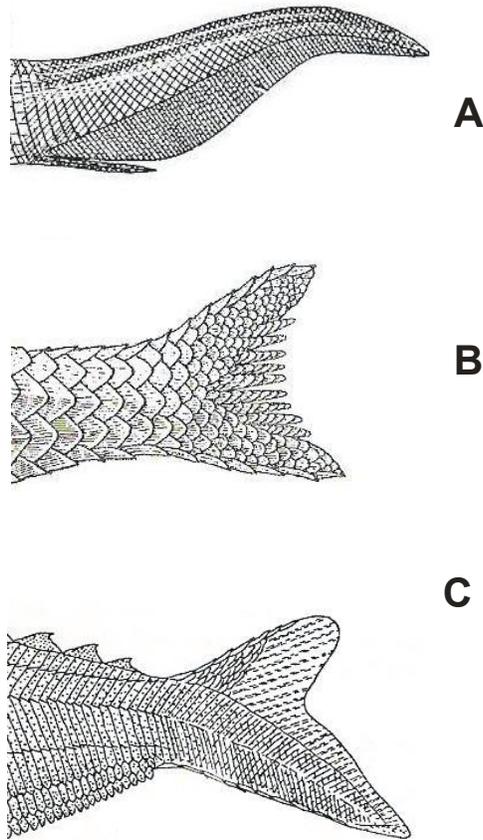


Fig 1. A comparison of caudal fin morphologies observed in extinct and extant fish. □A. The epicercal caudal fin is characterised by an elongate dorsal lobe. □B. The homocercal caudal fin is close to symmetrical and has dorsal and ventral lobes of equal size. □C. The hypocercal caudal fin has an elongate ventral lobe.

The homocercal tail is defined as a caudal fin with upper and lower lobes of equal proportions. It is found in fishes with a range of lifestyle from active species such as tuna to benthic forms with sedentary lifestyles. Species with homocercal tails, adapted for efficient, sustained cruising such as tuna, tend to have a caudal fin with a large dorsal span which are short dorsoventrally. Lauder (2000) found that the homocercal tail of the bluegill (*Lepomis macrochirus*) generated tilted and linked vortex rings with a central jet directed postero-ventrally resulting in an anteriodorsal reactive force. Extant species with longer homocercal caudal fins with a shorter span such as pike tend

to be adapted as accelerators (Woodward *et al.* 2006). The question of whether pteraspids had a hypocercal or homocercal tail is likely to have a critical impact on their locomotion and ecological niche. Species with an epicercal tail might provide some indicators as to how a homocercal tail would function. In extant species the epicercal tail creates posterior lift, usually to offset anterior lift. Harris (1936) demonstrated, using wind tunnels, that in the extant dogfish *Mustelus canis*, both the pectoral fins and epicercal tail generate lift. Alexander (1964) found that the epicercal tail in the dogfish *Mustellus canis* generated lift at the posterior end and negative pitch at the front which was counteracted by lift generated by the frontal part of the body. Lauder (2000) found that the epicercal tail could vary in effect according to mode of use. He found that the tail of the leopard shark *Triakis semifasciata* functioned according to the classical interpretation of the epicercal tail and generated lift. The tail of the sturgeon *Acipenser transmontanus* was found to have a more flexible dorsal lobe than that found in other species with an epicercal caudal fin. The result of this was that the upper lobe trailed the lower during the beat cycle. This caused the tail to generate propulsive forces orientated near the centre of mass of the body. This factor implies that the functional significance of an epicercal or hypocercal fin in an extinct species cannot necessarily be interpreted by external morphology alone.

There have been attempts made to infer the effect of the hypocercal caudal fin in extinct ostracoderms. Kermack (1943) investigated the hydrodynamic behaviour of *Errivaspis waynensis* using models in wind tunnels, and concluded that the body alone could generate enough lift to support the fish in water and that the hypocercal tail evolved to counteract this trend by producing anterior pitch. It has also been suggested that this type of tail evolved in anaspids to generate negative pitch, as an adaptation to aid feeding on the bottom (Parrington 1958). Ritchie (1964) concluded that the hypocercal anaspid tail would produce positive pitch. Hopson (1974) proposed that the pitch created by the tail might have counteracted the forces produced by the paired fins, which are believed to have been present in all anaspids (Ritchie 1964). While the epicercal tail is generally agreed to generate posterior lift based on experiments with

extant species, no clear consensus has emerged on the significance and hydrodynamic effects of the hypocercal tail in early vertebrates.

The morphology of the caudal fin in *Errivaspis* has extensive implications for the type of propulsive forces it would have produced and for the lifestyle of the genus. If the tail was hypocercal as previous researchers have suggested then extensive experimental research into its functional effect is required. If the hypocercal interpretation is incorrect then the functional significance of the tail would be better understood by comparison with extant species. It must be noted that there are inherent dangers in drawing functional and morphological comparisons between ostracoderms and extant fish. The nature of the musculature in ostracoderms is unknown and they do not display the same diversity of caudal fin morphology as extant teleosts, suggesting that there might have been constraints on morphological adaptations of their postcranial anatomy.

Previous interpretations of the caudal fin in *Errivaspis* and other ostracoderms.

White (1935) described the general postcranial morphology of *Errivaspis waynensis*, interpreting it as having a hypocercal caudal fin. He provided detailed drawings of the postcranial region in multiple specimens to justify his reconstruction but his reconstructions include no interpretation of the sediment surrounding the caudal fin. It is difficult to interpret from these illustrations whether the margins of the caudal fin as drawn, represent the actual outline of the specimen or margins that result from parts of it being overlain by sediment or missing. Blicek illustrated *Errivaspis* with a homocercal tail in his reconstruction (1984), which was produced by removing the lower tail lobe from Obruchev's (1964) reconstruction (Blicek pers. com.).

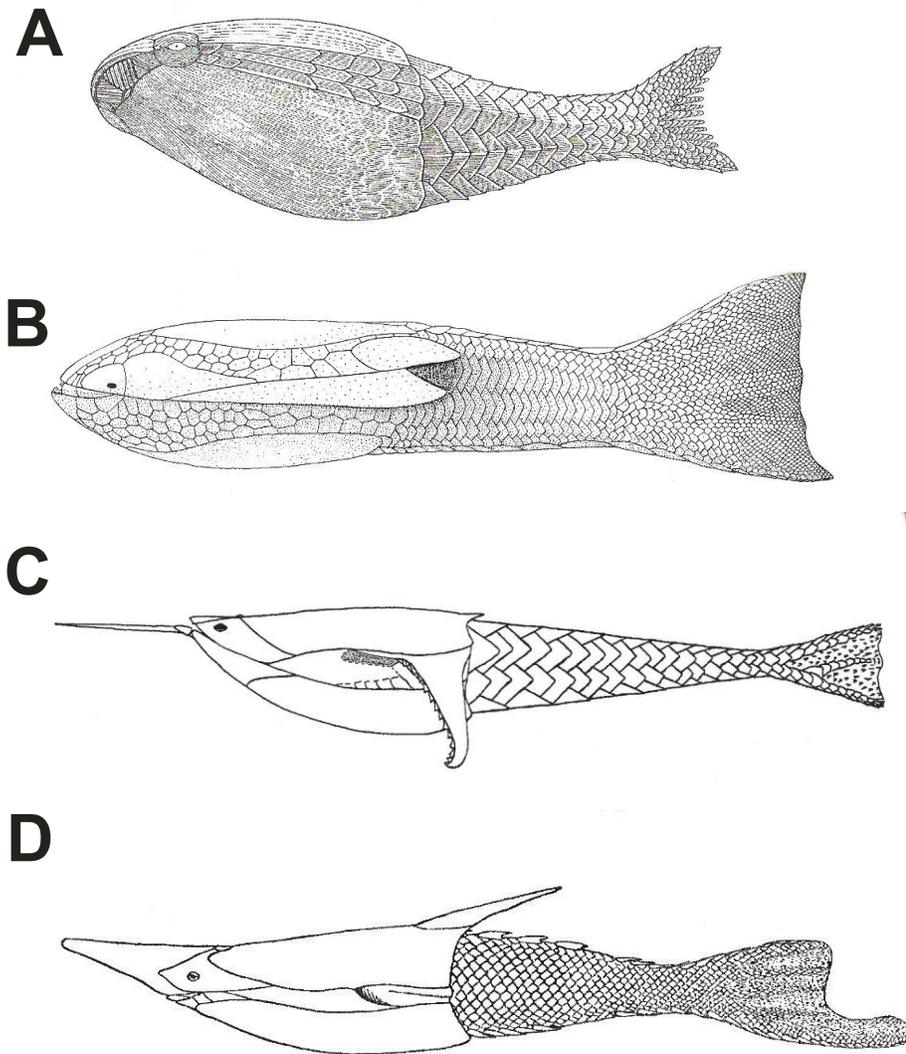


Fig. 2. A comparison of caudal fin morphologies observed in Heterostraci: □A. *Athenaegis* from Soehn & Wilson (1990). □B. *Drepanaspis* from Gross (1963). □C. *Doryaspis* from Pernegre (2003A, 2003B). □D. *Errivaspis* from White (1935).

The pteraspidiiform *Drepanaspis gemuendenensis* has been found to have a symmetrical, or “homocercal” caudal fin with five supporting lobes (Gross 1963). Some psammosteid heterostracans have been reconstructed with a ventral lobe pointing backward with the dorsal lobe pointing upward to form a hypocercal caudal fin (Tarlo 1964), but it does not resemble the extreme hypocercal morphology, previously attributed to *Errivaspis* (Fig. 2) and is might be functionally more akin to the homocercal morphology described in *Drepanaspis* by Gross (1963). Dineley (1976)

described the caudal fin of the cyathaspid *Ctenaspis* with symmetrical tail morphology. Denison (1971) in a review of the tails of heterostracans presented a number of homocercal types and covered *Errivaspis* but did not challenge the traditional hypocercal interpretation. Soehn & Wilson (1990) describe *Athenaegis*, a basal heterostracan with a homocercal caudal fin and supporting rays. *Doryaspis nathorsti* has previously been reconstructed with a hypocercal caudal fin (Blieck 1984) but Pernegre (2003A, 2003B, 2005) with the availability of more complete material reconstructed it with a symmetrical fin. The only reconstruction of *Errivaspis* that has been put forward without the extended ventral lobe, is by Blieck (1984).

While the most plesiomorphic Heterostraci display a homocercal tail with supporting ray like structures (Soehn & Wilson 1990), the Ordovician aranaspid *Sacabambaspis* has been shown to have a strongly hypocercal tail with the notochord extending into the lower lobe (Pradel *et al.* 2007). This downward flexure of the notochord is similar to the condition found in extant lampreys and hagfish. Anaspids display a hypocercal morphology but it is not known whether the notochord extends into the lower lobe. This has suggests that a hypocercal morphology might be the primitive condition of early vertebrates (Fig. 3). It is not known whether the notochord of Heterostraci extends into any of the supporting ray like structures.

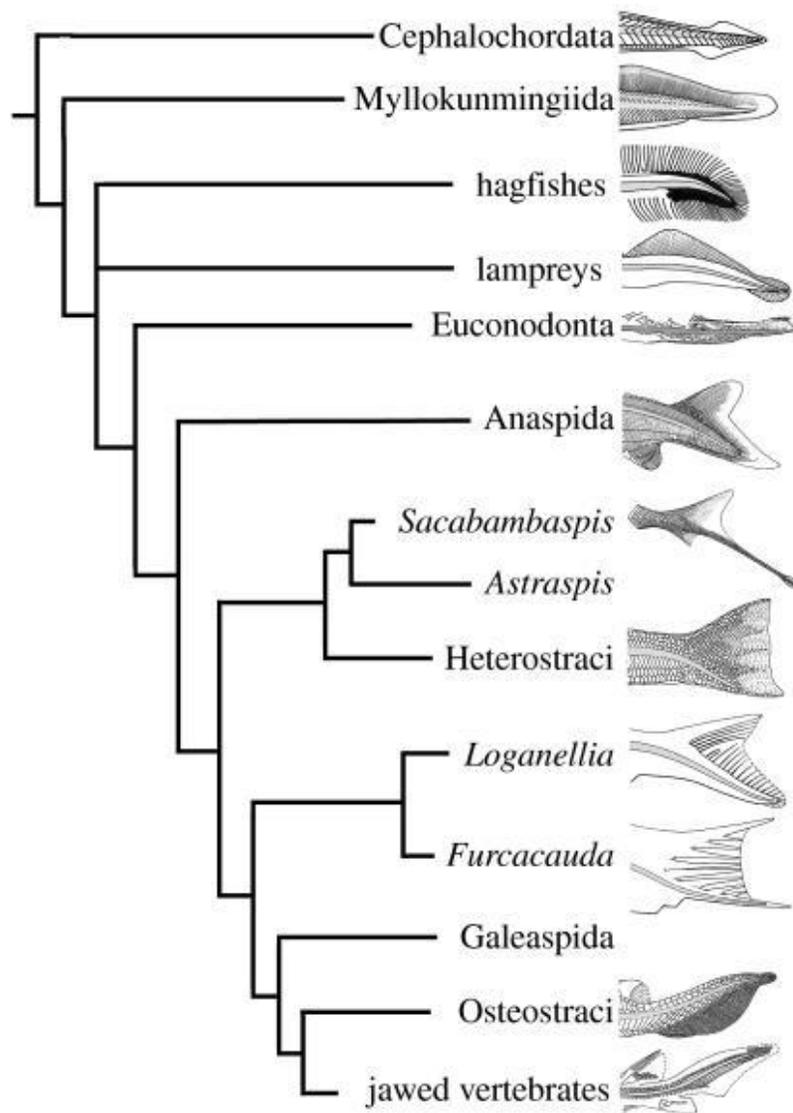


Fig 3. Phylogeny of early vertebrates and evolution of caudal fin morphology after Pradel *et al.* (2007). A downward flexure of the notochord is found in lampreys and hagfish while a similar condition combined with a hypocercal morphology is found in the anaspid *Sacabambaspis* suggesting that this is the plesiomorphic condition of early vertebrates.

In summary, the elongate ventral lobe attributed to *Errivaspis* is absent in all other heterostracans for which well preserved caudal fin material is available. Most heterostracans for which material is available have a homocercal tail and those that do not have a very different caudal fin morphology to that attributed to *Errivaspis* (Tarlo 1964). Given that these include basal forms thought to be similar to the types that gave rise to *Errivaspis* and other Pteraspidiformes such as *Doryaspis*, which are the closest

relatives of *Errivaspis* for which material is available, then the extended ventral lobe described by White (1935) would have been an autapomorphy unique to *Errivaspis* among the Heterostraci. At the time of this description there were no other well-preserved heterostracan caudal fins available for comparison and the groups most closely associated with them, the thelodonts and anaspids, did indeed have an extended lower tail lobe. This might have influenced contemporary researchers to interpret the caudal fin of *Errivaspis* in this manner.

In view of the discrepancy between the caudal fin morphology ascribed to *Errivaspis* and that of other Heterostraci discovered subsequently, it was decided to review the original material described by White and determine whether the reconstruction with a longer ventral lobe was justified. A further objective was to identification of implications of the caudal fin morphology for the locomotion of Pteraspidiiformes.

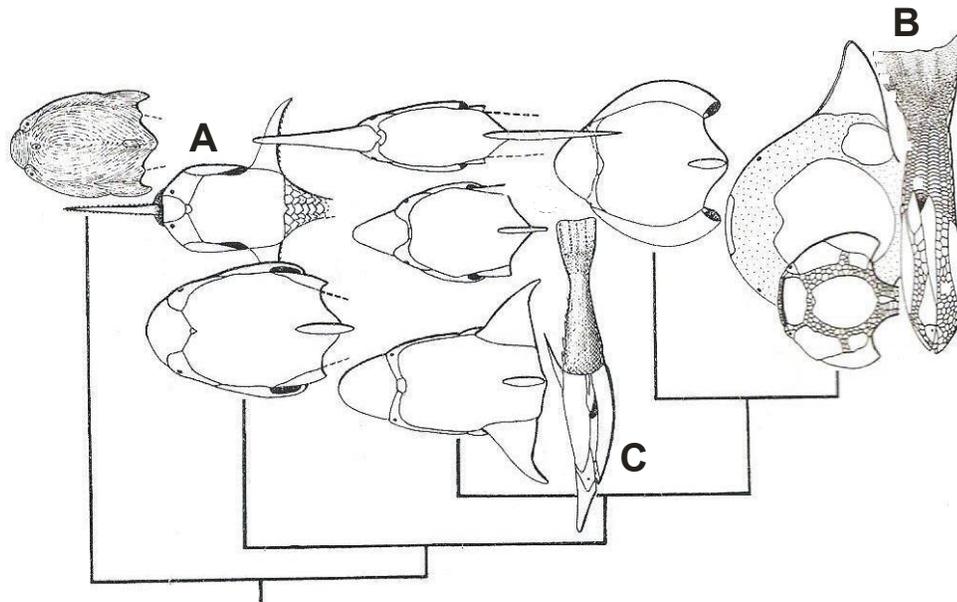


Fig. 4. Reconstructions and relationships of pteraspidiiform heterostracans after Janvier (1996). □A. *Drepanaspis gemundenensis* from Gross (1963). □B. *Doryaspis nathorsti* from Pernegre (2003A, 2003B). □C. White's (1935) reconstruction of *Errivaspis waynensis*.

Inherent uncertainties surrounding postcranial morphology in ostracoderms

The tails of pteraspid fossils are often distorted due to their fragility combined with the effects of decay prior to burial, collapse of soft body parts and sedimentary compression. It is therefore essential to identify the processes that have taken place in specimens and the likely consequences for observed morphology. Distortion of hard body parts due to compression can generally be identified by the presence of cracks. It must, however, be noted that Whittington (1977) found that in some mid-Cambrian trilobites distortion could occur without significant cracking. All of the specimens of *Errivaspis waynensis* looked at in this study displayed cracking in the head shields suggesting that they had been subject to significant compressive forces. To take the length of the upper part of the caudal fin as its total length as in Blicek's (1984) reconstruction, would imply that processes such as compression or disarticulation had lengthened the lower part of the fin giving the illusion of an elongate lower lobe. Previous taphonomic work suggests that expansion of fossils resulting from sedimentary compression is prevented by laterally confining pressures (Walton 1936, Harris 1974, Briggs & Williams 1981, Purnell & Donoghue 1999). The idea that the ventral lobe observed in *Errivaspis* was an artefact of expansion due to compressive forces should be discounted.

In soft-bodied organisms extensive collapse can occur due to decay before the subject is buried (Zangerl & Richardson 1963, Zangerl 1971, Conway-Moriss 1979). The head shield of an *Errivaspis* would be expected to retain its shape until crushed by compressive forces while the articulated scales of the postcranial region would be expected to become disassociated as soft body parts decayed. Even in a specimen where the postcranial region was preserved, the caudal fin could be expected to be subject to significant distortion due to decay because it is held together by soft tissue. It is possible that *Errivaspis* had a homocercal caudal fin with five supporting lobes as interpreted in other pteraspidiformes (Gross 1963, Obruchev 1964, Pernegre 2003A, 2003B, 2005). If rapid disarticulation of such caudal fin did not take place, it could

collapse due to decay, either from the top down, first causing the lobes to collapse together, or sideways coming to rest on its side. In either case the lowest supporting structure of the caudal fin would be likely to remain in place the longest and could conceivably create the illusion of a hypocercal tail fin. The nature of collapse would probably be determined by the type of sediment that the fish came to rest in. If it sank into a fine sediment it might be subject to some lateral confinement as the caudal fin broke down, while if it came to rest on a firm sediment it would be more likely to collapse sideways.

Materials and Methods

All of the specimens examined are of *Errivaspis waynensis* from the “Lower Old Red Sandstone”, held at the Natural History Museum London, originally described by White (1935). The specimens are from Wayne Herbett Quarry which is identified as being Devonian. Preservation is mouldic with the subject having been buried by the sediment and completely dissolved by late diagenetic processes. In all of the specimens a close examination was made of the margins of the caudal fin and the surrounding rock. Close scrutiny was given to where a distinct margin could be identified and where a margin was an artefact of sediment covering the specimen or of part of the specimen being missing. The intention was to critically analyze whether the margins from which the hypocercal morphology was interpreted reflected the dimensions of the caudal fin while the fish was alive, or could be better explained by other factors. The specimens are described below and identified by specimen number. For each specimen described a photograph is provided, highlighting the key features that led to the interpretations presented here (Figs 1-10).

Method of measurement

In order to compare dimensions of the postcranial regions in different specimens, measurements were taken. Where the specimen's postcranial region was twisted in collapse a piece of string was laid along the dorsal or ventral scales from the posterior of the head shield to the dorsal or ventral margin of the caudal fin respectively. This made it possible to determine the length of the postcranial region in life while the body axis was aligned straight. The dimensions obtained were consistently longer than those obtained by White (1935) and it is not clear from Whites description how he allowed for the fact that the postcranial region was twisted in some cases. The fact that his measurements are consistently lower than those presented here suggests that the discrepancy is due to procedural difference rather than error. It was necessary to determine whether part of the caudal fin was missing in some specimens, to see which ones most reliably represented its morphology in life. This could only be done by comparing the measurements of the caudal fin to the portion of the postcranial region that did not include the caudal fin, because the head shield was partially missing in some specimens. In order for this comparison to be valid it was necessary to distinguish a boundary between the caudal fin and the anterior portion of the postcranial region and the outline of the caudal fin. The size and shape of flank scales changes between the mobile postcranial region and the caudal fin, probably due to the need for scales in the former area to articulate. This change in scale morphology can be clearly seen in pictures of specimens P17477 and P17521 (Figs 5 and 7).

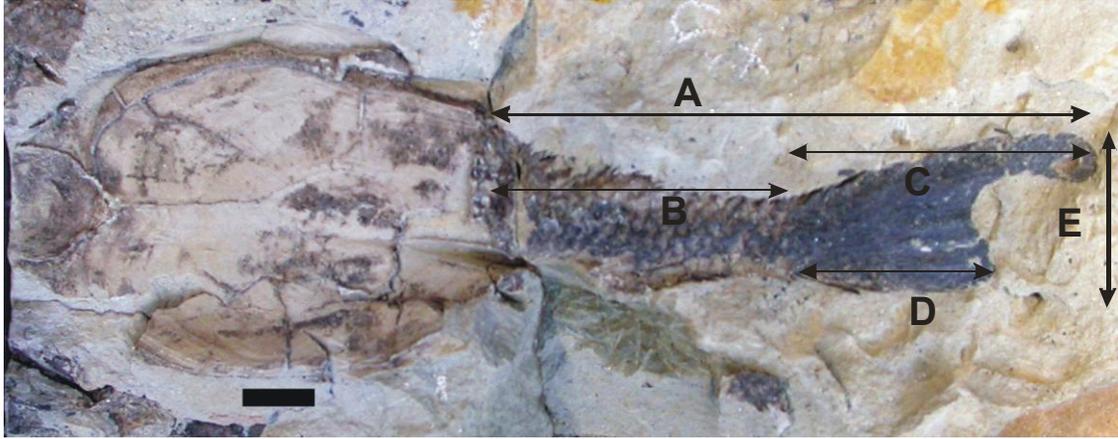


Fig. 5. Illustration of the measurements taken of the specimens P17477 (illustrated), P17485 and P17521. □A. Total length of postcranial region was taken along the dorsal margin which was the longest in all specimens. □B. Length of postcranial region minus the caudal fin was taken as the measurement from the head shield to the last articulating flank scale. □C. Ventral length of caudal fin. □D. Dorsal length of caudal fin. □E. Vertical span of caudal fin.

P17477 part and P17478 counterpart

Looking at White's (1935) reconstruction of *Errivaspis* it is apparent that this is the specimen that he has drawn on directly to interpret the outline of the caudal fin of *Errivaspis*. It is preserved in dorso-ventral collapse and displays the margins of the head shield and postcranial regions, although the anterior of the head shield is absent. The presence of a dorsal spine shows P17477 to be the dorsal surface of the fish. Progressive twisting of the postcranial region brings the caudal fin into lateral collapse. A structure resembling a lower tail lobe is present in both the part and counterpart. While the lobe has a rounded tip, part of the inner margin of the tip has not been fully prepared on the part rendering its outline doubtful. It must be noted however that comparison with the dimensions of other specimens suggests that the ventral margin does represent the maximum length of the caudal fin in life (see 'Analysis'). Scales are visible on the lower margin of the caudal fin showing that this margin is genuine but they are missing over the last 4 mm of the dorsal surface indicating that some material in this region has not been fully prepared. The orientation of the head shield shows that the lobe-like structure is ventral. Examination of the inner margin of the caudal fin

shows that an oval flake of missing material defines this margin on the part (Fig 5). A large crack runs across the counterpart, which corresponds to a flake of material that has broken away in the part. This suggests that a split in the specimen has caused a significant piece of the caudal fin to be lost and that the dorsal area was far more extensive in life. This is a critical finding given the importance of the outline of this specimen in forming previous interpretations of caudal fin morphology in *Errivaspis*. The presence of five ridges can be clearly made out resembling structures interpreted as fin rays in other Heterostraci (Gross 1963, Soehn & Wilson 1990). They cover a much less extensive portion of the caudal fin than those of other specimens such as P17485 and P17486 (Fig. 6). This also suggests that material is missing.

