



## Article

# The Life and Death of *Jamoytius kerwoodi* White; A Silurian Jawless Nektonic Herbivore?

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**Abstract:** *Jamoytius kerwoodi*, is a primitive, eel-like jawless vertebrate found uniquely in an Early Silurian (Llandovery epoch; 444–433 Ma) horizon near Lesmahagow, Scotland. This species is a rare component of a low-diversity dominantly nektonic detritus-feeding and herbivorous fauna living over an anoxic bottom and is found at the transition from a marine-influenced, probably brackish-water, deep-water basin to a shallower-water, less saline and likely freshwater basin. In the absence of true teeth, *Jamoytius* was probably a detritivore or herbivore feeding on *Dictyocaris*. *Jamoytius* may have a common ancestor with living lampreys, especially as their ectoparasitic mode of life might have evolved from ancestral detritivores or herbivores.

**Keywords:** vertebrate; *Jamoytius*; lamprey; herbivore; parasite; Silurian

## 1. Introduction

*Jamoytius kerwoodi* White was a primitive, eel-like jawless fish that lived in the Llandovery epoch (444–433 Ma) of the Early Silurian period [1] (Figure 1). The fossil is preserved as rare carbonized films on bedding planes in one laminated siltstone horizon in the bank of the Logan water in the Lesmahagow inlier of Lanarkshire, SW Scotland [2]. It was once considered the most primitive known vertebrate [1], but with additional studies, its affinities are now debatable [3–8]. Because the interpretations of such exceptionally preserved soft-bodied fossils is difficult, observed features can be interpreted in different ways [9–11] (Figure 2). Various cladistic analyses of *Jamoytius* with other jawless vertebrates, using different character codings, give divergent results [7,12–20]. Choice of the in-group taxa affects its placement [17,21,22]. The position of *Jamoytius* on cladograms has consequently not stabilized, though it often appears as a sister taxon to euphaneropids, and/or lampreys, and/or anaspids [5,15,17,23–25] (Figure 3).



**Citation:** Brookfield, M.E. The Life and Death of *Jamoytius kerwoodi* White; A Silurian Jawless Nektonic Herbivore? *Foss. Stud.* **2024**, *2*, 77–91. <https://doi.org/10.3390/fossils2020003>