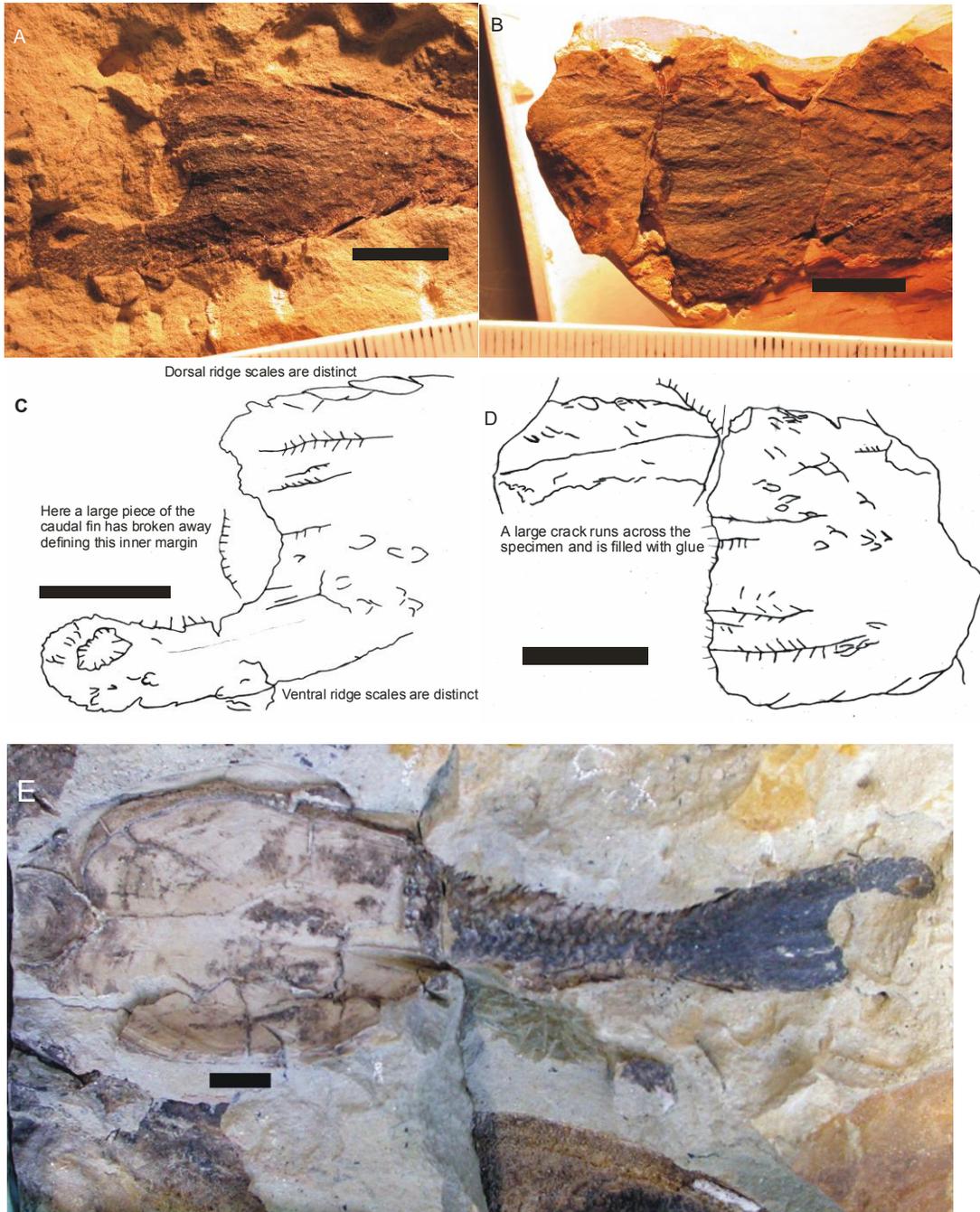


Fig. 5. Caudal fin of *Errivaspis waynensis* specimen P17477-8 illuminated in low angle relief.
 □A. P17478 shown in outline. □B. P17477 shown in outline. □C. P17477 is shown in a camera lucida illustration. □D. P17478 is shown in a camera lucida illustration. □E. P17478 is shown in its entirety displaying the dorsal spine that identifies this specimen as a ventral view.
 Scale bar = 1 cm.

P17485 part and P17486 counterpart

The specimen is preserved in dorso-ventral collapse and displays the margins of the head shield and postcranial regions. The presence of a dorsal spine on the part and oral plates on the counterpart shows that the part is the dorsal surface of the subject. A structure resembling a lower tail lobe with a rounded tip is present which the orientation of the head shield shows to be ventral. The rock surrounding the inner margin of the ventral lobe falls away sharply on the part while it is overlain by rock on the counterpart. It can clearly be seen that the dorsal margin of the caudal fin is overlain by matrix on the counterpart because of the way the rock has broken as it has split from the part (Fig. 6). Therefore the structure, identified as a ventral lobe by White (1935) cannot be regarded as having a reliably defined inner margin. The fact that much of the dorsal margin of the caudal fin is missing makes it impossible to determine whether the fin originally extended into this area. The presence of five ridges similar to those in P17477 and P17478 can be clearly made out though they are much longer, suggesting that material is missing from this area in the other specimen. The postcranial region has a progressively twisted morphology bringing the caudal fin into sideways collapse. This suggests that as the caudal fin has decomposed, supporting ray like structures (Fig. 6a) might have become disassociated from the connecting tissue and have collapsed together.

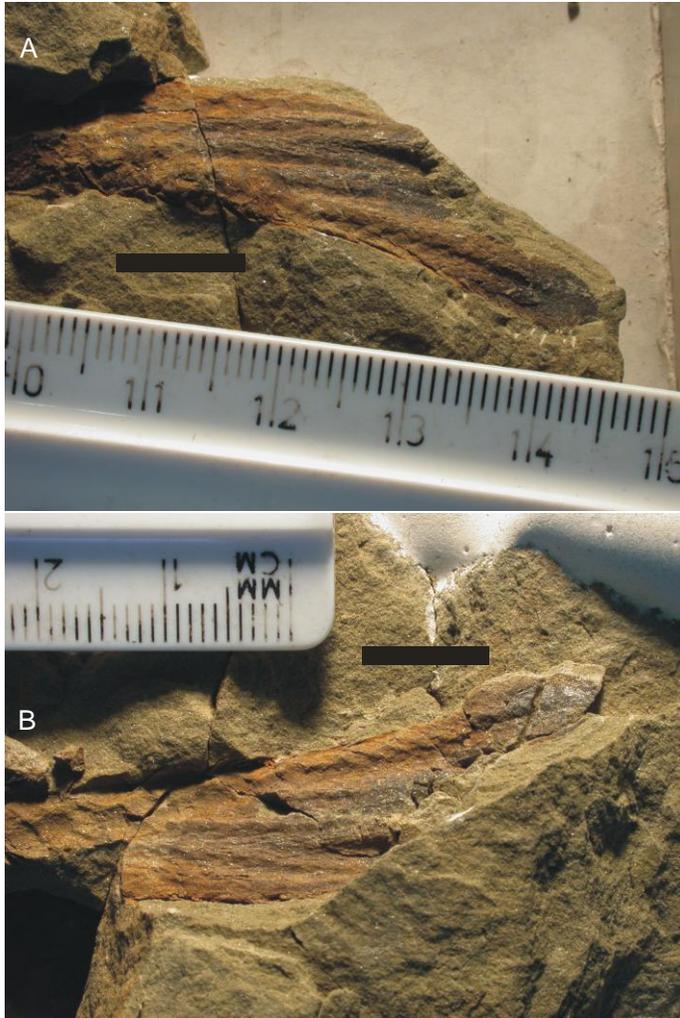


Fig. 6. Caudal fin of *Errivaspis waynensis* specimen P17485-6. □A. P17485. □B. P17486. Part and counterpart both display distinct ridge like structures but the outline of the rounded ventral ray is defined by the fracture between part and counterpart. Scale bar = 1 cm.

P17521 part and 17522 counterpart

This specimen is preserved in lateral collapse and includes postcranial elements and a partial head shield, which can be used to determine the length of the postcranial area between the head shield and caudal fin. There is a lot of material missing from the central part of the caudal fin with the dorsal and ventral margins surviving. The presence of dorsal and ventral ridge scales shows that these margins are not an artefact of the preparation of the specimen. The presence of loose scale fragments in the area

between the dorsal and ventral margins where material is missing suggests that this area was covered by the caudal fin during life (Fig. 7a). Preparation marks along this margin suggest a possible cause of flaking. One margin of the caudal fin is slightly longer than the other and the pattern of growth on the head shield fragment shows the longer lobe to be ventral. The shorter margin terminates due to overlayering of matrix rather than the presence of a clearly defined posterior edge (Fig. 7b). This makes it uncertain whether the length of the shorter margin in the specimen represents the actual length of the caudal fin in life or whether it was previously more extensive. Although one margin is shorter than the other, the difference is far less than in specimen P17477 and 17478. The orientation of the head shield fragment shows that the fish came to rest on its side prior to burial and allows us to determine the dorsal and ventral margins of the fin. This means that the caudal fin will not have been subject to the same vertical collapse as other examples described and the part of this specimen will provide the most reliable estimate of the proportions of the caudal fin prior to death. The position during burial may account for the preservation of parts of the dorsal and middle area of the caudal fin absent in other subjects. A downward turn in the direction of the most posterior dorsal ridge scale suggests that the dorsal margin of the caudal fin was shorter than the ventral margin prior to death (Fig. 7b). The counterpart preserves less material of the caudal fin as part of the anterior is missing (Fig. 7b).

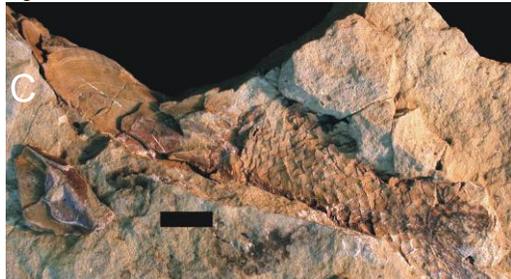
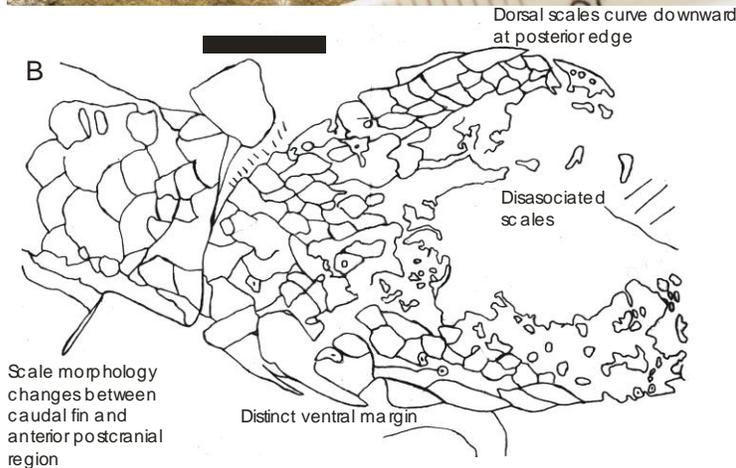
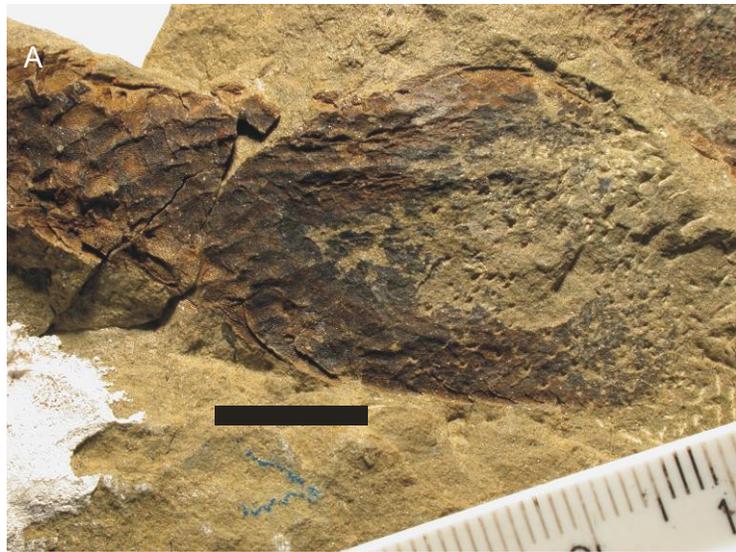


Fig. 7A. Caudal fin of *Errivaspis waynensis* specimen P17521 photographed in low angle relief.

Fig. 7B. Caudal fin of *Errivaspis waynensis* specimen P17521 is shown in a camera lucida illustration. Disassociated scales can be seen in the area between the dorsal and ventral lobes.. The longer margin which is ventral in this surface has clearly defined scales along the bottom but the interior margin is an artefact of missing material.

Fig. 7C. Specimen P17522 showing a fragment of head shield which identifies the dorsal and ventral margins of the caudal fin.

Fig. 7D. A closer view of specimen P17522 showing detail of the caudal fin.

Scale bar = 1cm in all cases.

P16789-90

P16789-90 is preserved in dorso-ventral collapse and displays the lateral margins of the head shield and postcranial regions. The presence of oral plates shows the part to be a ventral surface of the specimen. The postcranial region has a twisted morphology, progressively curving to the left, consistent with sideways collapse. The caudal fin displays ray like structures which appear to have become disorientated. The staggered orientation and collapse of the caudal fin makes its morphology in life impossible to interpret. The caudal fin is much shorter than in some of the other specimens and part of it is missing. The areas around the specimen have been filled in with plaster, making it impossible to determine whether these margins result from a fracture in the rock (Fig 8a).

P 17527 part and P17528 counterpart

The specimen displays an elongate lobe like structure. The nature of the collapse of the specimen cannot be satisfactorily be determined due to the complete absence of a head shield or other identifying landmarks. This also means that it is impossible to determine whether the lobe like structure is dorsal or ventral. The presence of three ridges similar to those observed in other specimens can be clearly made out. The inner margin of the lobe does not have a clear margin, and is surrounded by an area of raised matrix covered with chisel marks, suggesting that it could be a result of lack of preparation in this area (Fig. 8b, c). The presence of ridge scales on both the dorsal and ventral margins shows that they are not an artefact of the preparation of the specimen. The dorsal surface of the caudal fin displays a slight downward inflection.

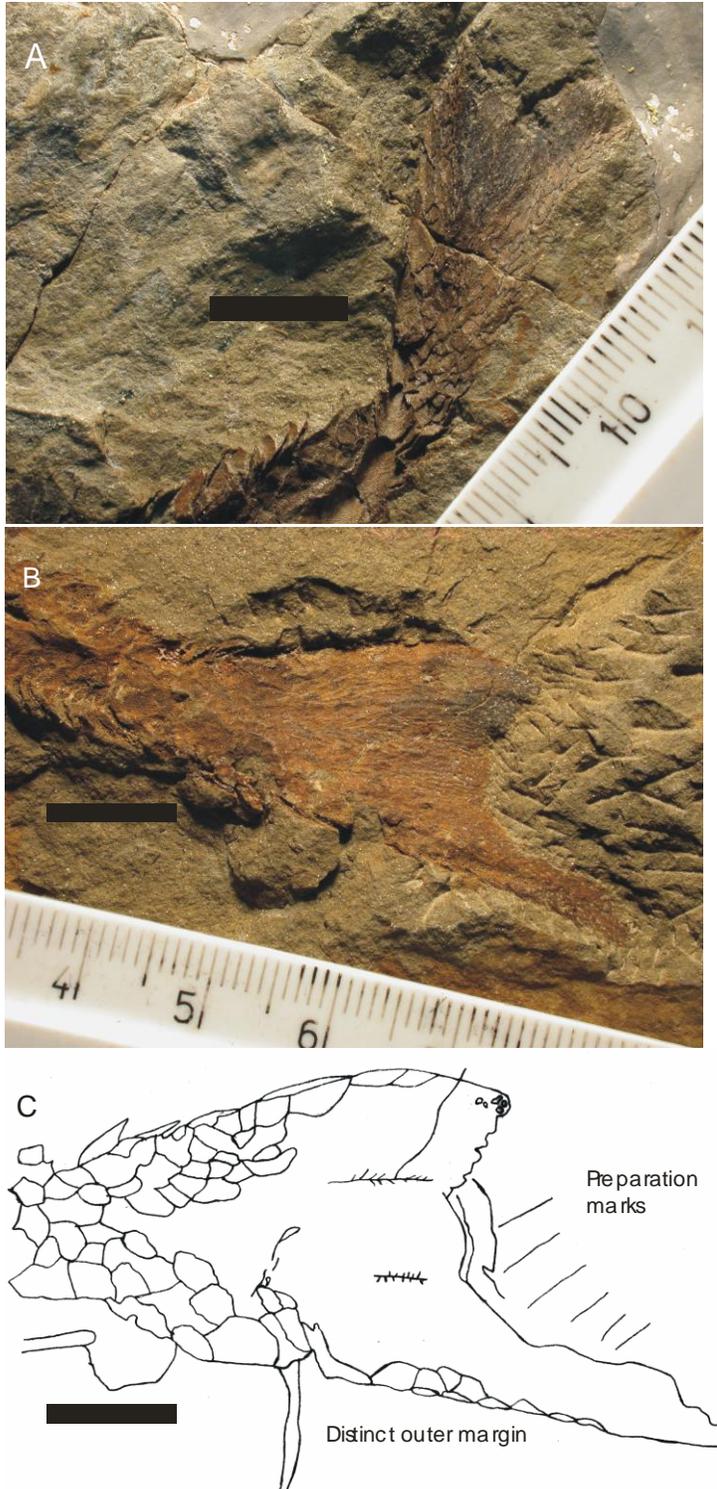


Fig. 8. □A. Caudal fin of *Errivaspis waynensis* specimen P16789-90 is photographed in low angle illumination. □B. Caudal fin of *Errivaspis waynensis* specimen P17527 is also photographed in low angle relief. □C. Specimen P17527 is shown in a camera lucida illustration. Scale bar = 1 cm in each case.

Analysis of postcranial measurements

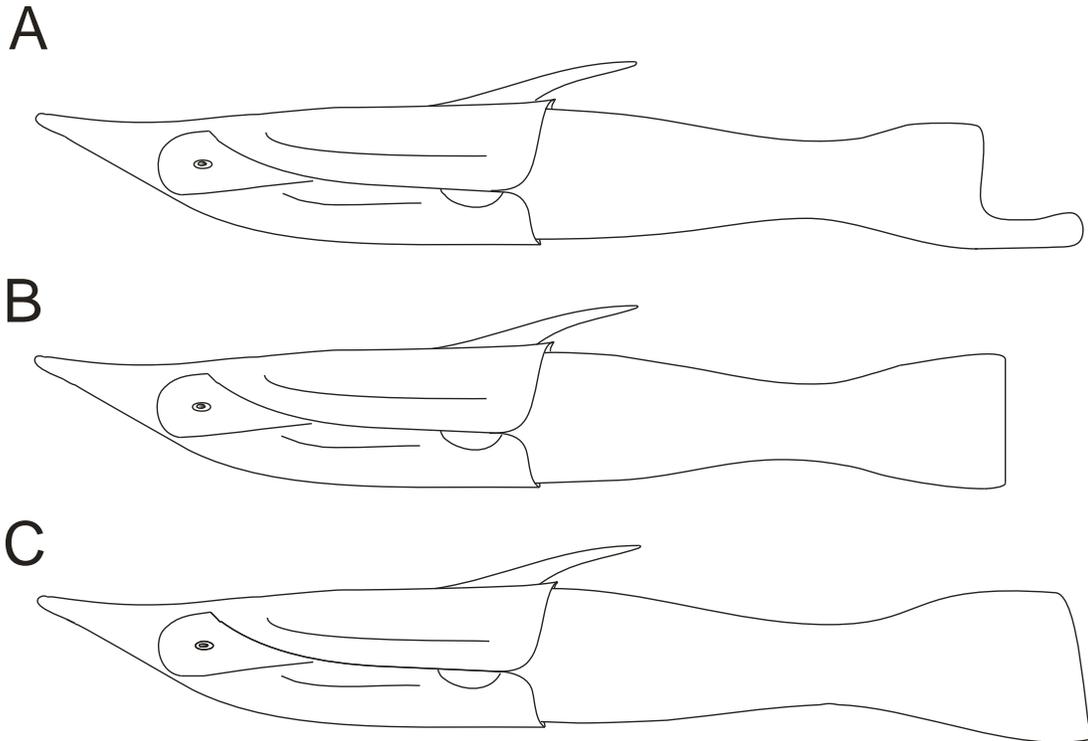


Fig. 9. Reconstructions of the caudal fin of *Errivaspis waynensis* past and present. □A. After White (1935). □B. After Blieck (1984). □C. A new reconstruction based on examination of the material described by White (1935) detailed in this chapter.

The measurements obtained suggest that neither White's (1935) reconstruction nor Blieck's (1984) reconstruction of the caudal fin of *Errivaspis* are consistent with the material present. It was found that White's (1935) reconstructions accurately recorded the visible detail of the specimens but that he concluded that the outline of the caudal fin as preserved reflected the outline in life. No attempt to interpret the matrix surrounding the caudal fins is apparent from White's diagrams or writing. There is therefore no clarification as to which margins might be artefacts of missing material or incomplete preparation. White also did not have the benefit of subsequent research in taphonomy and experimental taphonomy which would have suggested likely patterns of decay and collapse in the caudal fin. Blieck's (1984) reconstruction of the caudal fin was also found to be inconsistent with the material present since there was a much

longer ventral margin to the caudal fin in a number of specimens than his illustration allowed. This longer margin could not be attributed to any taphonomic processes.

In all eleven specimens of *Errivaspis waynensis* were examined, belonging to six individuals. In all three specimens, two of which showed evidence in the part and counterpart, displayed evidence of an elongate ventral lobe (P17477, 17478, P17521, P17527, P17485 and P17486) (Table. 1). None of them displayed a distinct margin along the dorsal edge of the lobe. It is clearly specimen P17477 that White (1935) drew on most directly for his reconstruction of the caudal fin of *Errivaspis*, and it is this reconstruction that has formed the basis for most subsequent illustrations. In this specimen, the lower lobe is clearly an artefact of a large area of the caudal fin having broken away either during the separation of the part and counterpart or preparation of the specimen. On the basis of this finding alone it is necessary to revise currently accepted interpretation of pteraspid fin morphology. In specimen P17527 the lower lobe does not have a distinct inner margin in contrast to its clearly defined outer margin. This makes it impossible to take it as representing the morphology of the caudal fin in life. In specimens P17477 and P17478 the inner margin of the lobe is defined by a fracture between the part and counterpart and cannot be accepted as a well defined margin. In specimen P17521 there is clearly a large amount of material missing between the dorsal and ventral margins and the shorter of the two margins is overlain by matrix at the dorsal extremity.

Specimen	Evidence of structure resembling elongate lower tail lobe	Evidence of structures resembling fin rays	Inner margin of inferred tail lobe is distinct	Dorsal margin of caudal fin is distinct	Ventral margin of caudal fin is distinct
P16789-90	No	Yes	No	Yes	No
P17477 and 17478	Yes	Yes	No	Yes	No
P17485 and P17486	Yes	Yes	No	No	No
P17521	Yes	No	No	Yes	Yes
P17527	Yes	Yes	No	Yes	Yes

Table. 1 Properties observed in the NHM specimens of *Errivaspis waynensis*. Identifies which subjects showed evidence of key features including dorsal tail lobes, and rays, and which margins were distinct.