Academic Editor: Eric Buffetaut

Received: 6 December 2023

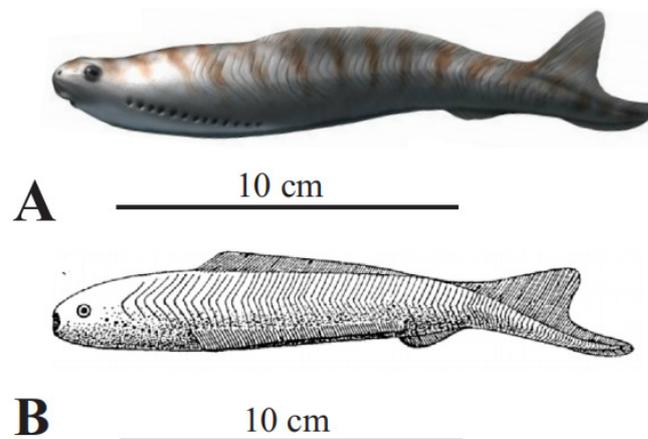
Revised: 22 March 2024

Accepted: 25 March 2024

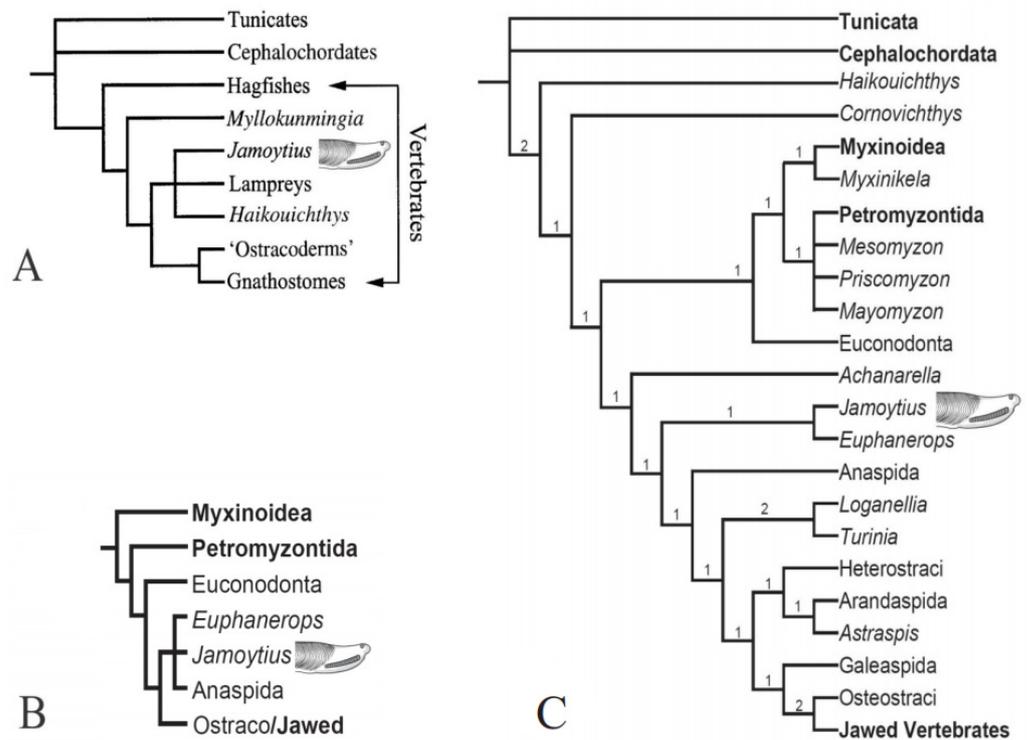
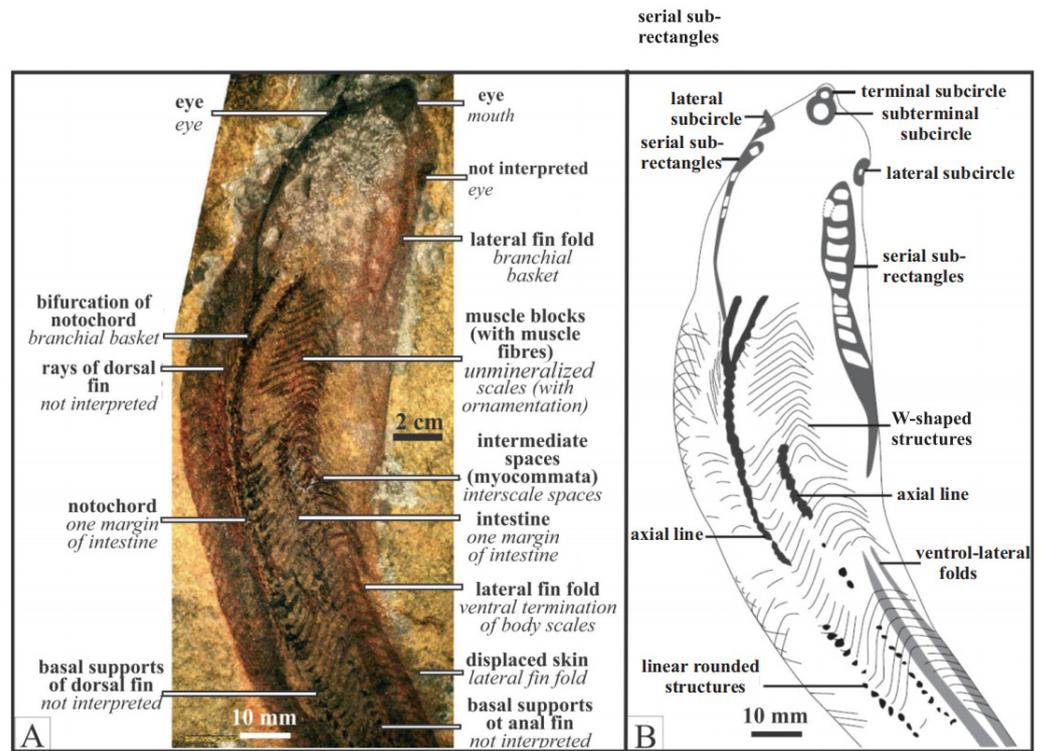
Published: 9 April 2024



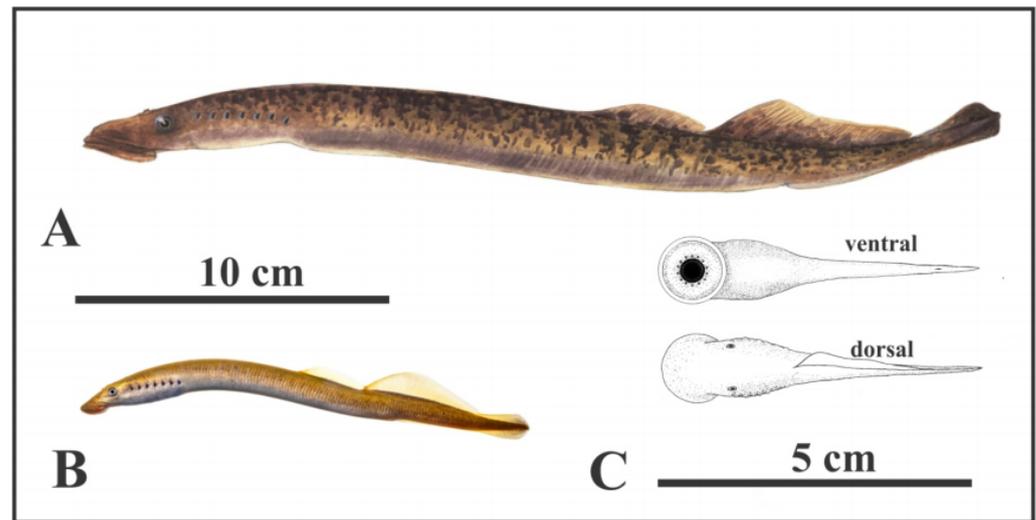
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**Figure 1.** *Jamoytius* reconstructions: (A) with ventral “lamprey” mouth (with permission from Nobu Tamura); (B) with terminal suspension/detritus feeding mouth ([2], plate 11).



As a sister taxon to the lampreys, *Jamoytius* has been compared with parasitic lampreys which attack fish. But, only 18 of the 38 known species of lamprey, are carnivorous [26]. Living nonparasitic lampreys appear to be derived from parasitic species with heterochronic shifts in metamorphosis [27]. Adult non-parasitic lampreys tend to be somewhat smaller (10 to 20 cm long) than adult parasitic lampreys (15 to 120 cm long) (Figure 4), whose size is related to life history trade offs; either become a parasite/predator with high growth potential, fecundity and mortality, or remain a detritivore with lower growth rates, fecundities and mortality [26,28]. Size is, however, not diagnostic and cannot be used to distinguish parasitic from non-parasitic forms [29], and the supposed parasitic Paleozoic forms may not have been such, but grazers or scavengers (see below).

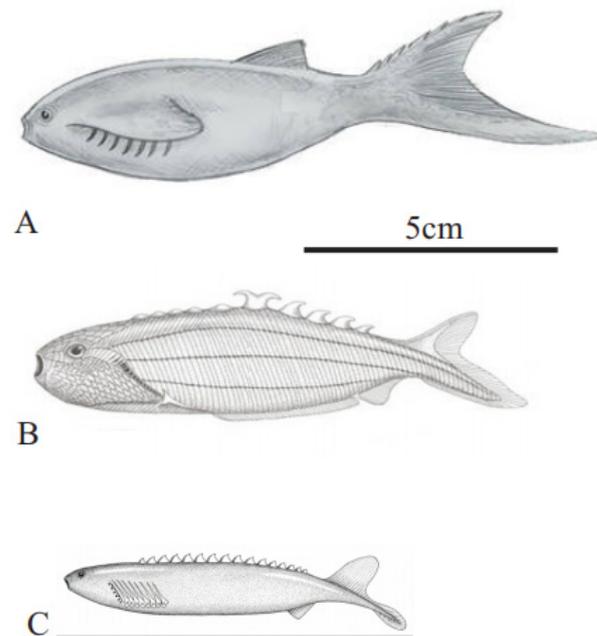


**Figure 4.** Living and oldest fossil (Devonian) lampreys. (A) Parasitic sea lamprey (*Petromyzon marinus* Linnaeus), 35–60 cm long; (B) American brook lamprey (*Lethenteron appendix* DeKay) 15–25 cm long (A,B) courtesy of North Carolina Wildlife Resources Commission; (C) Devonian parasitic fossil lamprey (*Priscomyzon riniensis* Gess et al. [22], ~5 cm long (public domain).

The fossil evidence for early evolution of lampreys is limited. Based on both morphological and molecular evidence, Brownstein and Near [32] estimated that 90% of living lamprey clades originated only since the late Cretaceous. As reconstructed by Reeves and Sansom [11], carnivorous lampreys evolved from non-carnivorous early Paleozoic forms in the Jurassic, when innovations of their feeding apparatus may underlie their evolutionary increase of the body size and the ‘modernization’ of their life-history during the Jurassic period [33], and then radiated from the late Cretaceous times (~100 Ma) and especially from Miocene times (~25 Ma) onwards into many both carnivorous and non-carnivorous forms.