Specimen P17521 appears to be the only specimen of the six to have come to rest on its side prior to burial. This makes it the best specimen to estimate the vertical span of the caudal fin as it will not have been subject to vertical collapse. It is also the only specimen that displays part of the shorter margin, taken to be the dorsal edge, undisrupted by collapse. While the area between the dorsal and ventral edges is extensively damaged some material can clearly be seen. On the face of it specimens P17447 and P17521 are not inconsistent with each other because the lower lobe could be absent in specimen P17521 simply because it has broken away post mortem. It must be noted however that specimen P17521 is the only individual that has come to rest on its side. In all the specimens where the fish has come to rest prior to burial, with the caudal fin in a more or less vertical orientation, it has clearly been subject to

vertical collapse. This makes measurements of the dorsoventral span of the caudal fin potentially misleading. It also makes specimen P17521 the most reliable indicator of the dorsal morphology of the caudal fin. It is necessary to look at the dimensions of the postcranial region as a whole to assess in which specimens material is missing. To assess whether specimen P17521 is representative of the total length of the caudal fin its dimensions were compared to the length of postcranial region excluding the caudal fin. In both specimens ridge scales are present along the dorsal and ventral margins, indicating that they are genuine margins and indicate the minimum length for the dorsal and ventral edges of the caudal fin. By measuring the distance from the head shield to the most posterior articulating scales and comparing it to the ventral margin of the caudal fin it was possible to calculate the proportion of the postcranial region made up by caudal fin. In specimens P17477, P17485 and P17521 the ventral margin of the caudal fin accounted for 47- 48 % of the total length of the postcranial region (Table. 2). This consistency between the specimens suggesting that the ventral margin of the caudal fin was complete in all three of these subjects.

Specimen	Length caudal fin mm	Length postcranial region – caudal fin	Length postcranial region/caudal fin	Caudal fin as % of postcranial length
P17477	44.2	48.3	1.1	47
P17485	40.689	45.517	1.119	47
P17521	65	58	1.1	47.

Table. 2. Comparison of the portion of the postcranial region made up by the dorsal margin of the caudal fin in specimens P17477, P17485, and P17521 (*Errivaspis waynensis*).

If we accept that the ventral margin of the caudal fin in specimens P17477, P17485, and P17521 probably represents maximum length prior to death, we can compare the dorsal margins of different specimens to see if part of them was missing. If the ventral margins are complete in P17477 and P17521 then clearly P17477 is missing a large portion of the dorsal margin of the caudal fin relative to P17521. This supports the

conclusion that the length of P17477s, dorsal surface is an artefact of part of it having broken away. This further shows that the caudal fin in P17477 has a lesser vertical span than that of P17521 relative to its length, suggesting that it has been subject to some collapse before it came to rest on its side (Table. 3).

Specimen	Vertical span mm	Ventral length mm	Dorsal length/span
P17477	18.8	29.9	1.3
P17521	22.7	31.6	1.1

Table. 3. Compares the dimensions of the caudal fins in specimens P17477 and P17521 (*Errivaspis waynensis*) in terms of the ratio between the length of the caudal fin and the vertical span.

Conclusions

The available material does not justify previous interpretations that the caudal fin of *Errivaspis* had a single extended ventral lobe. The hypocercal morphology proposed previously cannot be determined by a distinct margin at any point. All but one of the specimens shows ridges like those that have been observed in the tails of other Heterostraci and interpreted as supporting structures in either the part or counterpart (Gross 1963, Denison 1971, Soehn & Wilson 1990, Pernegre 2003A, 2003B, 2005). The absence of these ridges in P15721, which is the only specimen that has come to rest on its side, suggests that they might be an artefact of folding taking place during vertical collapse of the caudal fin post mortem. White (1935) satisfied himself that this was not the case and anatomical evidence from other ostracoderms supports his conclusion.

In the specimen that most influenced White in reconstructing the caudal fin with the hypocercal form (P17477) the interpretation of the morphology is clearly an artefact of missing material. If the fish comes to rest on the substrate ventral side down, which is the most likely orientation given its shape, and the caudal fin collapses vertically due to decay or sedimentary compression, then the lowest of the fin rays is the one most likely

to remain in position. Given that the ventral margin of the lower lobe is distinct in several specimens and fossils do not lengthen due to compression (Walton 1936, Harris 1974, Briggs & Williams 1981, Purnell & Donoghue 1999) it is reasonable to assume that the ventral margin represents the minimum length of the caudal fin. Based on the above considerations it is proposed that *Errivaspis waynensis* had an elongate homocercal caudal fin making up approximately 47% of the length of the postcranial region.

The caudal fin of *Errivaspis* would not have to differ from the morphology and general proportions observed in other Heterostraci to be consistent with the material present. The material suggests that *Errivaspis* had a morphology that was slightly hypocercal with the dorsal margin being shorter than the ventral margin but closer to a homocercal morphology than to the strongly hypocercal outline put forward by White (1935) or even the hypocercal morphology observed in psammolepids (Tarlo 1964). A new reconstruction of the caudal fin of *Errivaspis* is presented here with a near symmetrical morphology (Fig. 7) based on the available material and comparison with other pteraspidiformes which are the closest relatives of *Errivaspis* for which well preserved caudal fins are available.

The elongate caudal fin with a comparatively short dorsal span combined with the thickness of the caudal peduncle is consistent with extant species adapted primarily for acceleration, such as pike (*Esox lucius*) though such comparisons are dangerous as previously observed (see “previous research”). This morphology has a number of hydrodynamic and ecological implications. Since *Errivaspis* is thought to have been a filter feeder (Purnell 2001) it is far more likely to have developed the ability to accelerate rapidly to evade predators than to pursue prey. It is also possible that it used it to overcome fast flowing current while moving upstream, as extant migratory fish attain their highest power outputs in brief bursts while overcoming extreme flow regimes (Castro-Santos 2005). This would be especially significant since *Errivaspis* lacked pectoral fins which are used to counteract oncoming flow by extant fish (Arnold *et al.* 1991). The slightly longer ventral margin of the caudal fin described here for

Errivaspis and also observed in other heterostracans would probably be functionally intermediate between the caudal fins of extant fish with homocercal caudal fins producing fairly uniform posteroventral thrust and that of extant flying fish which produces positive anterior pitch. It is likely that *Errivaspis* would have been able to determine the nature of pitching moments produced by its caudal fin by the manner in which it beat it during the propulsive stroke as some extant fish do (see “previous research”).

Chapter 3

A wind tunnel based investigation into the hydrodynamic characteristics of three Palaeozoic jawless vertebrates, *Poraspis*, *Errivaspis* and *Ateleaspis*

Abstract

Ostracoderms, represent a crucial phase of vertebrate evolution during which many of the characters that are now taken as typical vertebrate features appeared for the first time. While recent work has gone a long way to clarifying relationships and patterns of character acquisition, understanding of the ecology and biomechanics of these early fishes has lagged behind. Very little is known, for example, about how they swam. Using models mounted in a wind tunnel, the hydrodynamic characteristics of three ostracoderm genera, *Poraspis*, *Errivaspis*, *Ateleaspis*, were compared with a view to constraining their hydrodynamic behaviour. The experimental data suggested that *Ateleaspis* was more suited to a benthic lifestyle than *Poraspis* or *Errivaspis*, being able to utilize ground effect while close to the bottom. This enabled it to swim with greater hydrodynamic efficiency and this probably drove the general pattern of morphological adaptation of osteostracans. Conversely it proved more subject to variations in lift and pitching moment while swimming in mid water column than the other two genera. *Poraspis* was found to have a morphology adapted to minimising drag for greater hydrodynamic efficiency while swimming in mid water column. *Errivaspis* was concluded to have had morphology suitable for both a benthic and pelagic lifestyle. All three genera were found to be subject to fluctuating levels of lift and moment which could have facilitated manoeuvring but would also have imposed metabolic costs and constraints on lifestyle.

Introduction

The Heterostraci and Osteostraci are two related groups of jawless fishes that traditionally fall under the heterogeneous grouping of stem gnathostomes or ostracoderms. They are characterised by a covering of plates or scales and have no living representatives. They represent a large and successful radiation of early vertebrates which lasted for 100 million years showing considerable diversity of body form and adaptive potential (Mark-Kurik 1992).

The three ostracoderm genera selected to form the basis of this study were *Poraspis*, *Errivaspis* and *Ateleaspis*. The hydrodynamic characteristics of these three genera were compared using models mounted in wind tunnels. *Ateleaspis tessellata* is one of the earliest known osteostracans, occurring in the Wenlockian of Scotland. It is thought to represent the plesiomorphic body plan of the Osteostraci and is the earliest vertebrate known to display paired appendages (Janvier 1987). It was included in the study to identify the hydrodynamic properties of the generalised osteostracan body form. It would then be possible in the future to extrapolate the likely hydrodynamic significance of specialized features in the more derived osteostracans, such as cornuae. Their effect could be further investigated by theoretical formulae or future experiments, which might indicate the evolutionary importance of such features. *Errivaspis* and *Poraspis* are generalised members of the two major heterostracan clades. *Errivaspis waynensis*, formerly described under the genus *Pteraspis*, is a pteraspidiform while *Poraspis polaris* is a cyathaspid. It was thought it desirable to compare the hydrodynamic properties of a generalised representative of the Cyathaspida, Pteraspidiformi and Cephalaspida, since these groups all represent large and geographically diverse radiations of early vertebrates. Little is known about the ecological interrelationships between these three groups despite the fact that they occur across many of the same faunas.

Novitskaya (2007) concluded that cyathaspids appeared in the Silurian and achieved the peak of diversity in the first half of the Early Devonian. Pteraspids appeared and

reached peak diversity at the same time as cyathaspids, though cyathaspids are absent from later beds. Pteraspids persisted to the end of the Early Devonian, although they sharply decreased in number in the second half of the Early Devonian. Novitskaya (2007) further proposed that both major heterostracan groups became extinct due to archaic locomotor adaptations and insufficient protection from predators. It has also been suggested that pteraspidiformes filled many of the niches vacated by the cyathaspids as they declined by the early Devonian, except in Siberia where the Amphiaspida remained abundant until the Pragian (Janvier 1996). While osteostracans are found in many of the same localities as heterostracans no data exists to constrain their niche differentiation relative to the Heterostraci. One of the objectives of this study was to compare hydrodynamic characteristics between representatives of each group and thus provide data to constrain hypotheses of lifestyles and competitive interactions.

The end of the Ordovician saw widespread glaciation and reduction in sea level which was accompanied by a reduction of biodiversity in marine faunas. The early Silurian saw a radiation of diverse vertebrate forms which included the heterostracans and osteostracans, which are the subject of this study. It is uncertain how the major ostracoderm groups came to colonise a globally distributed range of habitats. It was traditionally thought that the origin of early vertebrates took place in fresh water because most major localities bearing them were fresh water or marginal marine (Romer 1955, Dennison 1956, White 1958). In an extensive review of pre Devonian vertebrate localities Boucot & Janis (1983) concluded that fresh water habitats were not invaded until the Wenlock early Silurian and that most pre Wenlock localities were too distant from shorelines for the early vertebrate remains to be transported. Halstead (1985) later concluded that early vertebrates evolved in marine environments and started to colonise fresh water environments around the late Silurian. Elliot *et al.* (1991) suggested, based on the occurrence of early pteraspidomorphs, that the group originated in Australia and migrated through South American crossing an oceanic barrier to reach the Northern hemisphere. Sansom *et al.* (2009) described the aranaspid

Sacabambaspis from the middle Ordovician of Oman supporting a Gondwanan origin for the pteraspidomorphs.

Allen & Tarlo (1963) found, in an extensive review of osteostracan distribution in the Welsh borderland, that all genera were from fresh water environments with the exception of *Hemicyclaspis*, *Didymaspis*, *Sclerodus* and *Auchenaspis* which were all interpreted as being from marginal marine environments. Furthermore, they attributed the radiation of the Osteostraci to the emergence of fresh water flood plain environments at this time. A view supported by Janvier (1985). *Ateleaspis* remains have been identified in Scotland (Ritchie 1967), Norway (Heintz 1969), and Russia (Afanassieva & Karatajute-Talimaa 1998). The material of *Ateleaspis tessellata* on which the model used in the experiments was based was found in the Silurian Old Red Sandstone Beds of Slot Burn, Seggholm, Lanarkshire. This area was considered to be brackish or fresh water by Ritchie (1968) at the time he described the species, a view supported by Dineley & Metcalf (1999).

Locality	Interpretation	Author
Slot Burn (UK)	Brackish or fresh water lagoon	Ritchie (1968) Dineley & Metcalf (1999)
Shiel Burn (UK)	Low oxygen lake	Cocks (1992)
Ringerike Sandstone (Norway)	Marginal marine environment	Heintz (1969)
Severnaya Zemlya Formation (Russia)	Marginal marine environment	Afanassieva & Karatajute-Talimaa (1998) Lorenz <i>et al.</i> (2008)

Table 1. Localities bearing remains of *Ateleaspis tessellata* and environmental interpretation.

Poraspis polaris material has been identified from Spitzbergen (Kiaer 1932, Blicke & Heintz 1983), Britain, (Lankester 1873, Dineley & Metcalf 1999) Western Europe (Elliot *et al.* 1998) and Canada (Broad & Dinley 1973, Elliot *et al.* 1998). The material

of from which the morphology of the species is interpreted in this study, was described from the Lochkovian of the Red Bay group of Spitzbergen (Heintz 1932). The models display a head shield that is dimensionally identical to *Poraspis* while the postcranial region is based on Heintz' (1932) reconstruction of *Anglaspis*, a closely related genus for which well preserved articulated postcranial material was available. This locality has been identified as a marginal marine environment from examination of the depositional setting (Blieck & Heintz 1983, Goujet 1984, Janvier *et al.* 1993), and geochemical data (Schmitz *et al.* 1991). *Poraspis* material has also been found in Wayne Herbert Quarry, Herefordshire (Lankester 1873, Dineley & Metcalf 1999) which is interpreted as being a fluvial environment. The related *Anglaspis* has been found in the Lydney area of Gloucestershire that Dineley & Metcalf (1999) interpreted as a fluvial channel with a marine incursion (Allen 1964, Dineley & Metcalf 1999). *Poraspis* material has been identified in the Peel Sound formation of Prince of Wales island, of northwest Canada, late Silurian, by Elliot *et al.* (1998). The area is identified as having been deposited by a large delta system (Thorsteinsson & Tozer 1963). Elliot *et al* further suggested that the Canadian Arctic was the centre of origin for the genus *Poraspis*.

Locality	Interpretation	Author
Red Bay Spitzbergen	Marginal marine environment.	Blieck & Heintz (1983) Janvier <i>et al.</i> (1993)
Devils hole (UK)	Interdistributory bay formed in an alluvial plain.	Allen & Tarlo (1963) Halstead (1985)
Wayne Herbert Quarry (UK)	Fluvial flood plane that has dried out.	Allen & Tarlo (1963) Dineley & Metcalf (1999)
Peel Sound Formation (Canada)	Intertidal and shallow marine environment	(Thorsteinsson & Tozer 1963) Miall (1970)

Table. 2. Localities bearing remains of *Poraspis polaris* and environmental interpretation

The material of *Errivaspis waynensis* described by White (1935) was from Wayne Herbert Quarry, Herefordshire, of Devonian/Silurian age. This locality has been interpreted as being a fresh water fluvial environment (Dineley & Metcalf 1999). The similar *Pteraspis rostrata* is found at the Oak Dingle locality of Shropshire, the rocks of which are interpreted as being a river meandering across a floodplain (Allen 1964, Dineley, & Metcalf 1999). *Errivaspis* material has also been identified from Pool Quarry, Hertfordshire with possible remains identified in Jubilee Brook and Gildings Brook (Blieck 1984).

Locality	Interpretation	Author
Wayne Herbert Quarry (UK)	Fluvial flood plane that has dried out.	Allen & Tarlo (1963) Dineley & Metcalf (1999)
Pool Quarry (UK)	Fresh water environment.	Blieck (1984)

Table. 3 Localities bearing remains of *Errivaspis waynensis* and environmental interpretation.

Despite the palaeoenvironmental evidence there are uncertainties about the habitats of early vertebrates. While *Poraspis* was deposited in a near shore environment (Blieck & Heintz 1983, Janvier *et al.* 1993) it is theoretically possible that it died in a freshwater environment and was transported by river flow to a near shore environment where it was deposited. The hollow head shields of ostracoderms would make them especially prone to this type of transportation as many shelled invertebrates are. It also has to be taken into account that many genera or species that are anatomically very similar can occupy a wide range of differing environmental settings. While pteraspids from the “Old Red Sandstone” display a strontium isotope ratio consistent with a fresh water environment, a pteraspid from Podolia displays a ratio consistent with a saline environment (Schmitz *et al.* 1991).

While the debate around the origin of ostracoderms has been resolved in favour of a salt water origin, it is accepted that most major ostracoderm bearing faunas are fresh water or marginal marine environments.

Little is known about the role of ostracoderms within their ecosystems beyond that they are generally accepted to be suspension feeders (Purnell 2001). While previous research has gone a long way to clarifying relationships and patterns of character acquisition, understanding of the lifestyle and biomechanics of these early fishes has lagged behind. Very little is known, for example, about their locomotion or hydrodynamic characteristics. It is unclear from previous work whether they were benthic or free swimming and whether they were able to sustain an active lifestyle with high levels of mobility between separate environments. Previous research has provided few physical constraints on the hydrodynamic performance of ostracoderms and the limitations that it would place on their life style. The only extant jawless vertebrates are lampreys and hagfish. While cladistic analysis places them close to some basal ostracoderms, they have an eel-like morphology and employ anguilliform locomotion (Breder 1926, Braun & Reif 1985) which would not have been possible for ostracoderms with a covering of dermal scales. They do not therefore provide a living analogue for understanding the biomechanics of ostracoderms or how they might have swam.

While previous experimental work has looked at the hydrodynamic characteristics of heterostracans (Kermack 1943, Botella & Farina 2008) and osteostracans (Bunker & Machin 1991), there have been no attempts to compare representatives of separate ostracoderm groups in a single study. No previous attempt has been made to interpret the hydrodynamics of a cyathaspid genus by experimental methods.

Anatomical and hydrodynamic questions about ostracoderms

Anatomical questions about ostracoderms

While much research has been done on the gross anatomy and evolution of characters in Heterostraci and Osteostraci, very little has been done to relate physical shape to hydrodynamic function. What studies have been undertaken have each focused on a

single taxon, and have produced generalist interpretations. Previous work has not attempted to relate hydrodynamics and morphology to patterns of evolution and character acquisition. Gross morphology would have a considerable influence on manoeuvrability and hydrodynamic efficiency in these early vertebrates, which would determine their ability to move within their habitat and evade predators. The objective of this research was as far as possible to provide constraining data on how morphology related to hydrodynamic characteristics.

Ostracoderms have evolved a diverse and sometimes bizarre range of body forms. Previous work has done little to identify to what extent body form reflects optimisation for hydrodynamic efficiency and no previous experimental study has attempted to compare the body forms of different ostracoderm groups in terms of hydrodynamic characteristics or properties (Kermack 1943, Bunker & Machin 1991). Experiments were therefore devised to identify the comparative hydrodynamic and metabolic efficiency of different body forms, which might provide evidence of the ecological niche and lifestyle of different ostracoderm groups.

Ostracoderms differ from extant fish species in two crucial respects. Mobile pectoral fins are absent in heterostracans and reduced in size and range of mobility in many osteostracans. Extant fish use pectoral fins as the primary organ of steering, using them to make corrections in trajectory and counteract moment forces acting upon them as they swim. Ostracoderm genera lacking developed pectoral fins would have depended upon other features such as rigid body structures, and adjustments in the manner of movement of the caudal fin for stabilisation. They also lack obvious mechanisms to correct for pitching and yawing moments generated as they swam. Ostracoderms are also characterised by a head shield or carapace which limits the portion of the body that can be employed in a propulsive undulation. These differences mean that there are no satisfactory living analogues to help us interpret their mode of locomotion. Breder (1926) identified three key modes of locomotion in extant fish: anguiliform, carangiform and ostraciform. This terminology has since been updated (Webb 1975, Braun & Reif 1982, Braun & Reif 1985) Ostraciform locomotion

(caudal-suboscillatory) is defined as: “Body is rigid and not thrown into wave, propulsion by means of caudal fin oscillation” (Breder 1926). While the use of pectoral fins in propulsion is a major difference between extant ostraciform fish and ostracoderms, there is a similarity in that both have a large inflexible head shield.

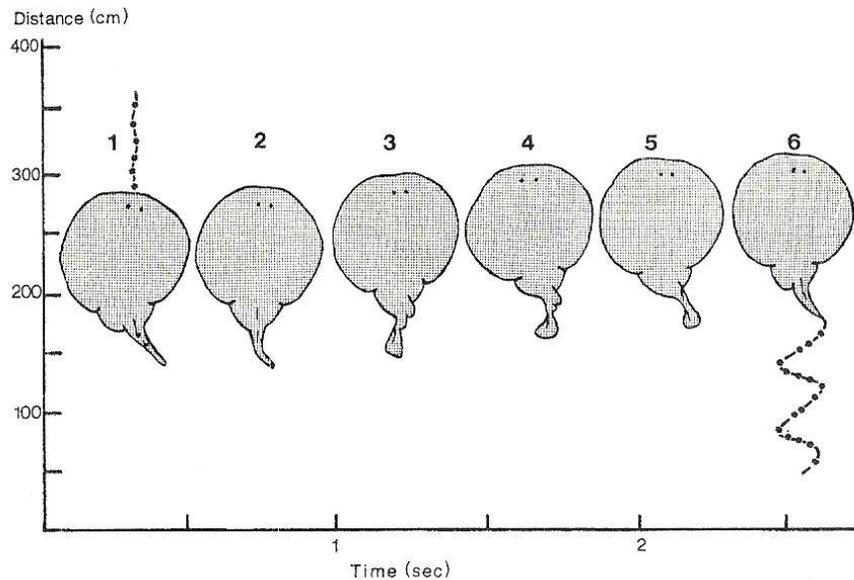


Fig 1 The pattern of ostraciform, or caudal-suboscillatory swimming as illustrated by Braun & Reif (1985).

Some ostraciform fish, such as the electric rays *Torpedinoidea*, achieve a stable body axis due to their large ventral surface area which generates lift (Braun & Reif 1985). In forms that do not have a dorsoventrally flattened morphology other mechanisms are employed to provide stability. The bony carapace of the smooth trunkfish *Lactophrys triqueter* has a morphology that generates counter rotating vortices. These provide a stabilising mechanism that self corrects for instabilities (Bartol *et al.* 2003). The stabilising vortices travel down ventro-lateral keels of the carapace. Subsequent work on other species of boxfish suggests that they too have keel like structures producing a similar capability (Bartol *et al.* 2005). Botella & Farina (2008) reported vortices on the margins of a model of *Errivaspis waynensis* placed in a flow visualisation tank. These might have had a stabilising effect similar to that observed in boxfish.

Hydrodynamic considerations

A wing or aerofoil produces lift because there is lower pressure on its upper surface than on its lower surface. Downwash, or the flow immediately behind a wing, reduces the amount of lift produced. In order to make up for that lost lift, the wing must go to a higher angle of attack, and this change in angle of attack increases the drag generated by the wing. This is known as induced drag because it is "induced" by the process of creating lift. A fish that generated lift in the same way as an aerofoil and utilized it for swimming in mid water column would be expected to display the same lift and drag characteristics with both lift and drag increasing at a positive angle of attack. The aerodynamic efficiency of an aircraft or submarine is measured as lift to drag ratio, or L/D. Its lift is equal to its weight, and the amount of propulsive thrust required is equal to the drag it produces. Therefore, the L/D is the weight that can be carried for a given amount of thrust. The higher the L/D ratio identified for an ostracoderm body form, the more efficient it would be hydrodynamically, and by extension metabolically. Identifying the extent to which generalised forms are optimized for hydrodynamic regimes would be an important first step in understanding the significance of some of the more derived forms, which have points of similarity in their body plan, but display extreme and sometimes bizarre adaptations. If the experimental data suggested that evolution of body form was not driven by pressures to improve hydrodynamic efficiency, then it would have to be explained by other variables such as sexual selection (Douglas *et al.* 2005).

The stability of an object travelling through air or water such as an aircraft is expressed in relation to each of the three axes. Stability in roll is called lateral stability, stability in yaw is called directional stability, and stability in pitch is called longitudinal stability. Lateral and directional stability are interdependent. Moments effecting a change of attitude about the centre of gravity in one plane tend to transfer to other planes. An object may have a different degree of stability around each of the three axes. This is because moments in different planes may, because of the morphology of the object, act differently in relation to the centre of gravity. This is known as 'roll

coupling'. 'Banking' an aeroplane, i.e. rolling relative to the horizontal, achieves a change of direction in that plane much more efficiently than by merely yawing to change direction (McCormick 1976). It may be the case that fish also employed this mechanism.