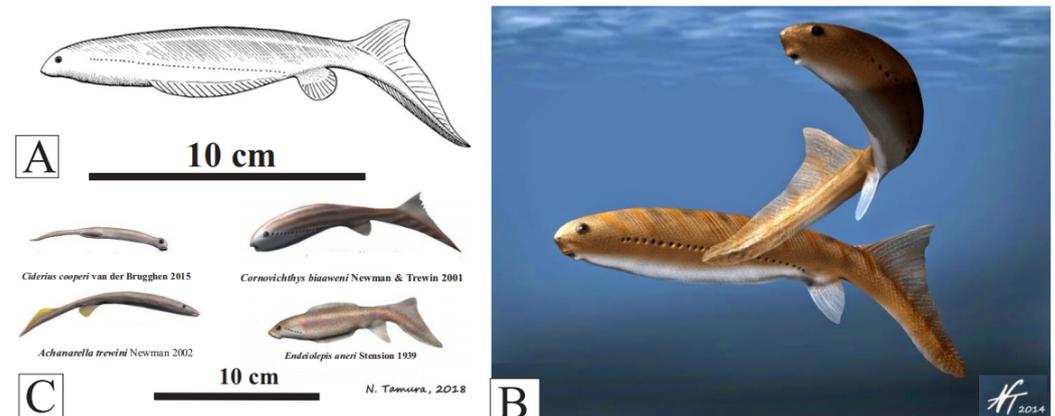
Only four undoubted Palaeozoic lamprey species have been recorded, the Devonian (419–359 Ma) *Priscomyzon riniensis*, from South Africa considered the oldest parasitic lamprey [22]. *Priscomyzon*, and three from the Carboniferous (359–299 Ma) [8]. These Paleozoic lampreys might not, however, be parasitic as conventionally assumed, as they have tiny dentition and a small buccal cavity (which accommodates the anti-coagulant secreting glands and food processing in living parasitic lampreys) and lack an ammocoete stage [8,34]. Wu et al. [33] speculated that the well-developed oral discs and attaching skills of these early lampreys might be adaptations to grazing algal mats, which would fit with the mode of life proposed here for *Jamoytius* and other similar forms like *Euthanerops*.

As a sister taxon to the anaspids (Figure 3B), *Jamoytius* resembles the genera, *Loganellia*, *Birkenia*, and, especially, *Lasanius* [35] (Figure 5). *Loganellia* also occurs in the *Jamoytius* bed, while *Birkenia* and *Lasanius* occur in slightly younger fish beds in the Lesmahagow succession [36,37].



**Figure 5.** Agnathan reconstructions: (A) Thelodont *Loganellia scotica* (<https://creativecommons.org/licenses/by-sa/4.0/>, permission Norbu Tamura); (B) Anaspid *Birkenia* (creative common, Highlander Fossils); (C) Anaspid? *Lasanius* (creative commons, permission Rob Van Assen).

*Jamoytius* is often classified as a sister taxon to the Upper Devonian fish, *Euphanerops*, originally grouped together in the Jamoytiforms [38] (Figure 3C), though many of the structures in the available fossils remain unexplained [24]. Several other euphaneropids have now been recognized: one, *Ciderius cooperi* van der Bruggen from the fish beds above the *Jamoytius* bed at Lesmahagow [39]. These are similar to *Jamoytius*, both in anatomy and possibly mode of life (Figure 6).



**Figure 6.** (A) *Euphanerops longaevus* reconstruction (Upper Devonian, Canada) <https://www.miguasha.ca/mig-en/euphanerops.php> (public domain) (consulted 7 August 2023); (B) *Euphanerops longaevus* as a swimming nektonic detritivore/herbivore (with permission from Nobu Tamura); (C) various euphaneropids; *Ciderius cooperi*, (Lower Silurian), *Achanarella trewinii*, *Cornovitchthys blaaweni* (Middle Devonian), *Endiolepis aneri* (Upper Devonian) (with permission from Nobu Tamura).

The mode of life of *Jamoytius kerwoodi* is thus unresolved; even its life orientation is still not certain [31]. In this paper I am not particularly concerned with its affinities, but with its mode of life as inferred from its anatomy (which bears, of course, on its affinities), adaptative morphology and palaeoenvironment based on the sedimentology of the enclosing strata and the lifestyles of it and its associated biota.

## 2. Anatomy

Because the preservation of soft-bodied organism like *Jamoytius* is so variable, and because there are often so few fossils of them preserved, then even their basic anatomy is subject to different interpretations, leading to radically different reconstructions and affinities [11].

*Jamoytius* had an elongated body, ranging from 14–18 cm long by 3–4 cm wide, a cartilaginous skeleton, akin to the branchial basket of lampreys, and weakly mineralized scales [31]. Earlier reconstructions show side-fins running the length of its body, but these are now interpreted as artifacts formed as a corpse was squashed post-burial. A ring-like stain, interpreted as cartilage, encircles the very small ‘mouth’ (seen as 0.5 to 0.7 mm in diameter in Figure 2), which suggested to Ritchie [2,18,25] that it was an ancestral parasitic lamprey. *Jamoytius*, however, apparently had no true teeth or teeth-like structures, in its ‘mouth’ [31]. If *Jamoytius* had rasping keratin teeth like living parasitic lampreys, as Stensiö [40] inferred for Norwegian anapsids, then these should probably be preserved carbonized, as is much of the rest of the animal (Figure 2). The third most abundant vertebrate fossils (after bones and teeth) are keratin-derived materials such as skin and feathers [41,42].