If an object is totally stable in a given axis then it will return to its trimmed state if moved out of it, without deliberate correction. If an object is positively stable in a given axis, then, when disturbed from its trimmed state, it will move back towards it but over-run it, then start a series of progressively damping oscillations about the original flight state. This damping process is referred to as dynamic stability. Dynamic stability can be quantified as the change in torque per unit rotation about an axis. If an object is neutrally dynamically stable about a given axis it will continue oscillating after disturbance but the magnitude of those oscillations will neither diminish nor increase. A negatively stable or fully unstable object may be statically unstable and have no tendency to return towards the trimmed state. Or it could be statically stable but dynamically unstable, where it will continue oscillating after disturbance with the magnitude of those oscillations getting progressively greater. If it can be demonstrated that the subject's morphology exaggerates the effect of pitch, or yaw when hydrodynamic forces are dominant it will demonstrate that the subject is dynamically unstable. Some modern fighter aircraft are highly dynamically unstable in this way, which greatly increases their manoeuvrability in any given plane, or combination of planes. However, the degree of instability present requires constant corrective inputs from computer control systems in order to retain controllability. If it can be shown that a fish is dynamically unstable in this way, to a less extreme extent, the implication may be that it is capable of relatively rapid changes in direction in the relevant plane, which may be an adaptive advantage, for example in evading predators. Roll coupling can transfer a relatively strong moment due to dynamic instability in a particular plane to other planes, allowing complex evasive trajectories to be followed.

The optimum dimensions to minimise drag in an aquatic animal would be a fusiform body approximately 4.5 times the length of the maximum diameter. Hertel (1966)

calculated that a depth/length ratio (D/L) of 0.22 would result in the lowest surface drag coefficient while a ratio of 0.24 would result in the lowest pressure drag. Videller (1993) wrote that most fast swimming animals had a ratio between 0.18 and 0.28, placing them within 10% of the optimum D/L ratio. Of the ostracoderm genera investigated *Poraspis polaris* comes closest to this morphology. Measurements taken from the model used in these experiments, based on Kiaer & Heintz's (1935) reconstruction suggest a D/L ratio of 0.227 and a fusiform morphology with a near-circular cross section. Based on Hertel's principles *Poraspis* approaches the optimum body shape for minimising drag and a fast swimming lifestyle. The implication is that it would be better suited to a mid water lifestyle than either *Ateleaspis* or *Errivaspis*.

Ecological questions raised

There has been no previous attempt to identify what hydrodynamic and energy budget problems ostracoderms would have encountered while trying to swim upstream or hold station on the bottom, in a fast flowing river. These factors could potentially limit their ability to move in high flow regimes, between habitats. A fish's energy expenditure during locomotion is directly related to the rate of flow in its habitat. Holding station against the flow for example requires continual expenditure of energy (Kemp *et al.* 2006). Migratory fish that have to move upstream as part of their life cycle have some of the highest power to weight ratios of any fish, with species such as blueback herring *Alosa pseudoharengus* being capable of velocities of up to 22 body lengths per second in bursts (Haro *et al.* 2004, Castro-Santos 2005). Higher flow rates also tend to increase the energy expenditure associated with foraging for food and thus limit foraging (Hill & Grossman 1993). To counter increased energy expenditure related to moving into flow, extant fishes have developed a range of mechanisms to counteract oncoming flow. The Atlantic salmon *Salmo salar* can use its pectoral fins as hydrofoils to hold position on the stream bed with negligible effort by adjusting their attitude (Arnold *et al.* 1991). Other species anchor themselves to the substrate using appendages and oral suction (Gerstner 2007). In a flow regime such as a river, an area

of reduced velocity flow close to the bottom, known as the boundary layer, is present. Migratory fish such as salmon utilize this region to reduce energy expenditure while moving upstream (Arnold *et al.* 1991). Experiments where fish are forced to swim into flow continuously show that they must periodically stop to recover (Lee-Jenkins *et al.* 2007) which means that they must either expend energy to remain stationary or evolve mechanisms to counteract flow. The absence of pectoral fins in many ostracoderms would have limited their ability to hold station either by anchorage or adjustment of attitude. This makes flow rates potentially a severe limitation on their ability to move upstream as part of their life cycle, and migrate between habitats.

There has been speculation in the literature that ostracoderms were benthic. This is supported by wear on the underside of carapaces of pteraspids (Denison 1973), and trace fossil evidence suggests that osteostracans were at least periodically benthic (Morrissey *et al.* 2004). Previous experimental investigations into the hydrodynamic properties of ostracoderms have not taken account of the possible physical interaction between ostracoderms and the bottom of the water body they inhabited. Ground effect is a term describing any aerodynamic or hydrodynamic effects occurring due to an objects body moving in close proximity to the ground.

To understand what ground effect is and how it relates to animals swimming in close proximity to the bottom, it is necessary to explain some aerodynamic properties of a wing or aerofoil. When an object in flow produces lift, swirling masses of air or other fluid form off its wingtips or margins. This creates the difference in pressure needed for lift, but the higher pressure flow beneath the wing is pushed around the wingtip to the lower pressure region above the wing. This motion is called a wingtip vortex. As the wing moves forward, this vortex trails behind the wing. This is referred to as a trailing vortex and its effect is to deflect the flow behind the wing downward, an effect known as downwash. When an aerofoil is moving close to a surface such as the ground, that surface partially blocks the trailing vortices and decreases the amount of downwash generated by the wing. This reduction in downwash increases the effective angle of attack of the wing so that it creates more lift and less drag than it would

otherwise (McCormick 1976). The impact of ground effect increases the closer to the ground that a wing operates. As the distance between the wing and ground decreases, the incoming air is forced in between the two surfaces and becomes more compressed. This effect increases the pressure on the lower surface of the wing to create additional lift called ram pressure (Fig. 2). Research into the utilization of ground effect among extant fish is sparse but there are examples. Blake (1978) found that the thrust required by mandarin fish *Synchropus picturatus* to hover was lower while it was in close proximity to the bottom due to ground effect.

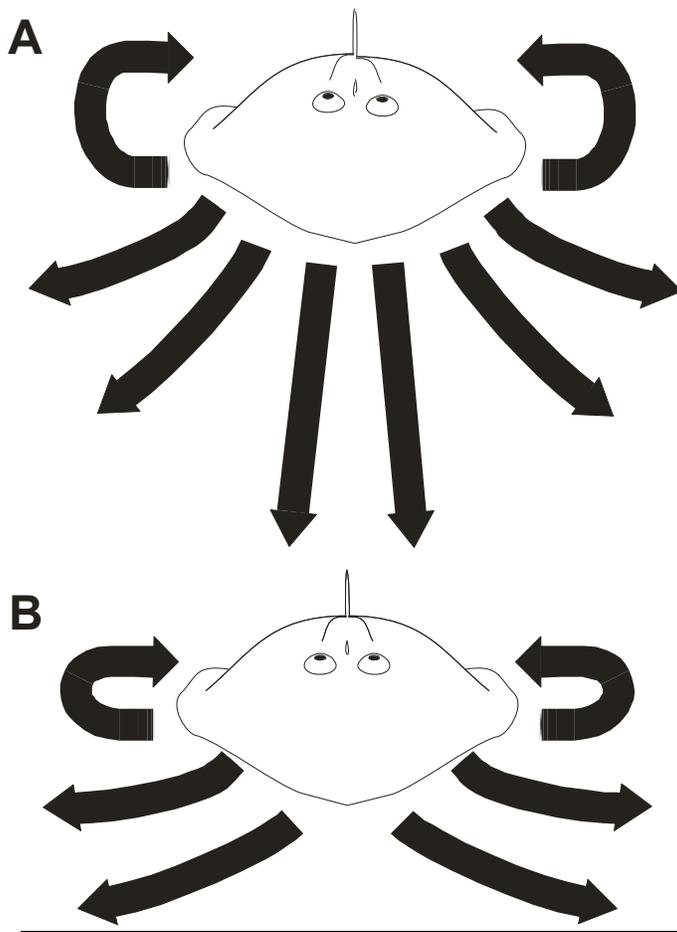


Fig 2. Schematic illustration of ground effect induced forces resulting from the interaction between trailing vortices produced by the fish, *Ateleaspis* and the bottom of the water body. □A. When the fish is swimming in mid flow the vortices produced by it are allowed to flow around the head shield unhindered. □B. When the fish is swimming close to the bottom the vortices are forced between the fish and the substrate producing induced lift or “ram pressure”.

If the fish had morphology prone to producing lift then it would be expected that ground effect would result in increased lift and reduction of drag while swimming in close proximity to the bottom. It would be expected that the area of higher pressure underneath the fish might effect moments in the pitch and yaw axis and therefore stability. Extant benthic fish have a density slightly greater than water which reduces the need to generate thrust to maintain station on the bottom but which also means that they must create thrust to generate lift like an aircraft (Arnold *et al.* 1991). If it could be established that close proximity to the bottom resulted in greater levels of lift in ostracoderm genera, then it would imply that they could utilize ground effect to swim with improved energy efficiency in this region. Ground effect could also have serious implications for the subject's ability to hold station while facing upstream as it might create lift which the fish would have to counteract with thrust. If it could be demonstrated that there was a reduction in pitching moment when the fish were close to bottom then it would suggest that ram pressure had a stabilizing effect.

Moments are used as a mechanism for climbing and diving in marine animals (Miklosovic *et al.* 2004) as well as manoeuvring in species such as the gliding tree frog *Polypedates dennysi* (McCay 2001). One objective of this research was to identify the nature of moments acting upon the three ostracoderm taxa and likely effect upon them. The objective of the project was that the data would identify not only what evolutionary patterns and developments reflect adaptations towards improved hydrodynamic performance, but also what lifestyle these hydrodynamic characteristics were optimised for.

Previous research

Comparisons with extant species

(Dollo 1910) drew comparisons between the ostracoderms and extant benthic rays, arguing that they probably had a similar lifestyle due to their similar cross section and

morphology. He further argued that the flattened bottom, triangular cross section and upward facing eyes of ostracoderms made them suited to a benthic lifestyle. The genera so compared included the osteostracans *Cephalaspis lyelli* and *Ateleaspis tessellata*, and the heterostracan *Drepanaspis gemundenensis*.

Belles-Isles (1987) used morphological comparisons between ostracoderms and extant species to interpret their hydrodynamic function. His work focused on a generalised osteostracan and the pteraspid *Errivaspis waynensis*. He concluded that the osteostracans were generalist swimmers able to employ three separate modes of swimming. He concluded that the pteraspids were specialist swimmers adapted to sustained high speed movement in the open sea but of poor manoeuvrability, like extant tuna.

Previous experimental interpretations of hydrodynamic characteristics

Kermack (1943) investigated *Errivaspis waynensis* using models in wind tunnels and concluded that the body alone could generate enough lift to support the fish in water and that the hypocercal tail evolved to counteract forward lift by depressing the postcranial region. His conclusions about the interaction between the tail and the head shield were based on the assumption that pteraspids had a hypocercal tail, which subsequent work suggests to be erroneous see (Chapter 2).

Bunker & Machin (1991) used a model of a generalised cephalaspid osteostracan in a wind tunnel to investigate the hydrodynamic characteristics of the group. They concluded that the head shield would produce lift even at zero incidence but that this could be offset by a slight deflection of the fins while the fish was stationary on the bottom. They further suggested that the cephalaspids could rest on the bottom even in strong water currents, cruise at moderate speed or swim rapidly at up to eight lengths

per second for short periods, and execute sharp manoeuvres at high speeds in the horizontal and vertical planes.

Botella & Farina (2008) have used wind tunnels to study flow patterns around the head shield of *Errivaspis waynensis*. They conclude that the flow pattern was dominated by leading edge vortices similar to the flow pattern over delta wing aircraft. They further conclude that these vortices not only generated lift but might also have had a stabilising effect. It is also worth noting that these are the type of vortices most instrumental in producing ground effect.

Materials and methods

Use of wind tunnels to interpret hydrodynamic behaviour of ostracoderms

A range of experimental techniques were examined for using actual size models to investigate the hydrodynamic properties of ostracoderms. The facilities at the Engineering Department of the University of Leicester included both wind tunnels and flume tanks. It was decided that a wind tunnel would be used because of the availability of the software package LabVIEW, which measures forces acting on a balance on which a model, in this case of an ostracoderm, is mounted. The use of this software package makes processing and interpreting the experimental data very rapid and efficient. The apparatus used in this investigation included an open ended wind tunnel, a three component force measuring balance from which the model is suspended, and a pitot static tube and manometer upstream of the model measuring velocity head. The three components of force measured by the balance are, fore lift in the vertical plane upstream of the centre of pressure of the model, aft lift in the vertical plane downstream of the centre of pressure of the model and drag acting horizontally. Moment is measured by subtracting the aft lift from the fore lift and multiplying it by half the distance between their action points. Pitching moment, defined as a vertical

force either forward or aft of the centre of balance, was used as an indicator of how the subjects are likely to behave when moving forward or while stationary in flow. Yawing moment, defined as a rotational force around the centre of balance could be measured by mounting the model on its side. The fore and aft lift are added together to produce total lift. The drag was measured directly by the balance. The angle of attack of the model is measured using a protractor built into the mechanism of the balance (Fig. 2). The independent variables which were altered to determine their effect on the dependant variables were the velocity of the airflow and the angle of attack of the model. The dependant variables could be measured in the pitch axis and yaw axis. The angle of attack could be changed to simulate a scenario where the fish was swimming in a straight line, climbing or diving.

Wind tunnels have been used extensively to investigate the dynamic performance characteristics of animals. The first application of this method to fish was undertaken by Harris (1936) who demonstrated that in the extant dogfish *Mustelus canis*, both the pectoral fins and epicercal tail generate lift. Since then they have been used to study both airborne and aquatic species. They have also been used to interpret the hydrodynamic characteristics of extinct species (Kermack 1943, Cruickshank & Skews 1980, Bunker & Machin 1991).

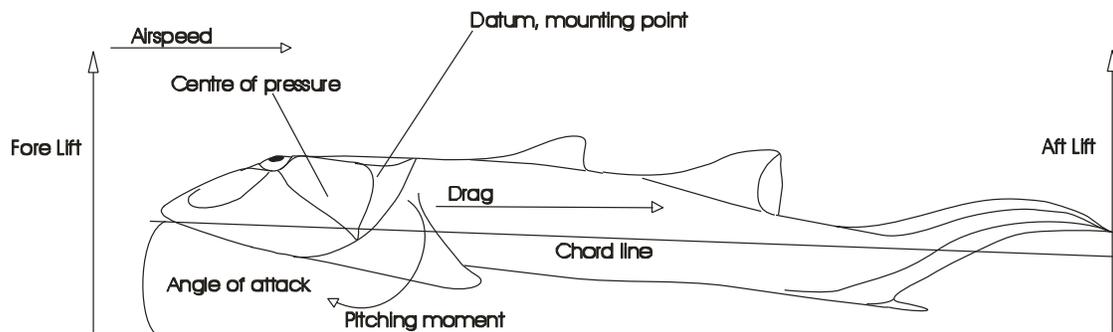


Fig. 2. Terminology and physical forces measured by the LabVIEW software in the wind tunnel experiments, illustrated with *Ateleaspis*.

Dynamic similitude

To understand how a wind tunnel can be used to investigate the performance characteristics of an aquatic animal it is necessary to understand dynamic similitude. This is the principle that all fluids, regardless of their physical properties, behave in much the same way. Dynamic similitude allows tests on a model in a wind tunnel to predict the behaviour of the subject in water if the velocity is increased to produce the same forces. For bodies moving while completely immersed in a fluid, the parameter used to establish dynamic similitude is the Reynolds number:

$$\text{Re} = \frac{\rho V d}{\mu}$$

Re is the ratio between the inertial and viscous forces on the body.

ρ Is the density of fluid (kg/m^3)

V is the velocity of the fluid relative to the body (m/s)

d is a characteristic dimension common to the model and subject (m)

μ is the dynamic viscosity of the fluid (kg/ms or Ns/m^2)

Re is dimensionless.

Similar conditions should be obtained for a model if the Reynolds number is made the same as for the subject being investigated. If the model is in air and the subject in water then:

$$\frac{\rho_a V_a d_a}{\mu_a} = \frac{\rho_w V_w d_w}{\mu_w}$$

Where the subscript 'a' refers to air properties and 'w' water properties.

Water density is affected by temperature and salinity. Based on palaeoenvironmental evidence that the fishes investigated typically lived in fresh or brackish water calculations were based on fresh water. Any effect resulting from moving between habitats was expected to be minimal.

No data currently exists to constrain the speed of ostracoderms. The simulated swimming velocity in the experiments was, of necessity, based on the typical swimming velocity of extant fish of a similar size. The experimental scenarios covered airspeeds corresponding to scenarios ranging from typical cruising speeds in extant fish in extant fish which can be up to two body lengths per second (Videller 1993) to maximum burst speeds that would only be attained while fleeing from predators or counteracting extreme flow regimes. The maximum airspeed of the wind tunnel was 38 m/s airspeed corresponding to 2 m/s in water or sixteen body lengths per second, which falls within the range observed in living migratory fish during short bursts, while fleeing from predators or attempting to counteract extreme flow regimes (Castro-Santos 2002, 2005). The models were the same size as the actual fish, which made it unnecessary to calculate the effects of scale in the equation. The ambient air properties at the time of the tests were determined by recording the atmospheric pressure and temperature prior to commencing each test. The building in which the wind tunnel is housed is heated so ambient temperature was fairly consistent. With the above data the relationship between airspeed and velocity of water can be determined by the following equation.

$$V_a = \frac{P_w \mu_a V_w}{P_w \mu_a} = \frac{999.19 * 1.82E^{-5}}{1.2 * 0.001139} \quad 1 = 13. \text{m/s}$$

That is to say that an airspeed of 13 m/s is equivalent to a water flow rate of 1 m/s or approximately four body lengths per second for any of the ostracoderm genera modelled.

Modifications to models reflecting latest research

The models used in the tests were based on casts of a set produced by the Open University. While the models were dimensionally correct in most respects they displayed a number of anatomical inaccuracies which made it necessary to modify them. The *Errivaspis* model had an elongate lower tail lobe or hypocercal caudal fin. *Errivaspis* has traditionally been reconstructed with an elongate ventral lobe as described by White (1935) which has since been challenged by (Blieck 1984) who produced a new reconstruction where the extended lower lobe was removed. The material described by White was examined and it was concluded that the elongate lower tail lobe was an artefact of material lost from the specimen. Measurement of the specimens suggested that the ventral margin reflects the actual length of the caudal fin which is of a homocercal or near homocercal morphology see (chapter 2). A new reconstruction of the caudal fin of *Errivaspis waynensis* is therefore proposed with a narrow homocercal morphology comparable to that observed in other pteraspidiformes (Gross 1963, Denison 1971, Dineley 1976, Soehn & Wilson 1990, Pernegre 2003A, Pernegre 2003B, Pernegre 2005). This type of morphology is typically found in extant fish that are adapted for rapid acceleration rather than high efficiency cruising (Woodward *et al.* 2006). Novitskaya (2000) has published a new reconstruction of the caudal fin of *Anglaspis* with a less downwardly pointed morphology and five supporting lobes. The postcranial region of the *Poraspis* model used is reconstructed on Heinz's (1932) illustration of the closely related *Anglaspis*. The caudal fin of the *Poraspis* model was modified to reflect Novitskaya's new reconstruction which was based on a more complete examination of the same material (Fig. 3).

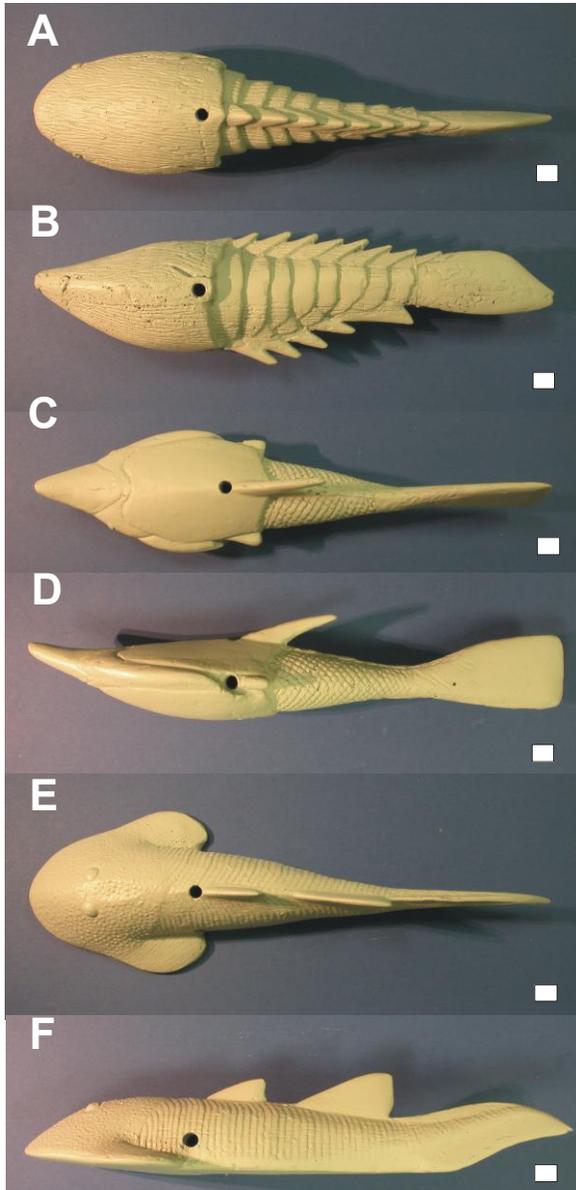


Fig. 3. Illustration of the models featured in the wind tunnel experiments. □A. *Poraspis polaris* in dorsal view. The shape and dimensions of the head shield are based on drawings by Kiaer & Heintz (1935). □B. *Poraspis polaris* in lateral view. The postcranial region is based on drawings of *Anglaspis* by Kiaer (1932) but the caudal fin has been modified to take account of Novitskaya's (2000) reconstruction. □C. *Errivaspis waynensis* in dorsal view based on Blicek's (1984) reconstruction. □D. *Errivaspis waynensis* in lateral view. The model is based on Blicek's (1984) reconstruction but modified with an elongate near symmetrical caudal fin morphology based in the research described in chapter 2. □E. *Ateleaspis tessellata* in dorsal view based on Janvier's (1996) reconstruction. □F. *Ateleaspis tessellata* in lateral view. Scale bar = 1 cm in all pictures.

Set-up and experimental procedure

A screw thread was drilled into each model transversely, allowing it to be suspended in a conventional swimming orientation for recording forces in the pitch axis. A second screw thread was drilled into each model dorsoventrally, allowing the models to be mounted on their side when recording forces in the yaw axis. The models were attached by the drilled thread to a threaded probe which attached to a two component balance. The angle of attack was altered manually using a protractor dial. The software package LabVIEW was used to record forces acting upon the balance. The software can be used to record a large number of physical parameters but the dependant variables relevant to this study were lift, drag and moment, which were studied in relation to flow velocity and angle of attack.

Fixed velocity test method.- In a fixed velocity test the angle of attack is altered at a chosen interval, in this case increments of 5° from -35° to $+40^\circ$, with the dependant variables being measured at each stage by the LabVIEW software. The velocity remains constant over the duration of the test. All of the fixed velocity experiments were carried out at an airspeed of 19 m/s, which corresponds to a swimming speed of 8 body lengths per second. This is a typical maximum burst speed observed in extant fish (Webb 1975), though much higher swimming speeds have been recorded in migratory fish (Castro-Santos 2005). The purpose of these tests was to determine how the dependant variables recorded by the software were affected by variation in the angle of attack of the fish. This identified the forces that acted upon the fish while they were either ascending or diving, and allowed us to compare the effects of angle of attack upon the three genera chosen for the study. The process was repeated ten times for each model to identify inconsistencies and potential sources of error in the data.

Fixed angle test method.- Fixed angle tests were conducted for all three ostracoderm genera. They were used to compare the hydrodynamic characteristics of the fish, at different velocities and a fixed attitude. A test with the model mounted facing into the flow at an angle of attack of 0° was used to test for lift drag and pitching moment that

the fish would have been subject to while swimming forward or facing into flow. A second set of tests were conducted with the models mounted on their sides, which measured yawing moment. In fixed angle tests the velocity of the air stream was progressively increased from 0-38 m/s, with the dependant variables being logged at nine increments starting at 20% of maximum airflow speed and increasing in increments of 10 % up to 100% or the maximum output possible for the wind tunnel. The highest velocities simulated at an airspeed of 38 m/s would correspond to speeds of sixteen body lengths per second which fall well within the maximum recorded for extant migratory fish (Castro-Santos 2005). While such velocities were theoretically possible for the genera, they would only occur in short bursts of 20 seconds or less while the fish was evading predators or trying to counteract the effects of oncoming flow. The mean velocity of most major rivers worldwide is under 1 m/s (Schulze *et al.* 2005). It was deemed desirable to simulate a similar flow in a situation where the fish was facing upstream, and to interpret the energetic demands that such an environment would place upon the fish. The apparatus could simulate scenarios where the fish was swimming upstream into flow velocities of up to 4 m/s which would be an extreme flow regime. The angle of attack remains constant throughout the test but it can be set to the desired level at the start. An angle of zero was chosen for the majority of tests.

Set-up of ground effect experiments

The interaction of the fish with the bottom of the water body was investigated to determine whether they were subject to any ground induced effects while close to the bottom which might have been relevant to their hydrodynamic performance. In order to do this, a conveyer belt was manufactured over which the models were mounted in the wind tunnel. The oncoming airflow was used to simulate both the forward motion of the fish and water flow that the fish was facing into. The conveyer belt was necessary not just to provide a surface for the models to be mounted over but also to simulate the movement of the fish relative to the bottom while it was swimming. In simulations where the fish was stationary on the bottom facing into the current the belt

remained stationary. The belt was covered with sand of a similar grade to river sediment to make the simulation as realistic as possible. When the experimental scenario involved the fish swimming close to the bottom, the belt turned in the opposite direction to the simulated direction in which the fish was swimming (Fig. 4). All tests involving the belt followed the pattern of data recording for the fixed angle tests where the belt was absent, to allow direct comparison. The fact that a range of flow velocities were investigated reduced the imperative for interpreting the environmental conditions that the fish lived in as the experiment simulates scenarios ranging from still water to a river with high flow velocity. The deep dorsoventral shape of *Poraspis* prevented the model from being mounted over the belt because the mounting point had to be higher than on the other two models, so the ground effect tests could only be conducted for *Ateleaspis* and *Errivaspis*.

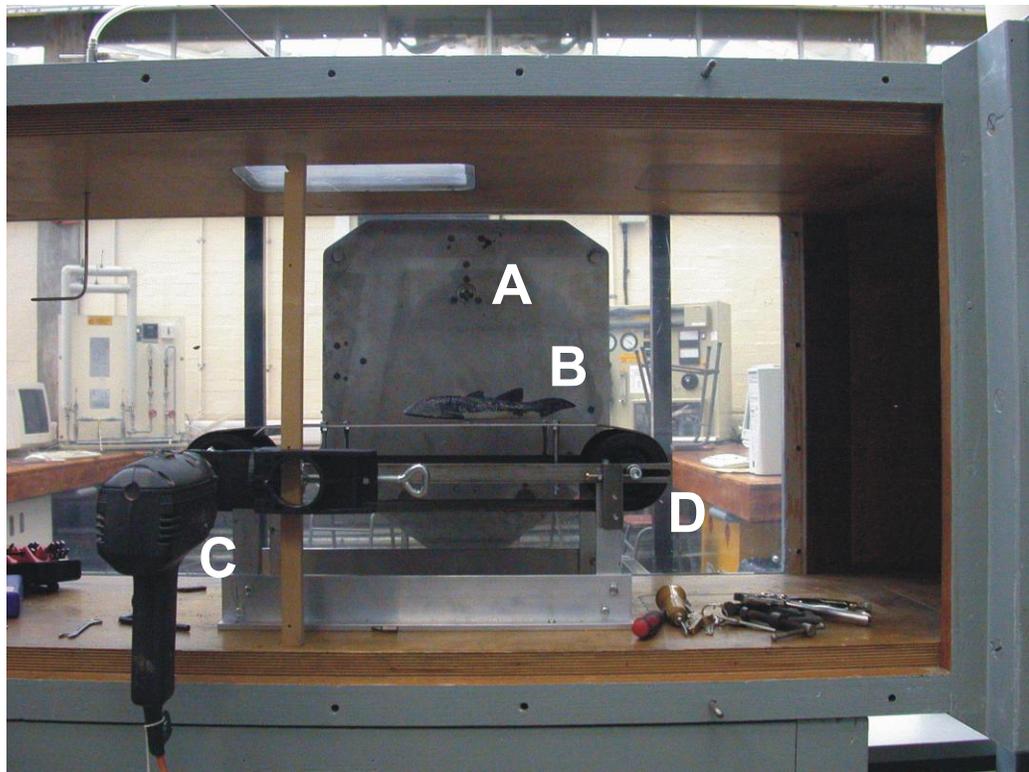


Fig. 4. Experimental setup of the ground effect simulations. □A. The protractor dial used to set the angle of attack of the model. □B. The model in this case *Ateleaspis*, is shown mounted over the conveyer belt. □C. An electric drill is used to power the conveyer belt. □D. The conveyer belt is bolted to the base of the wind tunnel and can be removed when required.

Ground effect test with a stationary fish.- To simulate a stationary fish, the model was mounted in the wind tunnel over the inactive conveyer belt facing into the oncoming airflow . The test was intended to determine what forces the fish would be subject to and what metabolic costs it might consequently incur holding station facing upstream. The scenarios simulated included the model facing into airflow with centre of balance 15 mm above the belt at 0° angle of attack and the same attitude with the fish moved to within 5mm of the belt to determine how forces acting upon the fish changed as it moved closer to the bottom. With the model mounted 15 mm above the belt it was possible to alter the angle of attack by up to 5°. This made it possible to simulate the forces that the fish would be subject to at the moment it attempted to move itself clear of the bottom at either positive or negative attitude. Simulations were run with the model mounted 15 mm above the belt with the nose facing 5° downward. The hypothesis being tested was that the fish might assume positive attitudes to utilize currents to gain lift when it wanted to get clear of the bottom and assume negative attitudes to reduce the lift-inducing effects of the current while attempting to maintain station on the bottom.

Ground effect test with a moving fish.- When investigating the implications of ground effect for swimming fish the model was mounted over a moving conveyer belt with the wind tunnel running. This simulates the fish swimming close to the bottom allowing for the effect of the movement of the fish relative to the bottom on ground effect. The conveyer belt was run at a velocity of 12 m/s corresponding to a swimming speed of about four body lengths per second. The airspeed was incrementally increased, as in other fixed angle tests, to simulate scenarios ranging from the fish swimming in still water and slower to scenarios where it was swimming into oncoming flow of 2 m/s or about 8 body lengths per second. The available motor and gearing did not make it possible to run the belt at velocities higher than 12 m/s. Comparing the data with the belt running to the tests where the belt was inactive made it possible to identify the effects of the movement of the fish relative to the bottom on ground effect induced forces.

Limitations and assumptions

A number of limitations are inherent to the experimental method. The models used are static and cannot take account of hydrodynamic variables resulting from deformation of the body. Forces likely to be relevant to the hydrodynamics of the fish include forces resulting from the tail beat cycle while the fish is swimming which might exaggerate or counteract the physical variables of lift drag and moment measured by the balance. This limitation does not however affect the experiments that simulate scenarios where the fish is attempting to maintain station on the bottom. The available apparatus cannot measure the effects of roll which is unfortunate because it might have helped to interpret the ability of the fish to maintain a stable trajectory without the aid of pectoral fins. The facilities did not permit flow visualisation which means that the forces acting on the fish must be interpreted solely from the forces measured by the balance.

Some of the velocities simulated were very high and in many cases would only correspond to maximum swimming speeds or extreme flow regimes. It was necessary in some cases to make inferences based on these higher swimming velocities because the data contained too much noise at velocities that would correspond to typical cruising speeds in extant fish. In hindsight it would have been desirable to work with much larger scale models, rather than the life size models used, in order to produce more sensitive data at lower velocities.

The morphology of the models was based on the best available interpretation of the gross anatomy of the fishes. All the models were compared to the best available material of the genera they represented to ensure that they were dimensionally accurate and were modified where appropriate. In some cases the material of the postcranial region was partially disarticulated and material was missing from the caudal fin area. It is possible that discovery of better specimens in the future could force re-evaluation of the postcranial anatomy of the genera investigated in these experiments. The hard body parts of the fossils such as the head shield were subject to sedimentary

compression which meant that the three dimensional anatomy had to be interpreted based on comparison of multiple specimens in some cases.

Initially the fixed velocity tests looked at angles of attack ranging from -40° - $+40^{\circ}$. An abnormally large amount of variation was found to be occurring specifically at an angle of attack of -40° . For this reason it was decided to run the fixed velocity test from angles of -35° to $+40^{\circ}$.

Summary of potential sources of error and their effects

Aerofoil tests.- The data for the fixed velocity tests produced a lot of variation between ten separate runs. It was necessary to identify whether this noise was an artefact of the low forces acting upon the models combined with the lack of sensitivity of the software, or a result of physical forces acting upon the models. In order to identify the processes taking place, the same experiment was conducted with a model aerofoil. The aerofoil was the same length as the ostracoderm models but much wider with a larger dorsal and ventral surface area. This was intended make the aerofoil more stable in flow than the model fish and identify whether oscillations in pitching moments and lift were an artefact of the fishes morphology or underlying error. The aerofoil tests produced data with very little noise in lift, drag or moment. Although the aerofoil produces greater lift than the models at equivalent velocities due to its shape it creates noise free data even at lower velocities where it produces levels of lift comparable to the ostracoderm models at higher velocities (see appendix). This suggested that the noise does not reflect lack of precision in the software but is a consequence of forces acting upon the models. Given that the variation in the data cannot be attributed to the lack of sensitivity of the apparatus it is concluded that there is considerable oscillations in the lift and moment acting upon the models at a given velocity or angle of attack. The most likely explanation for this is the process known as Karman vortex shedding. When a vortex is shed, an unsymmetrical flow pattern forms around the body, which therefore changes the pressure distribution. This means that the alternate shedding of

vortices can create periodic lateral forces on the body in question, causing it to vibrate. This phenomenon is observed in extant fish and several key features of the nervous system, such as the lateral line, have evolved to allow them to react to shedding vortices (Triantafyllou & Triantafyllou 1995, Triantafyllou *et al.* 2002).



Fig. 5. Tests were carried out with a model aerofoil to determine whether variations in the data were a result of underlying error in the balance and software or a result of turbulent flow around the models. The aerofoil was a shape well suited to producing laminar flow and the same length as the models.

Trouble shooting tests.- In order to assess the reliability of the wind tunnel data, trouble shooting tests were conducted using the *Ateleaspis* model. They consisted of re-running the experiments with the wind tunnel switched off and recording the physical variables of lift drag and moment as measured by the software. Any deviation of these variables from zero would be attributable to underlying error in the apparatus recording these forces. By comparing the underlying error to the trends in the wind tunnel data it was possible to determine whether they could be explained by the underlying error.

The data for *Ateleaspis* with the wind tunnel running was also examined for potential sources of error and to provide comparison with the “wind off” data. Comparison between the wind on and wind off data made it possible to distinguish the component of error that resulted from inaccuracies in reading of the dependant variables by the balance or software and any that resulted from inconsistencies in the dependent variables such as wind speed.

The data was examined to identify cumulative error in the independent variable and possible effects on the dependent variable. At the beginning of each experiment the angle is manually reset to 0° using a protractor dial. The fact that it has to be reset by eye, presents a potential source of error. An example of cumulative error would be protractor creep where an incremental change in angle of attack is imposed every time the protractor that regulates angle of attack is reset to zero between runs. The wind off and wind on data were both examined for any cumulative change taking place during the course of a single fixed velocity run out of a sequence of 10, and between subsequent runs. No pattern of cumulative change in the data was found in either the dependent or independent variables.

Testing for significance.- In order to determine the validity of experimental results significance tests had to be applied. It was also necessary to determine whether the error in the wind off data was sufficient to account for the observed trends in the wind on data. This was done by comparing the sample variance of the wind off data to the sample variance of the wind on data using an F test. None of the dependent variable produced P values that would imply that the wind on data could be an artefact of underlying error (see appendix).

Results

Effect of variation in angle of attack on *Poraspis*, *Errivaspis* and *Ateleaspis* (fixed velocity test)

The overriding finding of the fixed velocity tests is that *Poraspis* and *Errivaspis* behaved in a similar manner to one another in terms of the drag and moment characteristics and very differently from *Ateleaspis* suggesting that they were differentiated functionally from the osteostracan genus (see Figs. 6, 7).

Lift.- In the fixed velocity tests the all three of the ostracoderm models showed comparable and progressively increasing lift as the angle of attack was changed from 0° to +40° (Fig. 6). This is similar to the characteristics of an aerofoil which produces greater lift at higher angles of attack as they counteract downwash. At negative angles of attack from 0° to -35° *Errivaspis* and *Ateleaspis* both produced negative lift while *Poraspis* continued to produce neutral positive lift until it was at an angle of attack of -20° or greater. This would make *Poraspis* inherently less able to execute a steep dive. The *Poraspis* model also produced greater lift in a neutral angle of attack than the other two taxa.

Drag.- All three genera showed progressively increased levels of drag when the angle of attack deviated from 0° either positively or negatively (Fig. 7). While the drag produced by *Poraspis* and *Errivaspis* was comparable at all angles of attack, that produced by *Ateleaspis* was consistently higher. The lift to drag ratio at a given angle of attack can be taken as a measure of the hydrodynamic efficiency of the body form of the fish at that angle of attack. Comparison of figures 6 and 7 shows that *Ateleaspis* generates more drag than *Poraspis* and *Errivaspis* at all angles of attack from -35° to +40° while only generating equal or inferior lift. This means that it was less hydrodynamically efficient than the other two taxa at all angles of attack. It would have been least efficient relative to *Poraspis* and *Errivaspis* while diving at negative angles of attack. *Poraspis* and *Errivaspis* display comparable drag to one another at all angles

of attack but *Poraspis* displays greater levels of lift at neutral or negative angles of attack. This suggests that *Poraspis* was the most hydrodynamically efficient of the three at a neutral angle of attack in mid water column and indeed at all attitudes except steep ascents.

Pitching moment.- *Poraspis* and *Errivaspis* produced comparable pitching moments at all angles of attack with the recorded moment increasing incrementally from -35° to $+40^\circ$. *Ateleaspis* displays the same positive relationship between angle of attack and pitching moment but produces significantly lower recorded pitching moments at all angles of attack (Fig. 8).

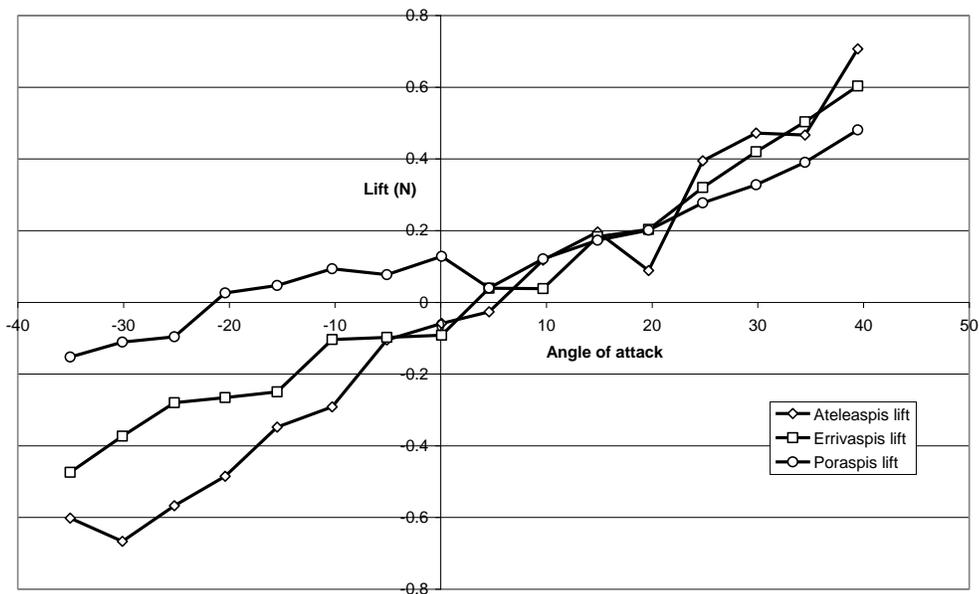


Fig. 6. Lift in *Poraspis*, *Errivaspis* and *Ateleaspis* in a fixed velocity test. Displayed data represents a mean of 10 runs for each of the three ostracoderm genera. The models were mounted on the wind tunnel balance and the angle of attack was incrementally changed from -35° to $+45^\circ$ with the lift being logged at increments of 5° . The airspeed remained at a constant 50% of wind tunnel output or 19 m/s airspeed which corresponds to a velocity in water of 2 m/s. or approximately eight body lengths per second

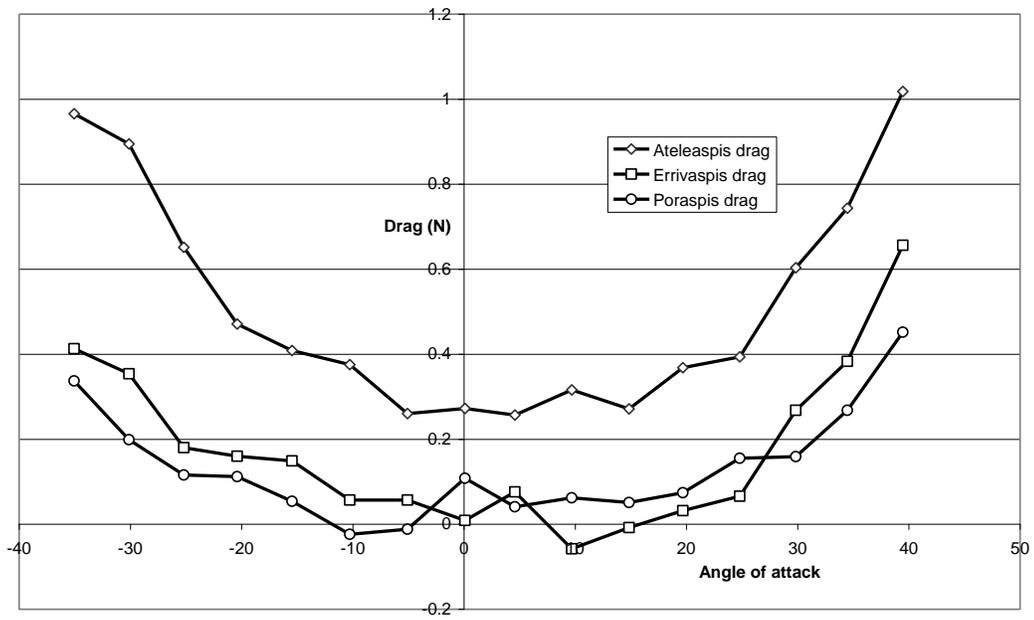


Fig. 7. Drag in *Poraspis*, *Errivaspis* and *Ateleaspis* in a fixed velocity test. All other experimental details are as with Fig. 5.

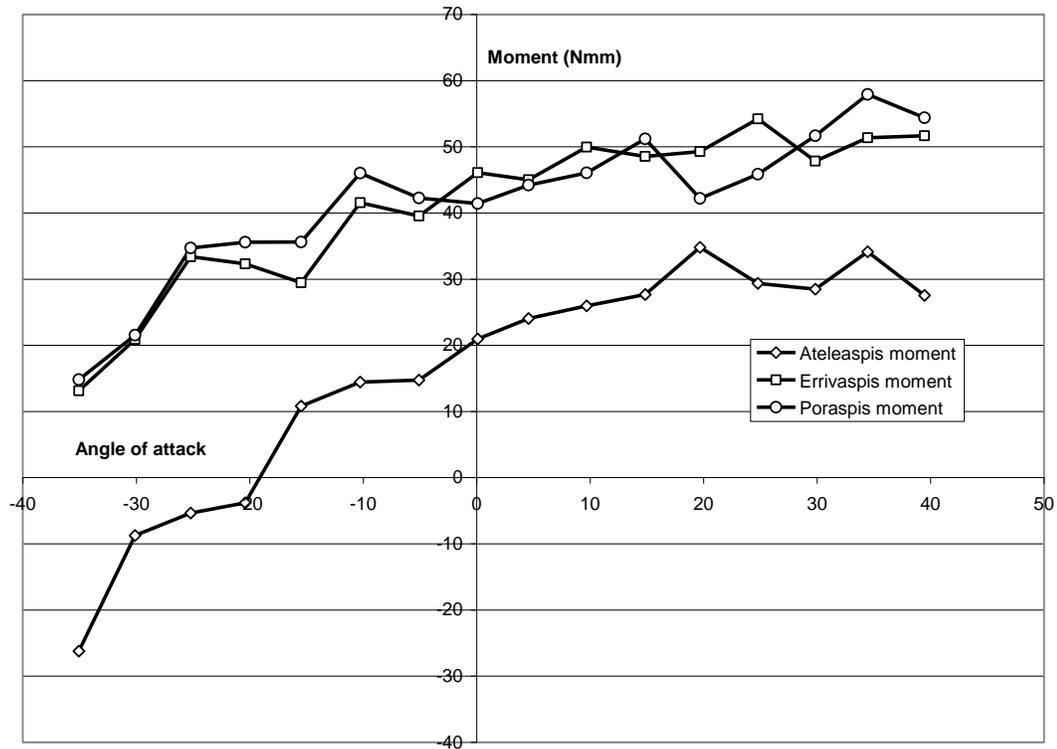


Fig. 8. Pitching moment in *Poraspis*, *Errivaspis* and *Ateleaspis* in a fixed velocity test. All other experimental details are as with Fig. 5.

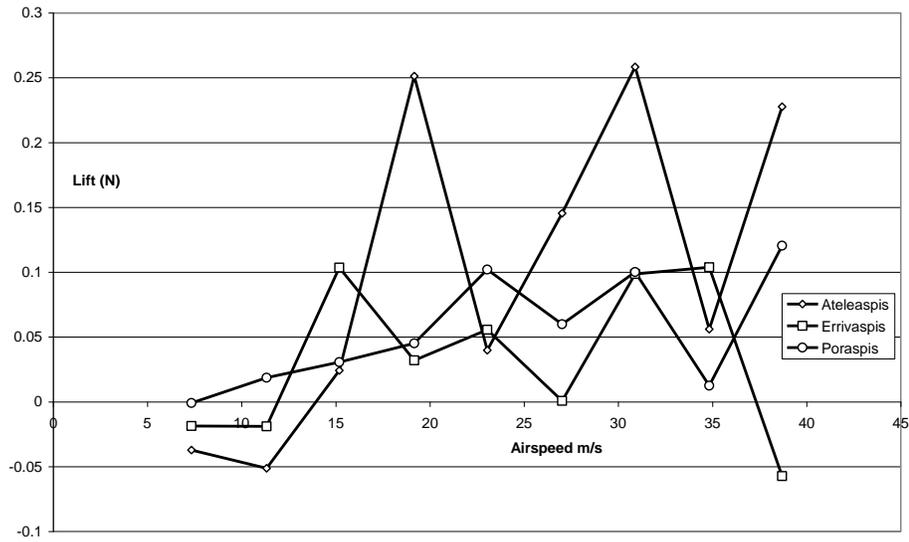
Effect of variation in velocity on *Poraspis*, *Errivaspis* and *Ateleaspis* (fixed angle tests)

Lift.- *Ateleaspis* displays more erratic lift than the other two taxa in the fixed angle tests. While its lift is generally at a similar level it displays sharp spikes (Fig. 9). This factor was not apparent from the fixed velocity tests and is attributable to pitching moments.

Drag.- There is little to separate the three genera in terms of the drag they produce in the fixed angle tests (Fig. 10). The differences only become significant at higher velocities which would only be attained when the subject was attempting to evade predators or overcome extreme flow regimes.

Pitching moment.- When looking at pitching moments in the fixed velocity tests it is apparent that pitching moments are greater at lower velocities, with higher moments and greater oscillations (Fig. 11). This holds true both for the tests where the model is suspended in mid airflow and those where it is mounted over the belt, (Fig. 14). This phenomenon is often observed in aeronautics as pressure produced at higher velocities can correct moments. The velocities where the fish would benefit from this correcting force would correspond to higher end burst speeds, and it would only be a factor when they were evading predators or attempting to counteract oncoming flow. It might however have made it easier for the fish to hold station in stronger water currents. The data suggests that ostracoderms would have been able to utilise positive and negative pitching moments to climb and dive respectively at normal cruising velocities.

Yawing moment.- When looking at yawing forces a different pattern emerged to that observed with pitching forces. All three ostracoderm taxa were subject to strong yawing forces at higher velocities but not at lower velocities that would correspond to typical swimming speeds. The *Ateleaspis* displays significantly higher yawing moments at speeds of eight body lengths per second or less than the other two taxa (Fig. 11). To put the likely effect of these moment forces on the fish into perspective, the pitching and yawing forces that the fish are subject to over the normal range of swimming speeds are significantly greater than recorded lift or drag. This means that of all the physical variables measured in the fixed angle tests, moment would have the most dominant effect on the fishes while they were swimming in mid water column.



Fi

g. 9. Lift in *Poraspis*, *Errivaspis* and *Ateleaspis* in a fixed angle test. Data represents a mean of ten runs for each of the three ostracoderm genera. The models were mounted on the balance at an angle of attack of 0° and the velocity was set at 20% of maximum wind tunnel output or airspeed of 7 m/s. The airspeed was increased in increments of 10% up to 100% of wind tunnel output and airspeed of 38 m/s.