The controversy about whether this ‘mouth’ was anterior terminal, or subterminal ventral, seems to be resolved in favour of the latter [31]. Towards the anterior end, many specimens preserve a pair of linear features composed of serially repeated, contiguous, sub-rectangular shapes, interpreted as branchial openings [31]. The anterior of *Jamoytius* has room for a piston-like tongue comparable with living parasitic lampreys [34]. In living parasitic lampreys, this holds the biting and cutting plates used to parasitize fish, which are not present in *Jamoytius*. On the other hand, such plates would not be required to eat soft vegetation, which is a possibility considering the holes in associated *Dictyoocaris* (see Section 5), and *Jamoytius* does not have the lamprey lips used for suction [43].

Most specimens do not preserve the posterior portion of *Jamoytius*, and where they do, it is too faint to be seen clearly [31]. So, the inferred hypocercal tail is reconstructed only by analogy with other near-contemporary anapsids, like *Birkenia* and *Lasanius* [17,44].

## 3. Mode of Life of *Jamoytius*

*Jamoytius* has been compared with parasitic lampreys which attack fish [2] (Figures 2A and 3). But, only 18 of the 38 known species of lamprey, are carnivorous. The ancestral crown lamprey was probably a freshwater nonparasitic species, some of which evolved into parasites [32]. Living non-parasitic lampreys are smaller (less than 40 cm long) than parasitic sea lampreys (35–120 cm long), and all inhabit freshwater [26]. The non-carnivorous lampreys do not eat at all, since they have a nonfunctional intestine, only live for four to six months on the energy stored when young; as a result, they typically have small mouths and poorly-developed teeth, useless for attaching to a host, and die after spawning [45]. For example, *Lethenteron appendix*, the American brook lamprey, has small larvae (1–2 cm long) that feed on algae and detritus for between three and seven years, before metamorphosing into sexually mature adults (15–25 cm long) [46]. The size and anatomy of *Jamoytius* is more compatible with non-carnivorous living lampreys, though the Devonian inferred parasitic lamprey, *Priscomyzon riniensis*, is also very small [22] (Figure 4C).

The comparable agnathans, have terminal anterior mouths which do not appear to be protrusible (Figure 5). Such mouths are often found among omnivorous mid-water feeders, which eating anything available, by grabbing bits of food as they move [47].

## 4. Paleoenvironments

The *Jamoytius*-bearing horizon is one of several eurypterid- and fish-bearing units in the Silurian (Llandoveryan; 444–433 Ma) Priesthill Group of the Lesmahagow inlier in the Midland Valley of Scotland [18,30,48]. It is exposed at Birk Knowes in a cliff next to the Logan Water (NS737346) (Figure 7A) near the top of the Patrick Burn Formation, an over 500-m-thick section of alternating grey sandstones, siltstones, and mudstones [37,49]

(Figure 7B). The sediments of the Patrick Burn Formation change gradually upwards from deeper water interbedded mudstone/turbidite sandstone facies into shallower water interbedded mudstone/cross-bedded and laminated sandstone facies [37,49]. This is accompanied by changes in the taxonomy and ecology of the fossil biotas from marine to freshwater [30,37,49] (Figure 7B).