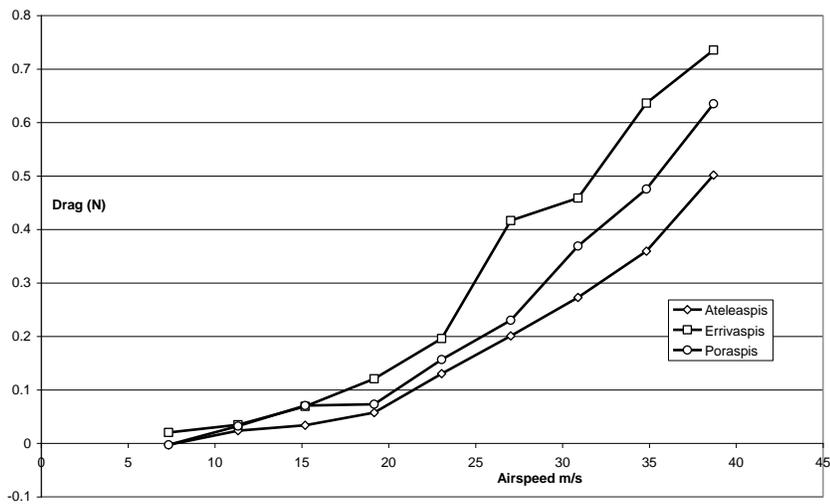


Fig. 10. Drag in *Poraspis*, *Errivaspis* and *Ateleaspis*, in a fixed angle test as a mean of ten runs. All other experimental details are as with Fig. 9.

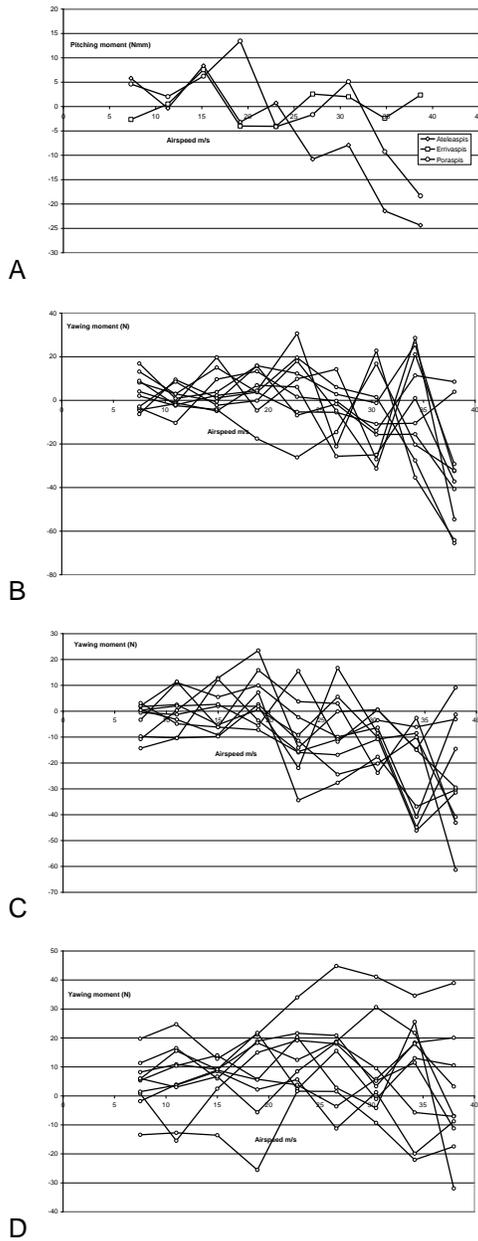


Fig. 11. Yawing Moments in *Poraspis*, *Errivaspis* and *Ateleaspis*, in a fixed angle test. □A. compares the mean pitching moments for each genus as a mean of ten runs. □B. Shows recorded yawing moments in all ten runs for *Poraspis*. □C. Shows recorded yawing moments in all ten runs for *Errivaspis*. □D. Shows recorded yawing moments in all ten runs for *Ateleaspis*. Yawing forces are not shown as means because the models are symmetrical, and recorded moments are equally likely to be positive or negative. Other experimental details are as with Fig. 9.

Impact of ground effect on *Ateleaspis* and *Errivaspis* (fixed angle tests)

Lift.- If the *Ateleaspis* model is mounted 15 mm above the conveyer belt at a given velocity, in a neutral angle of attack then lift is greater than in tests simulating the fish is in mid water column. Moving the model closer to the belt so that it is mounted 5mm above it produces a four fold increase in recorded lift over the scenario where it is mounted 15mm above the belt. The fact that the model produces higher lift in closer proximity to the belt demonstrates the presence of ground effect, the fact that the effect is exaggerated at higher velocity shows ram pressure. When comparing lift in *Errivaspis* to *Ateleaspis* it quickly becomes apparent that the *Ateleaspis* produces far stronger ground effect induced lift (Fig. 12a), and would be far better adapted to utilizing this lift while swimming, probably due to its flat bottomed cross section. It would be expected that both of them will generate more ground effect related lift than laterally compressed extant fish such as trout. *Errivaspis* does not produce higher levels of lift when mounted 5 mm above the belt relative to when it is mounted in mid flow. Indeed the recorded lift is actually less while the model is mounted over the belt (Fig. 12b). This could be explained by vortices flowing over the top of the fish being increased by ram pressure and producing pressure on the dorsal surface of the head shield. Such vortices were observed in wind tunnel tests conducted by Bottela & Farina (2008). The results suggest that *Errivaspis* would have produced minimal lift at typical cruising velocities, though it could still have benefited from some hydrodynamic and metabolic assistance while swimming in mid water

In terms of recorded lift the *Ateleaspis* model behaves very much like an aircraft moving in close proximity to the ground. Of the two genera subject to the ground effect tests, only *Ateleaspis* is likely to have been able to utilize ground induced forces to its metabolic advantage at typical swimming velocities for a fish of this size. Lowering the angle of attack of the model by a matter of five degrees, above the belt increases the lift and dramatically reduces the oscillations in the data. On tests before the belt was installed where ground effect was absent such slight changes in angle of attack did not produce significant changes in lift or noise levels. This suggests that lift

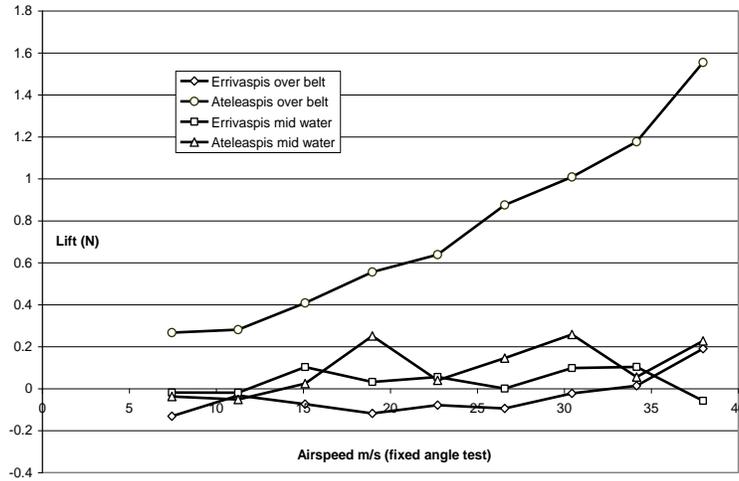
is more uniform under ground effect conditions and that *Ateleaspis* was well suited to getting itself clear of the bed quickly if threatened by a predator, for example. With negative angles of attack the trend runs counter to what has been observed with the model mounted in mid flow. Pointing the nose downward increases lift in proximity to the belt while it reduces lift in mid water column (Figs 6 and 13).

Drag.- The drag data shows little change in *Errivaspis* or *Ateleaspis* when mounted closer to the belt at airspeeds under 18 m/s which correspond to realistic swimming speeds. *Errivaspis* produces greatly elevated levels of drag at airspeeds greater than 18 m/s (Fig. 14). The fact that *Ateleaspis* is producing elevated lift for comparable levels of drag close to the belt means that it would have had a lower lift/drag ratio while swimming closer to the bottom and would therefore have been more hydrodynamically efficient. *Errivaspis* in contrast would have enjoyed no similar benefit. The elevated levels of drag produced by *Errivaspis* at higher flow velocities would not have affected it while swimming in still water but could have placed a significant energetic burden if it was trying to swim upstream in a fast flowing river. The critical consequence of the data is that swimming at maximum output, *Ateleaspis* would attain maximum hydrodynamic efficiency swimming close to the bottom while *Errivaspis* would be most efficient in mid water column. *Ateleaspis* would have been able to sustain an active benthic lifestyle far more efficiently than *Errivaspis* either in lacustrine or fluvial environments.

Pitching moment.- The *Errivaspis* model produces lower pitching moments when mounted above the belt relative to when it is mounted in mid flow. As with the lift there is no apparent ground effect induced trend. When the *Ateleaspis* model is mounted close to the belt it produces more uniformly high pitching moments than it does when mounted in mid flow (Fig. 15). This trend in *Ateleaspis* is probably attributable to ram pressure which would be expected to dampen random oscillations or pitching moments while producing higher levels of pressure. As with lift the flat ventral surface of *Ateleaspis* accounts for these trends. This produced an unexpected line of evidence when it was found that variation of recorded forces in the ground

effect tests, with the wind tunnel switched on, was less than in the control tests with the wind tunnel switched off. This confirmed that the underlying error in the data was not an artefact of the software since if this were the case it would be expected that the error would be at least as great with any “wind on” data. The implication of this trend is that the error is a result of instability in the balance and that the model fish has a stabilising influence when subject to ground effect. This combined with the fact that pitching moments are lower in the ground effect scenarios suggests that ground effect induced vortices might have stabilised ostracoderms while swimming close to the bottom.

A



B

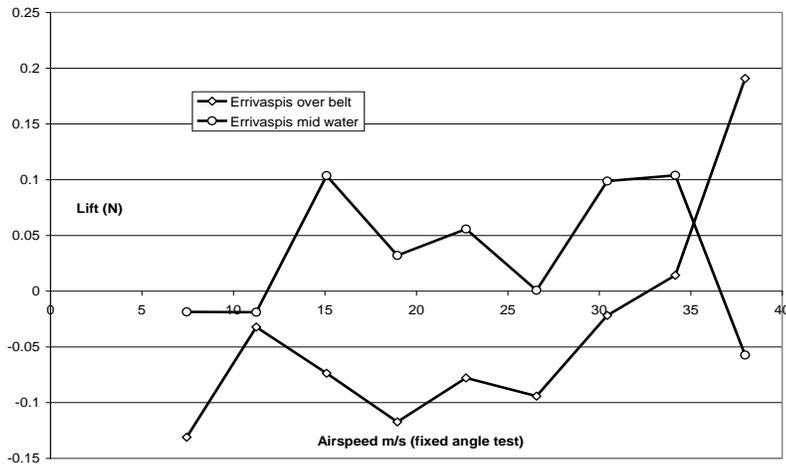


Fig. 12, Comparison of the impact of ground effect on *Errivaspis* and *Ateleaspis*. In all tests the angle of attack of the model is set at 0° and the velocity was set at 20% of maximum wind tunnel output or an airspeed of 7 m/s, then increased in increments of 10% up to 100% of wind tunnel output and an airspeed of 38 m/s with the lift being recorded at each increment. □A. Compares a simulation where the model is mounted in the wind tunnel clear of any surfaces to a simulation where the model is mounted 5 mm above a stationary conveyer belt in *Errivaspis* and *Ateleaspis*. □B. Focuses on the lift produced by the *Errivaspis* model mounted 5mm above the belt, compared to when the model is mounted in mid flow, as illustrated in 11A.

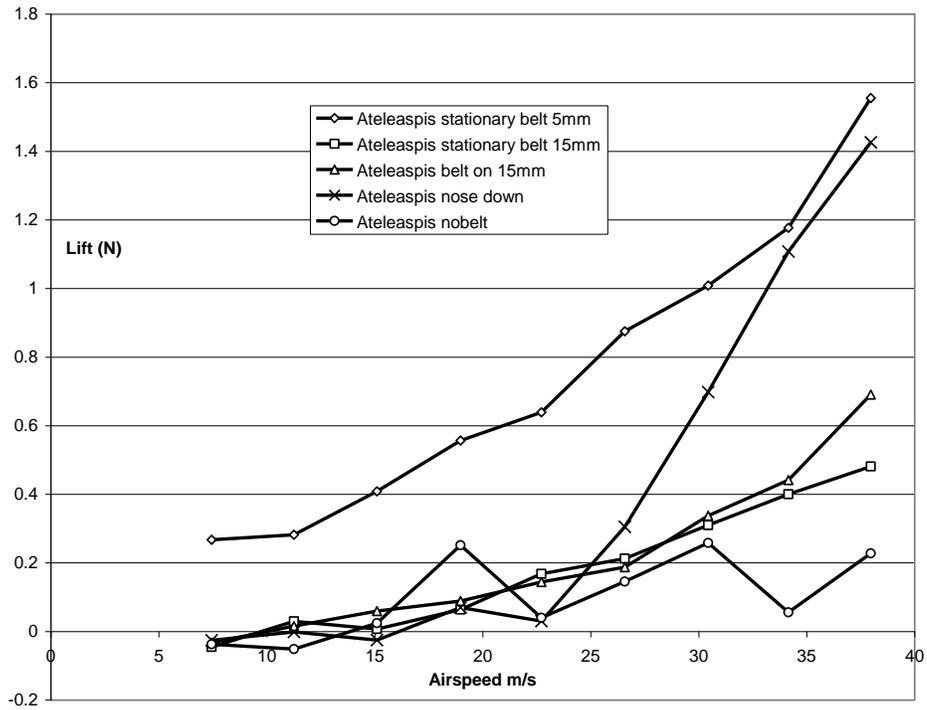


Fig. 13. The effect upon forces acting on the *Ateleaspis* model of mounting it closer to the belt. Compares a simulation where the model is mounted in the wind tunnel clear of any surfaces to a simulation where the model is mounted 15 mm above a stationary conveyer belt and a situation where the model is mounted 5mm above a stationary conveyer belt. Also shown are a scenario where the *Ateleaspis* model is mounted 15 mm above a moving conveyer belt and a scenario where it is mounted 15 mm above a stationary conveyer belt with the fore end angled 5° downward.

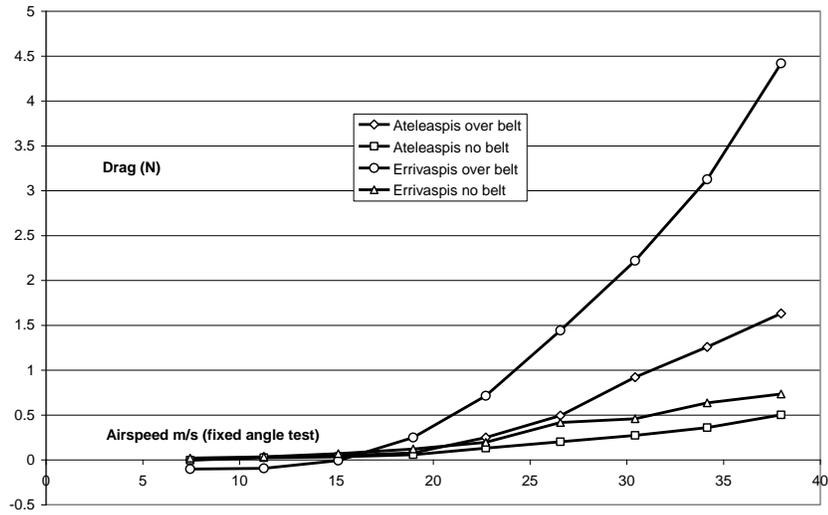


Fig. 14. Drag in *Errivaspis* and *Ateleaspis* in a fixed angle test while suspended 5 mm above a stationary conveyer belt compared to a scenario where the models are mounted in mid flow. All other experimental details are as with Fig. 12.

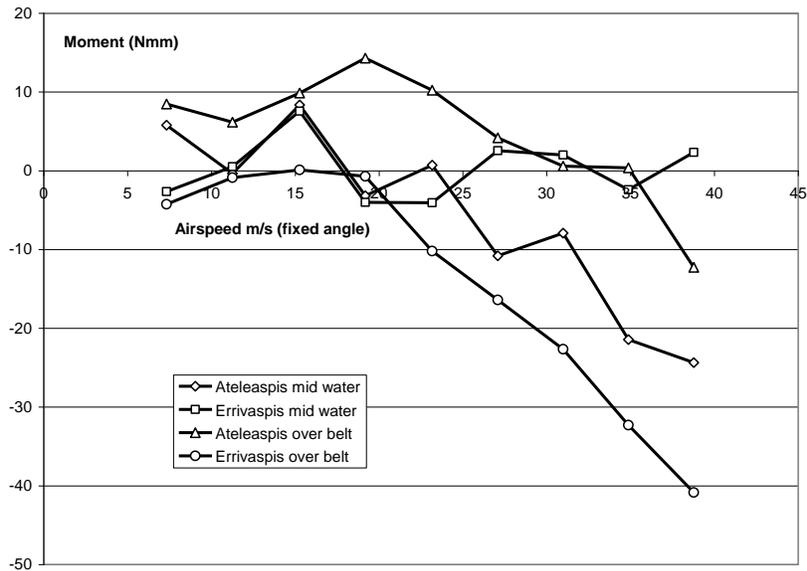


Fig. 15. Pitching moment in *Errivaspis* and *Ateleaspis*, in a fixed angle test while suspended 5 mm above a stationary conveyer belt compared to a scenario where the models are mounted in mid flow. Other experimental details are as with Fig. 11.

Effect of moving belt.- When the automated conveyer belt is moving at a speed of 12 m/s, lift produced by the *Ateleaspis* model mounted 15 mm above the belt increases moderately at high velocities (Fig. 14). The increase is minimal at biologically realistic speeds so it is acceptable to take data obtained with the belt stationary as being representative of scenarios when the fish is swimming. The increase is probably due to the interaction between the moving belt and the training vortices produced by the model. The data demonstrates that the *Ateleaspis* would have produced more lift while swimming in close proximity to the bottom than while resting on the bottom facing into flow but it would probably only be significant at the highest realistic swimming speeds.

Discussion

Ateleaspis

Ateleaspis has a lower lift/drag ratio than *Poraspis* and *Errivaspis* at all angles of attack in mid water column, (Figs 6 and 7). This means that it would be less hydrodynamically and therefore metabolically efficient than the two heterostracans while swimming under these conditions. *Ateleaspis* exhibits consistent lift forces at low, cruising velocities but there are erratic spikes of lift force in mid-water column at high velocities. These observations suggest that *Ateleaspis* was less well adapted than *Errivaspis* and *Poraspis* to fast swimming in mid-water (Fig. 9). *Ateleaspis* produces lower pitching moments at all angles of attack than the other two taxa, showing that it is more stable in the pitching plane. This suggests that it would be less able to execute sharp changes of direction in this plane in mid-water. Conversely, *Ateleaspis* exhibits the highest yawing moments in relation to velocity of all the taxa, especially velocities corresponding to swimming speeds ranging from two to eight body lengths per second (Figs 11 B, C, D), which encompasses the typical range between cruising speed and burst speed in most extant fish (Videller 1993). The implication of this is that *Ateleaspis* is dynamically unstable in the yaw axis. This would suggest a high degree

of manoeuvrability in the horizontal plane when constrained vertically by bottom of the habitat. This would be adaptive in a benthic mode for sequential lateral manoeuvring to avoid predators approaching from above or behind.

In the ground effect tests for *Ateleaspis*, it is apparent that lift is inversely proportional to distance from the bottom and is considerably higher than in the mid water column. This confirms that *Ateleaspis* benefited from ground effect induced lift and ram pressure (Fig. 13). Indeed it produces more lift at velocities equivalent to two body lengths per second close to the bottom than it does at velocities equivalent to sixteen body lengths per second in mid water. It also produces more lift over the belt at two body lengths per second than *Errivaspis* does at sixteen body lengths per second at any point in the water column. This shows that *Ateleaspis* would have had a huge advantage over other genera swimming in still water, near the bottom, and would have been much more efficient hydrodynamically and metabolically in this zone than it would be in mid water (Figs 12A, B). In addition, the experimental investigation of drag in the presence or absence of ground effect (Fig. 14) indicates that *Ateleaspis* produced higher levels of drag in close proximity to the bottom, which would imply that it would have to overcome higher forces when holding station facing into appreciable flow. *Ateleaspis* had an epicercal tail, which analogy with extant species suggests would tend to produce down-thrust (Chapter 2), keeping the animal in contact with a ‘cushion’ of water between its carapace and the bottom, thereby inducing optimal ground effect and ram pressure lift.

Poraspis

Poraspis shows lower drag in the fixed velocity tests at most angles of attack than the other two taxa while producing better lift. The data show that it would be substantially more hydrodynamically efficient in terms of lift/drag ratio than *Ateleaspis* in mid water column and have a small but significant advantage over *Errivaspis*. *Poraspis* is relatively stable in yaw compared to *Ateleaspis*, which, as discussed, gives the latter an

advantage in horizontal manoeuvre when constrained by the plane of the substrate (Fig. 10). However, *Poraspis* is less stable than both *Ateleaspis* and *Errivaspis* in the pitching plane, enabling relatively rapid changes of direction to be made in a free field. Due to roll-coupling effects facilitated by its relatively circular cross-section, this would enhance manoeuvrability in all planes, when clear of the bottom, suggesting adaptation for free swimming in mid water column (Fig. 9). Given its circular cross sectional and lack of pectoral fins combined with the moment forces it was subject to, it is possible that it would have turned onto its side and perhaps even upside down while executing rapid manoeuvres.

Errivaspis

Errivaspis behaves in a manner similar to *Poraspis* in experimental setups that place it in mid water column but apparently has certain adaptations for holding station on the bottom as shown by the low lift developed in the ground effect experiments. The idea that it had such a lifestyle is supported by wear observed on the underside of the head shield (Dennison 1973). Like *Poraspis*, and in contrast to *Ateleaspis*, it is relatively stable in mid-water at higher velocities, implying an ability to swim relatively fast in this environment (Figs 9 and 10). The only respect in which the experimental data show *Errivaspis* to be significantly less effective in mid water column than *Poraspis* is in that it produces much greater levels of drag at high velocities. Its principal difference with *Poraspis* is that its pitching moment is very flat at all experimental velocities, implying good longitudinal stability over a wide speed range which would have given it straight line stability at the expense of manoeuvrability (Fig. 12A). *Errivaspis*, like *Poraspis* produces much smaller yawing moments than *Ateleaspis* at all speeds. (Figs 11B, C, D). The inference from the low pitching and yawing moments of *Errivaspis* is that it would have a lower degree of manoeuvrability during swimming than the other two taxa in the study.

Errivaspis produces far less lift than *Ateleaspis* in the ground effect experiments, suggesting that this was not an important adaptive need for efficient locomotion. Indeed, it was shown to lose lift in ground effect (Fig. 12). This implies that it needed to expend less energy to hold station on or near the bottom, while facing into flow. The broad caudal peduncle of the tail is analogous with extant species capable of rapid acceleration. While it is dangerous to draw comparisons between extant teleosts and ostracoderms as discussed previously (Chapter 2), ability to accelerate rapidly is sometimes used as an adaptation to overcome fast flowing water. Such activity could have been interspersed with periods of resting on the bottom.

Implications for related taxa

Ateleaspis as stated previously would have been able to swim close to the bottom far more efficiently than *Errivaspis*, due to its ability to utilise ground effect induced lift. This ability can be attributed to its broad head shield with a large flattened ventral surface. The same feature makes it less able to hold a trajectory in mid water and gives it a lower lift to drag ratio. When comparing the dimensions of the head shield in the model of *Ateleaspis* to those published for other Osteostraci, it has one of the lowest aspect ratios of those measured (Table 1). This suggests that more derived Osteostraci would have benefited even more strongly from ground effect close to the bottom and would have encountered the same problems as *Ateleaspis*, while swimming in mid water to an even greater extent. More derived forms such as *Zenaspis salweyi* and *Cephalaspis lyelli* display features such as larger head shields, mobile pectoral fins, and a larger body. Features such as cornuae would have provided a broader ventral surface which the data suggest would be expected to counteract pitching and yawing moments with ram pressure. The larger head would exaggerate any ground effect induced trends which the more derived osteostracans were subject to. The mobile pectoral fins could have been used to push them clear of the bottom when commencing swimming from a stationary position and also to counteract lift while holding station on the bottom facing into flow. Some of the more derived forms also lack the dorsal

fin of *Ateleaspis* which would have served primarily to stabilise it while swimming in mid water column. All these features suggest further specialisation to a bottom dwelling lifestyle. It is possible that adaptations for a benthic environment in some osteostracan groups ultimately led to a less active lifestyle with a lower emphasis on hydrodynamic performance. This low activity benthic existence could have led to some of the forms with bizarre morphologies such as *Tauraspis*. While neither of the two heterostracan genera featured in the tests had the morphology to make use of ground effect induced lift, it is implicit in the data that some of the more dorsoventrally flattened Heterostraci such as the psammolepids, as well as some galeaspids, would have been able to employ a similar hydrodynamic strategy.

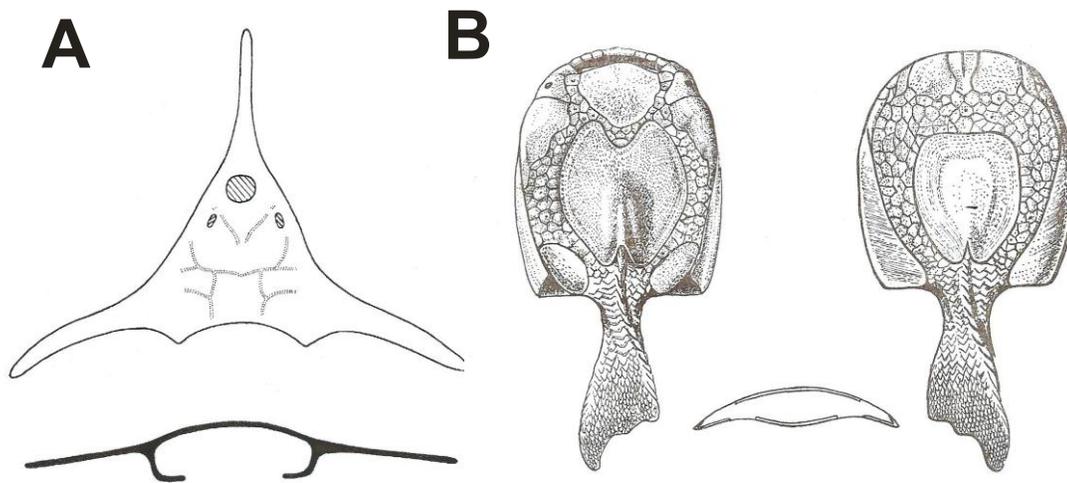


Fig. 15. Several ostracoderm groups have produced genera with head shields of large surface area that are dorsoventrally compressed. The fact that *Ateleaspis* is able to utilise ram pressure effectively to generate lift with its comparatively small head shield suggests that these genera would be able to do the same. □A. The head shield of the galeaspid *Asiaspis* is shown in dorsal view and cross section, after Pan (1984). □B. The psammolepid Heterostracan *Drepanaspis* is shown in is shown in dorsal view and cross section, after Tarlo (1964).

Species	Reference	Aspect ratio
<i>Ateleaspis tessellata</i>	Ritchie 1967	0.84
<i>Aceraspis robusta</i>	Heintz 1939	1.06
<i>Hirella gracilis</i>	Heintz 1939	1.20
<i>Hemiteleaspis heintzii</i>	Westol 1945	1.11
<i>Hemicyclaspis murchisoni</i>	Stensio 1932	0.97
<i>Tremataspis mammillata</i>	Mark-Kurik 1992	0.73
<i>Cephalaspis lyelli</i>	Mark-Kurik 1992	0.95
<i>Trewinia magnifica</i>	Janvier 1987	1.72
<i>Zenaspis salweyi</i>	Measurement by author	0.93
<i>Boreaspis rostrata</i>	Mark-Kurik 1992	1.33
<i>Hoelaspis angulata</i>	Mark-Kurik 1993	1.47
<i>Benneviaspis lankesteri</i>	Mark-Kurik & Janvier 1995	1.83
<i>Benneviaspis urvantsevi</i>	Mark-Kurik & Janvier 1995	2.83
<i>Benneviaspis holtedhali</i>	Mark-Kurik & Janvier 1995	2.22
<i>Benneviaspis longicornis</i>	Mark-Kurik & Janvier 1995	2.63
<i>Benneviaspis anglica</i>	Mark-Kurik & Janvier 1995	1.75
<i>Hapilaspis apheles</i>	Mark-Kurik & Janvier 1995	1.38
<i>Severaspis rostralis</i>	Mark-Kurik & Janvier 1995	1.42
<i>Tauraspis rara</i>	Mark-Kurik & Janvier 1995	0.85

Table 4. Aspect ratios or span of head shield/cord, in a number of osteostracans, and the references from which the measurements were taken

Errivaspis waynensis has a fairly elongate head shield relative to other pteraspids (Table 2). Among extant fish forms adapted for maneuverability tend to be short relative to their girth (Webb 1975). The experimental data suggest that pteraspids with shorter head shields such as *Protopteraspis* would have had lower resistance to pitching and yawing moments but would have been able to utilize them to execute a tighter turning circle, as was observed in yaw data (Fig. 11D). These factors all suggest that they had a lifestyle more adapted to maneuverability than *Errivaspis* which was found in the experimental data presented here to have a fairly restrictive

turning circle. There are derived forms with highly elongate head shields such as *Rhinopteraspis* which would have had a lot more resistance to moment forces but a very restrictive turning circle. This makes it likely that they had an ecological niche less dependant on ability to maneuver in tight spaces and were likely to occupy larger water bodies.

Species	Reference	Aspect ratio
<i>Protopteraspis viogti</i>	Tarlo 1964	0.73
<i>Protopteraspis pygmaea</i>	Blieck 1984	0.85
<i>Protopteraspis siliktokia</i>	Blieck 1984	0.79
<i>Protopteraspis corniga</i>	Blieck 1984	0.82
<i>Protopteraspis arctica</i>	Blieck 1984	0.67
<i>Protopteraspis primaeva</i>	Blieck 1984	0.82
<i>Protopteraspis aquilonia</i>	Blieck 1984	0.62
<i>Protopteraspis leathensis</i>	Blieck 1984	0.68
<i>Protopteraspis gosseleti</i>	Blieck 1984	0.64
<i>Protopteraspis whitei</i>	Blieck 1984	0.64
<i>Protopteraspis sartokia</i>	Mark-Kurik 1992	0.67
<i>Pteraspis rostrata</i>	Blieck 1984	0.55
<i>Pteraspis mitchelli</i>	Blieck 1984	0.68
<i>Errivaspis waynensis</i>	Blieck 1984	0.49
<i>Errivaspis depressa</i>	Blieck 1984	0.42
<i>Loricopteraspis althi</i>	Blieck 1984	0.46
<i>Loricopteraspis dairydinglensis</i>	Blieck 1984	0.68
<i>Parapteraspis jackana</i>	Blieck 1984	0.54
<i>Canadapteraspis alocostomata</i>	Blieck 1984	0.55
<i>Europteraspis crenulata</i>	Blieck 1984	0.69
<i>Europteraspis arnelli</i>	Blieck 1984	0.74

<i>Gigantaspis bocki</i>	Blieck 1984	0.62
<i>Rodenaspis brevispina</i>	Blieck 1984	0.83
<i>Cyrtaspidichthys ovata</i>	Blieck 1984	0.95
<i>Cosmaspis transversa</i>	Blieck 1984	0.97
<i>Eucyclaspis erroli</i>	Blieck 1984	1.13
<i>Oreaspis dunklei</i>	Blieck 1984	0.79
<i>Oreaspis williamsi</i>	Blieck 1984	0.72
<i>Oreaspis ampla</i>	Blieck 1984	0.86
<i>Lampraspis tuberculata</i>	Blieck 1984	1.00
<i>Miltaspis anatirostrata</i>	Blieck 1984	0.44
<i>Larnovaspis gougeti</i>	Mark-Kurik 1992	0.78
<i>Larnovaspis stensioei</i>	Blieck 1984	0.67
<i>Larnovaspis kneri</i>	Blieck 1984	0.63
<i>Larnovaspis iwaniensis</i>	Blieck 1984	0.49
<i>Larnovaspis major</i>	Blieck 1984	0.58
<i>Larnovaspis mogielnensis</i>	Blieck 1984	0.50
<i>Brachipteraspis latissima</i>	Blieck 1984	0.81
<i>Brachipteraspis monmouthensis</i>	Blieck 1984	0.61
<i>Rhinopteraspis dunensis</i>	Mark-Kurik 1992	0.11
<i>Rhinopteraspis crouchi</i>	Blieck 1984	0.45
<i>Zascinaspis heintzi</i>	Blieck 1984	0.71
<i>Zascinaspis carmani</i>	Blieck 1984	0.80
<i>Zascinaspis laticephla</i>	Blieck 1984	0.71
<i>Protaspis macgrewi</i>	Mark-Kurik 1992	0.96
<i>Protaspis bucheri</i>	Blieck 1984	0.72
<i>Protaspis dorfi</i>	Blieck 1984	0.76
<i>Althaspis elongata</i>	Blieck 1984	0.32
<i>Althaspis leachi</i>	Blieck 1984	0.47
<i>Unarkaspis schultzei</i>	Mark-Kurik 1992	0.16

<i>Mylopteraspidella robusta</i>	Blieck 1984	1.09
<i>Podolaspis lerichei</i>	Novitskaya 2000	0.21
<i>Podolaspis zychi</i>	Blieck 1984	0.43
<i>Podolaspis lata</i>	Blieck 1984	0.53
<i>Liliaspis philippovae</i>	Novitskaya 1971	0.80

Table. 5. Aspect ratios or span of head shield/cord, in a number of pteraspidiformes, and the references from which the measurements were taken.

Comparisons between *Poraspis polaris* and related cyathaspids reveal some interesting points. *Anglaspis* has a head shield with a comparable aspect ratio to that of *Poraspis* but with a less streamlined morphology unlike the torpedo shaped head shield found in *Poraspis*. This would be expected to produce greater drag and perhaps better lift as well. Genera with longer head shields such as *Torpedaspis* would be expected to be more resistant to yawing forces but would suffer some increase in drag because they fall outside the idealized proportions for minimizing drag outlined by (Hertel 1966) and (Videller 1993) to which *Poraspis* conforms.

Station holding

Both *Errivaspis* and *Ateleaspis* would have encountered problems in holding station on the bottom facing into flow because pectoral fins, absent in the two Heterostraci and underdeveloped in *Ateleaspis*, are used as hydrofoils to counteract lift and moment by extant fish. While *Ateleaspis* would be able to travel close to the bottom far more economically than *Errivaspis*, either in still water or flowing water, it would have to expend more energy to hold station on the bottom in fast flow due to its propensity for producing ground effect induced lift. It might have been able to counteract this by partially burrowing into the sediment to prevent water flowing underneath it and direct it over the top. It is likely that the evolution of more derived pectoral fins in osteostracans was driven by need to counteract lift resulting from oncoming flow, since

counteracting flow is a major energy budget constraint in extant fish, often overcome by use of pectoral fins (Arnold et al. 1991), and data presented by Bunker & Machin (1991) suggests that the pectoral fins of osteostracans could have been used this way. It is also likely that more plesiomorphic forms such as *Ateleaspis* generally inhabited still water environments while more derived forms moved more actively in rivers with high flow regimes. The fact that *Errivaspis* had to expend less energy to hold station on the bottom than *Ateleaspis* suggests that it would have been better able metabolically to sustain a lifestyle that involved migrating upstream. The new homocercal caudal fin morphology that has been proposed for *Errivaspis* (Chapter 2) would be better suited than the epicercal caudal fin of *Ateleaspis*, to producing the rapid bursts of speed that migratory fish need to overcome fast flowing currents (Castro-Santos 2005).

How this work relates to previous interpretations

Differences between the experimental setup and physical variables measured in (Kermack 1943, Bunker & Machin 1991) and the methodology presented here, make direct comparisons between results problematic. However some comparisons are appropriate. Kermack's experimental setup assumed that *Errivaspis* had a hypocercal caudal fin now shown to be unlikely (Fig. 3). His conclusion that the caudal fin depressed the postcranial area is therefore redundant. Kermack also concluded that the head shield of *Errivaspis* could have generated enough lift to support the front of the fish while it was swimming in mid water column and that it might have assumed a positive angle of attack to increase lift. The experimental data presented here upholds this conclusion (Fig. 6). It further suggest that *Errivaspis* could have generated the kind of lift predicted by Kermack at typical swimming velocities, but that it would have been erratic and perhaps intermittent unless corrected for (Fig. 12B). Given Bunker and Machin's (1991) calculations for the mass of a 38 cm cephalaspid, an ostracoderm of the size of those featured in this work would be expected to weigh around 0.6 N. All of the genera featured in the experiments presented here would have

morphologies that would produce enough lift to carry their mass at steep angles of attack and *Ateleaspis* would have been able to generate similar levels of lift at a neutral angle of attack while swimming close to the bottom, even at cruising speeds. Bunker & Machin tested for lift and drag at angles of attack ranging from 0° to + 20° but conducted all tests at a velocity corresponding to a typical cruising speed of two body lengths per second. They observed the same pattern of drag increasing at higher angles of attack ultimately leading to induced drag generating lift that were observed in the wind tunnel tests presented here for *Ateleaspis*. They concluded that cephalaspids would have no difficulty maintaining station on the bottom in strong water currents, seemingly based on forces measured in tests where a model mounted in mid flow. The ground effect experiments presented here with the conveyer belt in place show that this experimental method would produce misleading data (Fig. 12A). Their data does however suggest that the mobile pectoral fins in more derived osteostracans would have been effective for counteracting ground effect induced lift while the fish was holding station on the bottom.

Conclusions

Many of the findings presented here align with previous inferences about the lifestyles and adaptive significance of ostracoderms however; this is the first time that they have been supported by constraining experimental data. The data strongly suggests that ostracoderm morphology tends towards optimisation for performance under different hydrodynamic and environmental regimes.

Ateleaspis has a morphology adapted for hydrodynamic efficiency in a benthic lifestyle, producing higher lift under these conditions, and enjoying a considerable metabolic advantage relative to *Errivaspis*. It is highly likely that *Ateleaspis* would have travelled along the bottom while evading predators as the ground effect induced lift combined with its ability to turn rapidly while swimming benthically would have enabled it to maintain burst speeds for longer and manoeuvre more effectively in this

zone. It would also have been able to swim much faster relative to the thrust it produced, and it was probably not very manoeuvrable in mid water column. It would have encountered more problems than *Errivaspis* while trying to hold station on the bottom facing into flow as a result of the ground effect induced lift. Given that the head shield of *Ateleaspis* is an ideal shape for locomotion close to the bottom, it is likely that more derived osteostracans would be even better adapted to such a lifestyle (see discussion). Most of the hydrodynamic trends identified by the experimental data would be maladaptive for a free swimming lifestyle but beneficial for a benthic lifestyle. The conclusion is that *Ateleaspis* had a slow-cruising, benthic lifestyle and probably predominantly inhabited lacustrine or slow-flowing river environments where it would not have needed to overcome extreme flow regimes.

Poraspis has a torpedo-shaped morphology dimensionally suited for producing low drag in mid water column. This morphology is inherently unsuitable for a benthic lifestyle and well suited to a free swimming lifestyle. This interpretation is supported by the experimental data which show that it produces lower levels of drag than the other two genera in both the fixed angle and fixed velocity tests. It is however very unstable in the pitch, yaw, and roll by extrapolation of its cross section. It would have had problems holding trajectory while being very manoeuvrable in mid water.

The gross morphology of *Errivaspis* appears intermediate between *Poraspis* and *Ateleaspis* and the experimental data suggest that it occupied a generalist position with adaptations for swimming benthically and in mid water column. In mid water, *Errivaspis* behaved much more like *Poraspis* in terms of lift and drag characteristics than *Ateleaspis*. The fact that it produces low levels of lift while close to the substrate combined with previous research showing that wear is often found on the underside of the head shield in pteraspids, suggests that they periodically rested on the bottom. The hydrodynamic data suggest that it was fairly well adapted to swimming in mid water, and the new proposed reconstruction of the caudal fin with a homocercal morphology (Chapter 2) is consistent with extant marine animals that are free swimming and adapted for rapid acceleration. This indicates that it would have been both benthic and

mobile in mid water column for significant periods. The combination of adaptations for swimming in mid water and holding station on the bottom suggest that *Errivaspis* would have been well adapted to a migratory lifestyle being able to hold with low energy expenditure and swim efficiently in rapid bursts in mid water column. Such a lifestyle is consistent with the abrasion observed on the head shield by Dennison (1973).

This investigation answers some questions about distinguishing anatomical features in ostracoderms and raises others. The rigid head shield, while constraining the range of movement of the body, is shown to be shaped to aid hydrodynamic performance in the three ostracoderm genera investigated. The data also strongly imply that the same is the case for other genera not included in the study. The data do however raise questions about how the subjects could have stabilised themselves in mid water column. All three of the ostracoderm taxa in the experiment would have been subject to significant moment forces in both the pitch axis and the yaw axis. While aquatic animals utilise moments for manoeuvring they also have to be controlled. Without pectoral fins it is difficult to see how the two heterostracan genera could have done this. *Poraspis* has a morphology that is optimised for minimising drag at a given velocity but is highly prone to both pitching moments and yawing moments and without pectoral fins it has no obvious mechanism to correct for them. While the apparatus did not permit the investigation of roll, the almost circular cross section of the *Poraspis* would be expected to offer little resistance to it. It is possible that controlling moment forces drove the evolution of more derived pectoral fins in cephalaspids and head shield structures such as cornuae and enlarged dorsal spines in pteraspids.

Further work

The data suggest a number of directions for future research. The revelation that *Ateleaspis* produced ground effect induced lift close to the bottom raises questions

about other taxa. A similar experiment could be conducted with a model of a more derived cephalaspid. *Cephalaspis lyeli* or *Zenaspis sawleyi* would be the obvious choices given the availability of good postcranial material. It would also be instructive to do a similar test on a psammosteid heterostracan known from complete material such as *Drepanaspis gemunendensis* and the pteraspidiform *Doryaspis nathorsti*. The radiation of pteraspids resulted in acquisition of a number of characters of unknown functional significance such as dorsal spines and cornuae in genera that were otherwise of very similar morphology. Taking the *Errivaspis* model used in these experiments as a starting point it would be possible to remove the dorsal spine or add structures found in other genera such as cornuae and repeat the experiments to see what difference it made.

Appendix

Analysis of trouble shooting data

Wind tunnel data will typically display noise due to limitations of the accuracy of the apparatus and minor procedural inconsistencies. It was necessary to assess whether trends in the data could be a result of error. The LabVIEW software was used to record three dependant variables lift, drag and moment. The two independent variables which they are compared against are angle of attack and velocity. The first trouble shooting tests were to determine accuracy with which the software interpreted the dependent variables. In order to do this a series of trial runs were done with the wind tunnel switched off which meant that any deviation from zero would represent error in the software reading of dependant variables. All troubleshooting tests were conducted with the *Ateleaspis* model for the sake of consistency. The angle of attack of the was incrementally changed from -35° to $+45^{\circ}$ with the dependant variables being logged at increments of 5° to allow for any effects resulting from manipulation of angle of attack, during the fixed velocity tests. The wind off data showed considerable variation in the recorded variables, (Figs 15 and 16), but no significant trend was found in the error. It was also found that there was less error in the tests conducted with the model aerofoil, than in both the wind on and wind off data with the model fish, even at the lowest recorded forces (Fig. 17). This suggests that much of the noise in the data results from inherent instability of the ostracoderm models, rather than lack of sensitivity of the equipment.

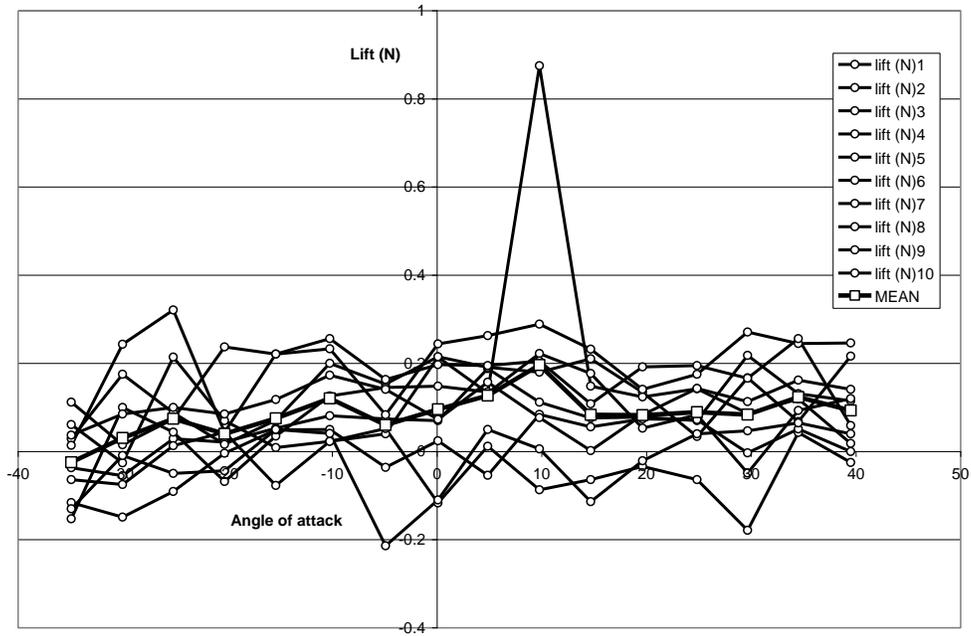


Fig. 15. Mean recorded lift over ten runs with airspeed of 0 m/s compared to the distribution of the data. All other experimental details are as with the “wind on” fixed angle tests.

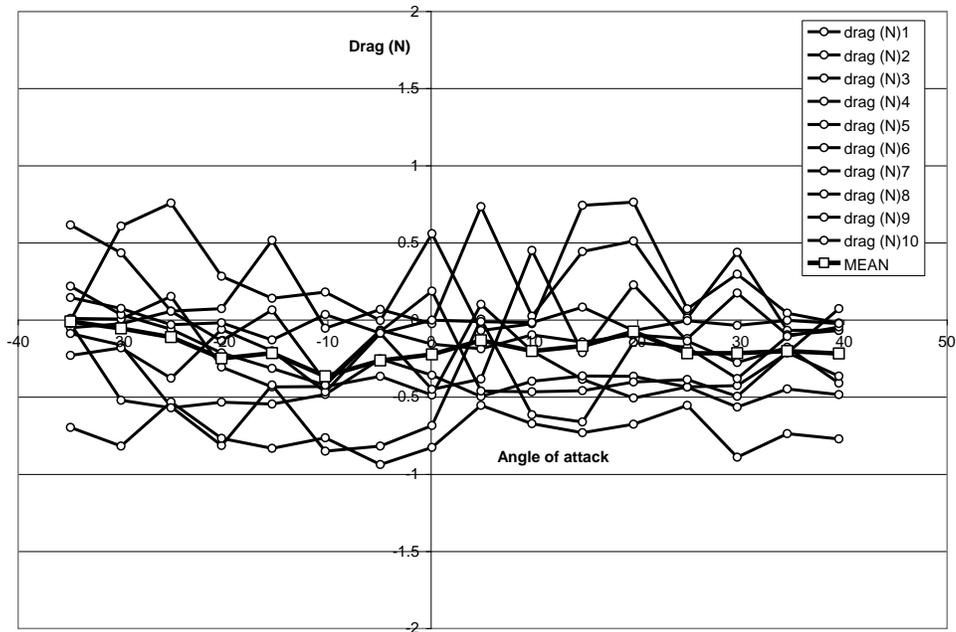


Fig. 16. Mean recorded drag over ten runs with airspeed of 0 m/s compared to the distribution of the data. All other experimental details are as with the “wind on” fixed angle tests.

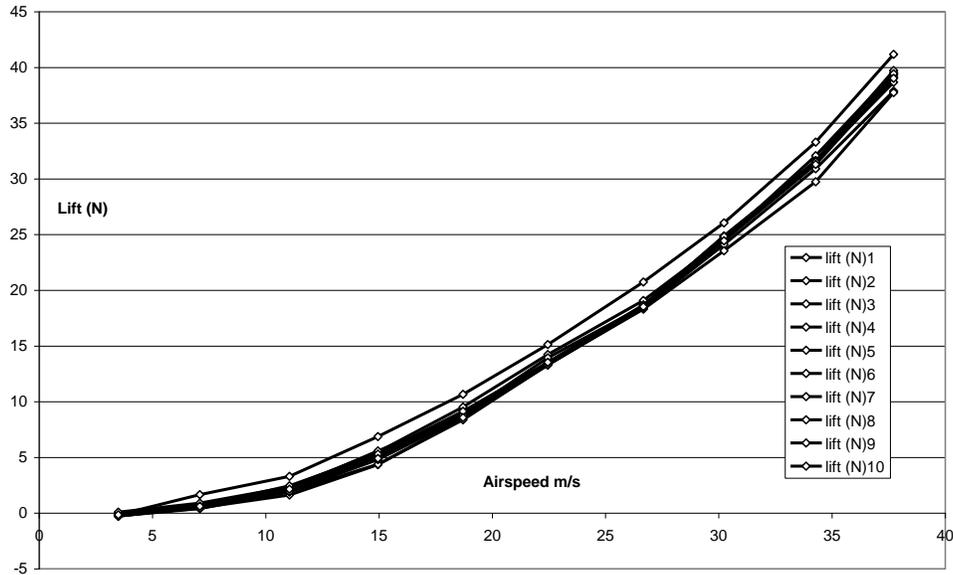


Fig. 17. Lift over ten runs in a fixed angle test with a model aerofoil with the wind tunnel running. All other experimental details are the same as for the fixed angle tests using model fish.