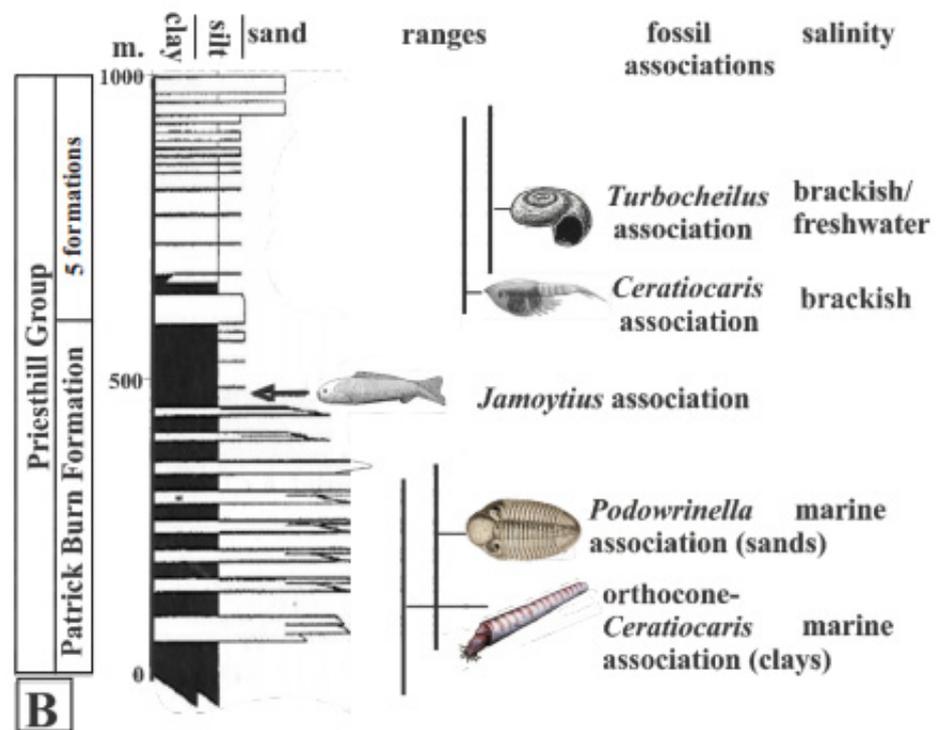
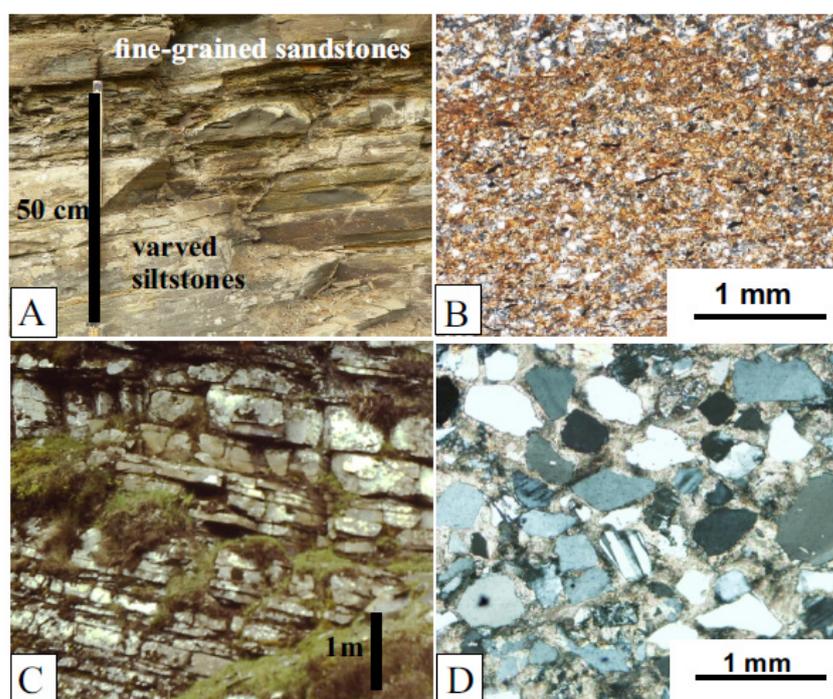


Figure 7. (A) Birk Knowes exposure of *Jamoytius* beds. (B) Section of Priesthill Group with fossil associations, ranges, and inferred salinity (modified from Lovelock, 1998 [22]).

Throughout the Patrick Burn Formation, and in the *Jamoytius* bed itself, there is a complete absence of burrowing organisms and there are no tracks or trails on the bedding plane surfaces [37]. The undisturbed nature of the sediments, together with abundant pyrite and organic matter, indicates anaerobic bottom conditions in very quiet water subject to periodic underflows [30]; in keeping with the abundance of *Ceratiocaris*. Geochemical evidence indicates a gradual salinity drop through the upper part of the Priesthill Group, which contains all the fish beds [49].

The *Jamoytius* bed itself is about 10 m thick and consists of alternating fine-grained thin sandstones, deposited by turbidity currents, and varved siltstones in which the varves consist of a lower graded siltstone overlain by an organic-rich muddy layer: the latter enclose most of the fossils [30,49] (Figure 8A,B). The bounding sandstones are low-angle tabular cross-bedded fine-grained mature muddy quartz- and feldspathic-sandstones [49], deposited by sand waves in shallow water by storms [37,50] (Figure 8C,D). The deeper water *Jamoytius* bed with its turbidite sandstones and laminated siltstone contrasts markedly with the enclosing shallow water cross-bedded fine sandstones and testify to great fluctuations in water levels and climate at millennial scales typical of marginal marine and semi-arid lake basins such as those of Lake Cariaco in northern Venezuela and Lake Chad in the central Sahara [51,52].



**Figure 8.** Sediments; (A) view of part of *Jamoytius* bed showing varved siltstones alternating with graded fine-grained sandstones; (B) photomicrograph of *Jamoytius* bed varved siltstone showing lower graded silt layer overlain by organic-rich silt cap, then coarser basal silt layer of overlying varve; (C) view of outcrop of fine-grained quartz-sandstones overlying *Jamoytius* bed; (D) photomicrograph of fine-grained sandstone from (C), dominated by subangular quartz grains with rare plagioclase feldspar, in carbonate cement.