An F test was used to assess the significance of the wind-on data by comparing its distribution to the troubleshooting data recorded with airspeed of 0 m/s.

Null hypothesis.- The null hypothesis for each dependent variable is that there is a correlation between the distribution of in the wind on and wind off data, and that any apparent trend is a result of error in the data.

Alternative hypothesis.- The alternative hypothesis for each dependent variable is that there is not a correlation between the distribution of lift in the wind on and wind off data.

A P value close to 1 suggests that there is very little difference between the samples. A P value of 0.05 or less is taken to imply that the chance of the two samples being related is almost nonexistent. . The tables below compare the distribution of the wind on and wind off data for each dependent variable. All the P values are significantly lower than 0.05 suggesting that the null hypothesis should be rejected.

In summary, the data produced by the wind tunnel is sufficiently accurate to permit broad interpretations of the hydrodynamic behaviour of the fishes at medium to high velocities while they are in mid water column. Much more accurate interpretations are possible when they are moving close to the belt and generate more uniform forces. If a high level of accuracy were needed when investigating the subject moving in mid water column at lower velocities, then it would be necessary either to use a larger model or to use a correction factor.

F test results for comparison between the wind on and wind off data.

Lift

F-Test Two-Sample for Variances

	<i>Lift 18</i> <i>m/s</i>	<i>Lift 0 m/s</i>
Mean	-0.04431	0.084331
Variance	0.180721	0.00233
Observations	16	16
df	15	15
F	77.55068	
P(F<=f) one-tail	1.89E-11	
F Critical one-tail	2.403447	

Drag

F-Test Two-Sample for Variances

	<i>Drag 18</i> <i>m/s</i>	<i>Drag 0</i> <i>m/s</i>
Mean	0.516993	-0.18247
Variance	0.069157	0.007775
Observations	16	16
df	15	15
F	8.894592	
P(F<=f) one-tail	6.21E-05	
F Critical one-tail	2.403447	

Moment

F-Test Two-Sample for Variances

	<i>Moment</i> <i>18 m/s</i>	<i>Moment</i> <i>0 m/s</i>
Mean	28.03394	15.54371
Variance	88.16113	316.3226
Observations	16	16
df	15	15
F	0.278706	
P(F<=f) one-tail	0.009173	
F Critical one-tail	0.416069	

Detailed clarification of wind tunnel equations

Moment

The pitching moment is given by the equation

$$M = -x (L \cos\alpha + D \sin \alpha)$$

Where x Distance from centre of rotation to centre of pressure
L Lift force
D Drag force
 α Angle of attack

Pressure

Coefficient of pressure is calculated by

$$C_{cop} = \frac{\text{distance from leading edge to COP}}{\text{chord length}}$$

Lift

Coefficients of lift, moment and drag may also be defined and are used to establish how a subject behaves while moving forward. These are given by the following equations:

$$C_L = \frac{L}{\frac{1}{2}\rho V^2 S}$$

$$C_d = \frac{D}{\frac{1}{2}\rho V^2 S}$$

$$C_m = \frac{M}{\frac{1}{2}\rho V^2 S c}$$

Where: C_L, D, M coefficients of lift, drag, and pitching moment

L, D, M total lift force, drag force, pitching moment (N or Nm)

$\frac{1}{2}\rho V^2$ Dynamic pressure (Pa)

ρ Air density (kg/m^3)

V air velocity (m/s)

S model plan area = chord length x span (m^2)

c chord length (m)

(Douglas *et al.* 2005)

Mode of manufacture of the models

Models of the three ostracoderm taxa were based on a series of casts produced by the Open University and were modified with Miliput plaster to correct for any inaccuracies. Using the modified models as positives, moulds were manufactured from silicone. Silicone was chosen due to its ability to record minute detail, and minimal shrinkage (Rose 1981, Goodwin & Channey 1994:). The first positives produced from the mould were used as blanks to be modified by filing away material as required. Once this was done a second mould was made to allow multiple casts to be made of the updated model. The material from which the first positive was made had to have a plastic phase to allow the models to be manipulated and modified. It also had to be suitable for working with tools. Epoxy resin was the obvious choice since it becomes plastic at comparatively low temperatures which can be produced with a jet of hot air.

The mixture of epoxy resin used to produce the models consisted of 100parts MY793 resin to 33 parts XD716 hardener. Once mixed it was left to stand for an hour to allow air bubbles to escape before pouring. After twenty four hours the resin was in a plastic phase where it could be manipulated. This allowed the curvature of the postcranial area to be removed from the models. It normally takes a further two days to achieve complete rigidity but it was achieved in four hours by heating the models in an oven at 40 °C. The epoxy resin used was transparent so orasol blue was added to the mixture to make the detail of the models more visible.

References

- Afanassieva, O. B. & Karatajute-Talimaa, V. N. 1998: New osteostracans (Agnatha) from the Silurian and Lower Devonian of the Severnaya Zemlya Archipelago (Russia). *Paleontological Journal* 6, 60-64.
- Alexander, R. M. 1964: The lift produced by the hetrocercal tails of selachi. *Journal of Experimental Biology* 43, 131-138.
- Allen, J. R. L. 1964: Fluviatile sedimentation, six cyclotherms from the lower Old Red Sandstone, Anglo Welsh basin. *Sedimentology* 3, 163-198.
- Allen, J. R. L. & Tarlo, L. B. 1963: The Downtonian and Dittonian facies of the Welsh borderland *Geological Magazine* 100, 129-155.
- Arnold, G. P. Webb, P. W. & Holford, B. H. 1991: The role of the pectoral fins in station holding of Atlantic Salmon (*Salmo salar*). *Journal of Experimental Biology* 156, 625-629.
- Bartol, I. K. M. Gharib, D. Weihs, P. W. Webb, P. W. Hove, J. R. & Gordon, M. S. 2003: Hydrodynamic stability of swimming in ostraciid fishes: role of the carapace in the smooth trunkfish *Lactophrys triqueter* (Teleostei: Ostraciidae). *Journal of Experimental Biology* 206, 725-744.
- Bartol, I. K. M. Gharib, D. Webb, P. W. Weihs, P. W. & Gordon, M. S. 2005: Body-induced vortical flows: a common mechanism for self-corrective trimming control in boxfishes. *Journal of Experimental Biology* 208, 327-344.
- Belles-Isles, M. 1987: La nage et l'hydrodynamique de deux Agnathes du Paleozoique: *Alaspis macrotuberculata* et *Pteraspis rostrata*. *Jb Geol Palaeont.* 175, 347-376.
- Blake, R. W. 1978: The energetics of hovering in the mandarin fish (*Synchropus picturatus*). *Journal of Experimental Biology* 82, 25-33.
- Blicck, A. 1984: Les Heterostraces Pteraspidiiformes, systematique, phylogenie, biostratigraphie, biogeography. *Cahires de Palaeontologie.* 27-91.
- Blicck, A. Heintz, N. 1983: Cyathaspids of the Red Bay group (Lower Devonian) of Spitzbergen. *Polar Research* 1, 49-74.
- Botella, H. & Farina, R. A. 2008: Flow patterns around the rigid cephalic shield of the

- Devonian Agnathan *Errivaspis waynensis* (Pteraspidiformes Heterostraci)
Paleontology 51 (5), 1141-1150.
- Boucot, A. J. & Janis, C. 1983: Environment of the early Palaeozoic vertebrates.
Palaeogeography Palaeoclimatology Palaeoecology 41, 251-287.
- Braun, J. & Reif, E. 1982: A new terminology of aquatic propulsion in vertebrates. *N. Jb Geol Palaeont, Abh* 164, 162-167.
- Braun, J. & Reif, E. 1985: A survey of aquatic locomotion in Fishes and Tetrapods.
Jb Geol Palaeont 169, 307-332.
- Breder, C. M. 1926: The locomotion of fishes. *Zoologica Scripta* 4, 159-256.
- Briggs, D. & Williams, M. 1981: Restoration of flattened fossils. *Lethaia* 14, 157-164.
- Broad, S. & Dineley, D. 1973: *Torpedaspis*, A new upper Silurian and lower Devonian genus of Cyathaspididae. *Bulletin of the Geological Society of Canada* 222, 53-91.
- Bunker, S. E. & Machin, K. E. 1991: The Hydrodynamics of the Cephalaspids. *In: Soc. Exp. Biol. Seminar Ser* 36, 113-129.
- Castro-Santos, T. 2005: Optimal swim speeds for traversing velocity barriers: an analysis of volitional high-speed swimming behavior of migratory fishes.
Journal of Experimental Biology 208, 421-431.
- Cocks, L. L. M. Holland, C. H. & Rickards, R. B. 1992: A Revised Correlation of Silurian rocks in the British Isle *Geological Society of London Special Report* 21
- Conway-Morris, S. 1979: Middle Cambrian Polychaetes from the Burgess Shale of British Columbia. *Philosophical transactions of the Royal Society of London* 1007, 227-274.
- Cruickshank, A., R. I. & Skews, B.W. 1980: The functional significance of nectridean tabular horns. *Proceedings of the Royal Society of London Series B-Biological Sciences* 209, 512-527.
- Denison, R. H 1971: On the tail of the Heterostraci. *Forma et Functio*, 4, 87-99.
- Denison, R. H. 1956: A review of the habitat of the earliest vertebrates. *Fieldiana Geology* 11, 357-457.
- Denison, R. H. 1973: Growth and wear on the head shield in Pteraspidae (Agnatha).

Palaeontographica 143, 11-24.

Dineley, D. L. 1976: New species of *Ctenaspis* (Ostracodermi) from the Devonian of Arctic Canada. In C. S. Churcher (ed): *Essays in Palaeontology in honour of L. S. Russel*, Geology Department University of Bristol. 26-45.

Dineley, D. L. Metcalf, S. J. 1999: *Fossil fishes of the British Isles* Geological conservation review series 16. 675 pages.

Dollo, L. 1910: Paleontologie ethologique. *La Palaeontologie Ecologique Bulletin de la Societe Belge de Geologie de Paleontologie et d Hydrologie* 23, 377-412.

Douglas, J. F. Gasiorek, J. & Swaffield, J. 2005: *Fluid mechanics* 5th edition. John Willey & Sons New York. 114-163.

Elliot, D. K. Loeffler, E. J. & Liu, Y. 1998: New species of the cyathaspidid

Poraspis

(Agnatha: Heterostraci) from the Late Silurian and Early Devonian of Northwest Territories, Canada. *Journal of Paleontology* 72(2),360-370.

Elliot, D. K. Blicek, A. R. M. & Gainer, P. Y. 1991: Ordovician Vertebrates In Advances in Ordovician Geology. *Paper of the Geological Survey of Canada* 90-9 366, 93-106.

Gerstner, C. L. 2007: Effect of oral suction and other friction-enhancing behaviors on the station-holding performance of suckermouth catfish (*Hypostomus spp*). *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 85, 133-140.

Goodwin, M. B. & Channey, D. S. 1994: Moulding, Casting and Painting. In Loggi, P. & May, P (eds). *Vertebrate Paleontological techniques*. 235-271. Cambridge University Press.

Goujet, D. 1984: Les Possions Placoderms du Spitzberg. Arthrodires Dolichothoraci de la formation de wood Bay (Devonien inferieur). *Cahiers de Palaeontologie*, Centre National de la recherche scientifique Paris. 325 pages.

Gross, W. 1963: *Drepanaspis gemuendensis* Schuler Neuntersuchung. *Palaeontographica* 121, 133-155.

Halsted, B. L. 1985: The Vertebrate Invasion of Fresh Water. *Philosophical*

- transactions of the Royal Society of London Series B* 309, 243-258.
- Haro, A. T. Castro-Santos, J. Noreika, M. & Odeh. 2004: Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic sciences* 61, 1590-1601.
- Harris, J. E. 1936: The role of the fins in the equilibrium of the swimming fish. Wind tunnel tests on a model of *Mustelus canis*. *Journal of Experimental Biology* 13, 474-493.
- Harris, T. M. 1974: *Williamsoniella lignieri*: its pollen and the compression of spherical pollen grains. *Palaeontology* 17, 125-148.
- Heintz, A. 1939: Cephalaspids from the Downtonian of Norway. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. Mat.-Naturv. Klasse*, 1-119.
- Heintz, A. 1969: New Agnaths from Ringerike Sandstone. *Norske Videnskapsakademiens Skrifter (Matematiske-naturvetenskapslige Klasse)*, 1-28.
- Hertel, H. 1966: *Structure, Form and Movement*. Reinhold, New York. 251 pages.
- Hill, J. & Grossman G. D. 1993: An energetic model of microhabitat use for rainbow trout and royside dace. *Ecology* 74, 685-698.
- Hopson, J. 1974: The functional significance of the hypocercal tail and lateral fin fold of Anaspid Ostracoderms. *Fieldiana Geology* 33, 83-93.
- Janvier, P. 1981: The phylogeny of the craniata, with particular reference to the significance of the fossil Agnathans. *Journal of Vertebrate Palaeontology* 1, 121-159.
- Janvier, P. 1985: Environmental framework of the diversification of the Osteostraci during the Silurian and Devonian. *Philosophical Transactions of the Royal Society of London b* 309, 259-272.
- Janvier, P. 1987: The paired fins in Anaspids: one more hypothesis about their function. *Journal of Palaeontology* 61 (4), 84-87.
- Janvier, P. 1996: *Early Vertebrates*. Oxford University Press. 408 pages.
- Janvier, P. Thanh T. D. & Phuong, T. H. 1993: A New Early Devonian Galeaspid from Bac Thai Province, Vietnam. *Palaeontology* 36, 297-309.

- Jasinoski, S. C. Rayfield, E. J. & Chinsamy, A. 2007: Elucidation of Dicynodont cranial function using finite element analysis. *Journal of Vertebrate Paleontology* 27, 95A-95A.
- Kermack, K. 1943: The functional significance of the hypocercal tail in *Pteraspis rostrata*. *Journal of Experimental Biology* 20, 23-27.
- Kiaer, J. 1932: The Downtonian and Devonian Vertebrates of Spitzbergen. *Skrifter Svalbard Ishavet* 52, 1-26.
- Kiaer, J. & Heintz, A. 1935: The Downtonian and Devonian Vertebrates of Spitzberge. *Skrifter om Svalbard og Ishavet* 40(1), 8-137.
- Lankester, R. 1873: On *Holaspis sericeus* and on the relationships of fish genera *Pteraspis*, *Cyathaspis* and *Scaphaspis*. *Geol Mag* 10, 241-245.
- Lauder, G. 2000: Function of the caudal fin during locomotion in fishes: Kinematics, Flow Visualisation and Evolutionary Patterns. *American Zoology* 40, 101-122.
- Lee-Jenkins, S. S. Y. Binder, T. R. Karch A. P. & McDonald D. G. 2007: The recovery of locomotory activity following exhaustive exercise in juvenile rainbow trout (*Oncorhynchus mykiss*). *Physiological and Biochemical Zoology* 80, 88-98.
- Lorenz, H. Mannik, P. Gee, D. & Proskurnin, V. 2008: Geology of the Severnaya Zemlya Archipelago and the North Kara Terrane in the Russian high Arctic *Internationa Journal of Earth Sciences* 97, 519-547.
- Mark, E. 1961: Certain adaptation phenomena in the psamosteids *Geological notes (Estonian Academy of Sciences)* 1, 30-34.
- Mark-Kurik, E. 1992: Functional aspects of the armour in the early vertebrates. In E. Mark-Kurik (ed): *Fossil fishes as living animals* 1 107-115, Akademia.
- MarkKurik, E. & Janvier, P 1995: Early Devonian osteostracans from Severnaya Zemlya, Russia. *Journal of Vertebrate Paleontology* 15, 449-462.
- McCay, M. G. 2001: Aerodynamic stability and manoeuvrability of the Gliding Frog *Polypedates dennysi*. *Journal of Experimental Biology* 204, 2817-2826.
- McCormick, B. W. 1976: *Aerodynamics aeronautics and flight control*. John Willey & Sons, New York. 477-561.
- Miall, A. D. 1970: Continental marine transition of the Devonian of Prince of Wales Island Northwest Territories. *Canadian Journal of Earth Sciences* 7, 124-144.

- Miklosovic, D. S. Murray, M. M. Howle, L. E. & Fish F. E. 2004: Leading-edge tubercles delay stall on humpback whale (*Megaptera novaeangliae*) flippers. *Physics of Fluids* 16, L39-L42.
- Morrissey, L. B. Braddy, S. J. Bennett, J. P. Marriott, S. B. & Tarrant, P. R. 2004: Fish trails from the Lower Old Red Sandstone of Tredomen Quarry, Powys, southeast Wales. *Geological Journal* 39, 337-358.
- Novitskaya, L. I. 1971: Les (Amphiaspides) Heterostraci du Devonien de la Sibirie. *Cahiers de paleontologie*. 1-130.
- Novitskaya, L. I. 1986: Fossil Agnathans of the USSR. *Trudy Paleontologicheskogo Instituta* 219, 1-159.
- Novitskaya, L. I. 2000: Adaptation for swimming in the external morphology and skeleton of early vertebrates (Agnatha: Heterostraci). *Paleontologicheskii Zhurnal*. 3-13.
- Novitskaya, L. I. 2007: Evolution of generic and species diversity in agnathans (Heterostraci: orders Cyathaspidiformes, Pteraspidiformes). *Paleontological Journal* 41, 268-280.
- Obruchev, D. V. 1964: Subclass Heterostraci (Pteraspidides). In Orlov, J. A. (ed): *Fundamentals of Palaeontology*, I, A, 11, Agnatha and Pisces, 45-82, Moscow Academy of Sciences.
- Pan, J. 1984: The Phylogenetic Position of the Eugaleaspida in China. *Proceedings of the Linnean Society of New South Wales* 107, 309-319.
- Parrington, F. R. 1958: On the nature of the Anaspida. In Westoll T. S. (ed): *Studies of fossil Vertebrates*, 108-128, Athlone Press London.
- Pernegre, V. N. 2003A: The genus *Doryaspis* White (Heterostraci) from the Lower Devonian of Vestspitsbergen, Svalbard. *Journal of Vertebrate Paleontology* 22, 735-746.
- Pernegre, V. N. 2003B: A new Pteraspidiformes genus (Vertebrata, Heterostraci) from the Wood Bay Formation (Lower Devonian, Spitsbergen). *Geodiversitas* 25, 261-272.
- Pernegre, V. N. 2005: Description of a new species and morpho-functional analysis of

- the genus *Doryaspis* White (Heterostraci) from the Devonian of Spitsbergen. *Geobios* 38, 257-268.
- Pradel, A. Sansom, I. J. Garnier, P. Cespedes, R. & Janvier, P. 2007: The tail of the Ordovician fish *Sacabambaspis*. *Biology Letters* 3, 72-75.
- Purnell, M. A. 2001: Feeding in extinct jawless heterostracan fishes and testing scenarios of early vertebrate evolution. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269, 83-88.
- Purnell, M. A. & Donoghue, P. 1999: Flattened Fossils, Physical Modelling and the Restoration of Collapsed Skeletons. In: Savazzie, E. (ed) *Functional Morphology of the Invertebrate Skeleton*. 91-99.
- Rigby, S. Tabor, G. 2006: The use of computational fluid dynamics in reconstructing the hydrodynamic properties of graptolites. *Transactions of the Geological Society of Stockholm* 128, 189-194.
- Ritchie, A. 1964: New lights on the morphology of the Norwegian Anaspida. *Videnskapsakademiens Skrifter (Matematisk-Naturvidenskaplige Klasse)* 14, 1-35.
- Ritchie, A. 1967: *Atelaspis tessellata* Traquair, a non cornuate cephalaspid from the upper Silurian of Scotland. *Zoological Journal of the Linnean Society* 47, 69-81.
- Ritchie, A. 1968: New evidence on *Jamoytius kerwoodi* White, an important ostracoderm from the Silurian of Lankashire, Scotland. *Palaeontology*, 21-39.
- Romer, A. S. 1955: Fish origins-Fresh or salt water. *Papers in marine biology and oceanography*.
- Rose, J. 1981: A replication technique for scanning Electron microscopy. *American Journal of Physical Anthropology* 62, 255-261.
- Sansom, I. J. Miller, C. G. Heward, A. Davies, N. S. Booth, G. A. Fortey, R. A. & Paris, F. 2009: Ordovician fish from the Arabian Peninsula. *Palaeontology* 52 (2), 337-342.
- Schmitz, B. Aberg, G. Werdelin, L. Forey P. & Bendix-Almgren, S. E. 1991: Sr-

- 87/Sr-86, Na, F, Sr, and La in Skeletal Fish Debris as a Measure of the Paleosalinity of Fossil-Fish Habitats. *Geological Society of America Bulletin* 103, 786-794.
- Schulze, K. Hunger, M. Döll, P. 2005: Simulating river flow velocity on global scale *Advanced Geoscience* 5, 133-136.
- Shadwick, R. E. & Pitman R. L. 2007: Morphology and biomechanics of a "three-wing" flying fish: *Parexocoetus brachypterus*. *Journal of Morphology* 268, 1133-1133.
- Soehn, K. L. & Wilson, M. V. H. 1990: A complete articulated heterostracan from the Wenlockian (Silurian) beds of the Delmore Group Mackenzie Mountains, Northwest Territories Canada. *Journal of Vertebrate Paleontology* 10 (4), 405-419.
- Stensio, E. A. 1932: The cephalaspids of the Great Britain. *British Museum (Natural History) London* 220.
- Tarlo, L. B. H. 1964: Psammosteiformes (Agnatha) A review with descriptions of new material from the lower Devonian of Poland. *Palaeontologica polonica* 13. 1-118.
- Thorsteinsson, R. & Tozer, W. 1963: Geology of northern Prince of Wales Island and Northwestern Somerset Island. in Fortier, Y. (ed) *Geology of the North Central part of the Arctic Archipelago, Northwest Territories (Operation Franklin)* *Geological survey of Canada* 320, 117-129.
- Triantafyllou, M. S. & Triantafyllou, S. G. 1995: An efficient swimming machine. *Scientific American March*. 40-46.
- Triantafyllou, M. S. Techet, A. H. Zhu, Q. Beal, D. F. Hover, N. S. & Yue, P. 2002: Vorticity Control in Fish-like Propulsion and Maneuvering. *Integrative and Comparative Biology*. 42, 1026-1031.
- Videller, J. 1993: *Fish Swimming*. Chapman & Hall London. p 73-97.
- Walton, J. 1936: On the factors which influence the external form of fossil plants: with descriptions of the foliage of some species of the Palaeozoicequisetalian genus *Annularia* Steinberg. *Philosophical transactions of the Royal Society of London Series B*. 226, 219-237.

- Webb, P. W. 1975: Hydrodynamics and energetics of fish propulsion. *Bulletin of the Fisheries Research Board Canada*. 190, 1-159.
- Westol, T. S. 1945: A new Cephalaspid fish from the Downtonian of Scotland, with notes on the structure and classification of Ostracoderms. *Transactions of the Royal Society of Edinburgh-Earth Sciences*. 61, 341-357.
- White, E. I. 1935: The Ostracoderm *Pteraspis kneri* and the relationship of the Agnathous Vertebrates. *Philosophical transactions of the Royal Society, London*. B 225, 381-457.
- White, E. I. 1958: Original environment of the craniates. In Westol, T. S. (ed): *Studies of Fossil Vertebrates*, The Athlone, London.
- White, E. I. & Toombs, H. A. 1983: The Cephalaspids from the Dittonian section at Cwm Mill, near Abergavenny, Gwent. *Bulletin of the British Museum, Natural History (Geology)*. 37, 149-171.
- Whittington, H. B. 1977: The middle Cambrian Trilobite *Naraoia* Burgess Shale British Columbia. *Philosophical transactions of the Royal Society of London*. 280 (974), 409-443.
- Woodward, B. L. Winn, J. Winn, P. & Fish, F. E. 2006: Morphological Specializations of Baleen Whales Associated With Hydrodynamic Performance and Ecological Niche *Journal of Morphology*. 267, 1284–1294.
- Zangerl, R. 1971: On the Geological significance of perfectly preserved fossils. *Proceedings of the North American Palaeontological Convention Chicago.1*, 1207-1222.
- Zangerl, R. & Richardson E. S. 1963: The Palaeoecological history of two Pennsylvanian black shales. *Fieldiana Geology Mem.* 4, 1-352.