Both the *Jamoytius* bed, and higher fish-bearing beds at Lesmahagow, have alternations of fine silt-clay couplets (varves) which contain the biota, and olive-grey massive mudstones which are barren [53]. In the *Jamoytius* horizon, itself, the alternations of laminated siltstones and graded quartz sandstones are almost identical to those of Cariaco basin in Venezuela [54,55]. Water circulation inside this partially isolated basin is restricted, which, combined with high annual primary productivity, causes it to be permanently anoxic at depth, where alternating light and dark coloured varved sediments correspond respectively to the winter-spring dry season and the summer-fall rainy season [56].

The tectonic situation of the Midland basin Silurian inliers is also comparable with that of the Cariaco and related basins along the northern Venezuelan coast. Both are complex basins between ocean and continent, which evolved through time from marine to freshwater continental conditions due to shortening and inversion caused by major strike-slip faulting, occupying about the same ~100 Ma time period, Cretaceous to Recent for Venezuela, and Silurian through Devonian for the Midland Valley [57,58].

## 5. Palaeoecology

Though the lower Partick Burn Formation has transported marine, or brackish water, fossils in turbidite sandstone, which shows source connections with the sea, the lack of normal marine planktonic organisms above these basal beds is clear evidence that the oceanic connection was tenuous at best [37].

The *Jamoytius* bed lies above the *Podowrinella* (sands) and orthocone-*Ceratiocaris* (clays) biofacies, between shallow water unfossiliferous sandstones [37] (Figure 6). The *Podowrinella* biofacies is in turbidite sandstones and has been transported from shallower water. It has benthonic scavengers (4 trilobite species, 1 ostracod), attached filter feeders (3 brachiopods, 1 bivalve, crinoid ossicles, bryozoa), herbivores (1 gastropod), free living filter feeders (Tentaculites, Cornulitids). This fauna suggests living conditions in shallow turbulent marine, possibly slightly brackish, water [37]. The orthocone-*Ceratiocaris* biofacies is in the clays and has only the podshrimp, *Ceratiocaris papilio*, rare orthocones and the occasional patch of thelodont scales. The orthocones are upright in the sediment and have floated in and settled with decomposition gas in chambers holding them upright as they settled through the water. The *Ceratiocaris* and thelodonts, in the absence of marine fossils in situ, indicate brackish to freshwater environments [37].

For the fossil biota of the *Jamoytius* bed, I use the list of Lovelock [37], which list only those fossils from the actual laminated siltstones. Peach and Horne [59] believed the Birk Knowes outcrop to be equivalent to those at Shank Castle, which was later shown to be incorrect [49]. Unfortunately, this mis-correlation has led to confusion over the attribution of some fossils to the *Jamoytius* bed [37] (pp. 166–167), an error repeated through successive editions of ‘The Geology of Scotland’ [60]. The single example of the blind “horseshoe crab”, *Cyamocephalus loganensis* Currie 1927, is a museum specimen, attributed to the *Jamoytius* bed only on similar lithology [61]. Hunter [62] never recorded from where he got his single specimen of the scorpion *Palaeophonus caledonicus*, though this might be a plant (Ritchie, 1963), and it was dubiously assigned to the *Jamoytius* horizon by Peach and Horne [59] (p. 574).

The actual fossil biota of the *Jamoytius* bearing laminated siltstone is dominated by the crustacean *Ceratiocaris papilio*, accompanied by the thelodont, *Loganellia scotica*, the enigmatic thylacocephalan crustacean? *Aniktozoon loganense* [63], *Dictyocaris slimoni*, most likely a plant thallus [30], and disc- and stem-shaped plants. Other members are rare to very rare. Rare members are the eurypterids *Slimonia acuminata*, *Jamoytius kerwoodi* itself and the molluscs. Very rare members are the eurypterids, *Errepterus bilobus*, *Hughmilleria* sp., the ostracod, *Beyrichia* sp. (one specimen), and the problematica, *Taitia catena* and *Striatuncus scoticus* [30] (Table 1).

The phyllocarid, *Ceratiocaris*, or pod shrimp, is up to 30 cm long, and is the most abundant fossil. Living phyllocarids (leptostracans) are little known, but seem to prefer low energy conditions over mud bottoms, and are tolerant of low oxygen concentrations [64,65]. Although usually considered filter feeders, they can like shrimps, be opportunistic scavengers, eating plants, organic detritus, and any living or dead organism that does not eat them first [66–68].

*Loganellia scoticus* is up to 30 cm long, and was originally reconstructed as a bottom detritus feeder with heterocercal tail [69]: but it more likely lived as a nektonic feeder with hypocercal tail, as supposed for the anaspid *Birkenia*, especially considering the anoxic bottom over which it lived [30,70,71]. Indirect evidence comes from fossil scroll coprolites assigned to the anaspids *Birkenia* and *Loganellia*, which occur in post-Llandoveryan varved siltstones in Northern Ireland, and are ascribed to detritus feeders [72].

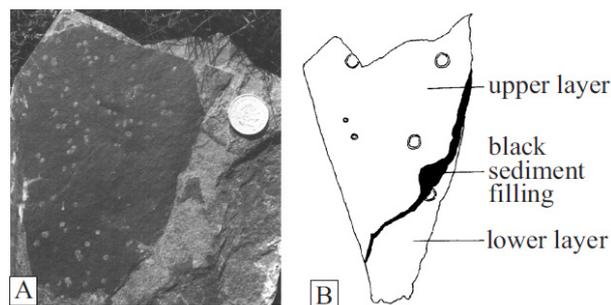
**Table 1.** Taxa, ecology, and abundance of *Jamoytius* association biota.

| Taxa                               | Feeding Strategy                   | Frequency   |
|------------------------------------|------------------------------------|-------------|
| Arthropods                         |                                    |             |
| <i>Ceratiocaris papilio</i>        | nektonic omnivore                  | very common |
| <i>Slimonia acuminata</i>          | nektonic scavenger                 | rare        |
| <i>Erreptoerus bilobus</i>         | nektonic carnivore                 | very rare   |
| <i>Ainiktozoon loganense</i>       | unknown                            | common      |
| <i>Beyrichias</i> sp. (1 specimen) | detritivore                        | very rare   |
| Chordata                           |                                    |             |
| <i>Loganellia scotica</i>          | nektonic detritus/herbivore?       | common      |
| <i>Jamoytius kerwoodi</i>          | nektonic detritus/herbivore?       | rare        |
| <i>Loganellia grossi</i>           | nektonic detritus/herbivore?       | very rare   |
| Cephalopoda                        |                                    |             |
| ? <i>Orthocone</i> indeterminate   | nektonic carnivore                 | very rare   |
| Small (2 specimens)                |                                    |             |
| Gastropoda                         |                                    |             |
| <i>Platyschisma helicites</i>      | mobile herbivore, grazer           | rare        |
| (7 specimens)                      |                                    |             |
| Bivalvia                           |                                    |             |
| <i>Pteritonella</i> sp.            | bysally attached suspension feeder | rare        |
| Unknown                            |                                    |             |
| <i>Dictyocaris slimoni</i>         | plant primary producer?            | very common |
| Plant                              |                                    |             |
| <i>Tatia catena</i>                | primary producer                   | very rare   |

*Ainiktozoon*, is about 12 cm long, and though originally described as an early chordate [73], is now more plausibly an arthropod, more precisely a thylacocephalan crustacean [63]. Its mode of life is unknown, though its abundance suggests an herbivore or detritus feeder rather than a carnivore as postulated for other thylacocephalans [74].

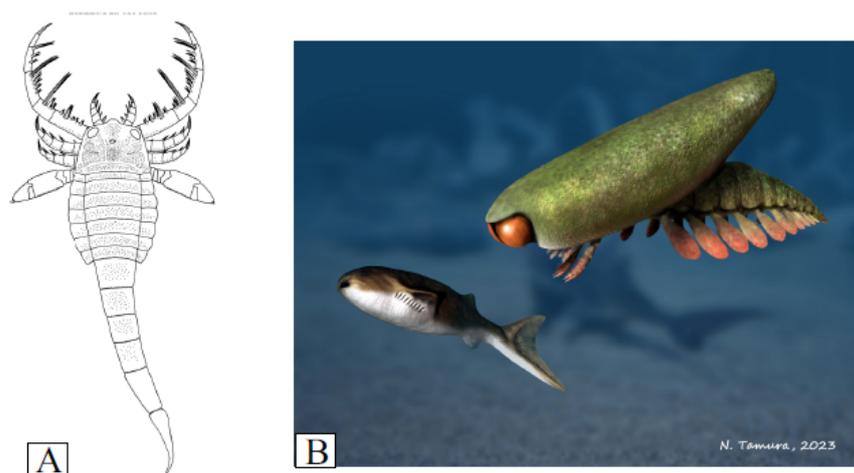
Other arthropods, which are sometimes attributed to the *Jamoytius* bed, come from the overlying Kip Burn Formation, now mostly covered by the waters of the Logan reservoir, including the millipede *Archidesmus loganensis* Peach, 1899 [59].

*Dictyocaris slimoni*, forms large carbonaceous sheets up to 30 cm in diameter, commonly pierced by variably sized circular holes up to 5 mm across, with raised rims [75,76] (Figure 9). *Dictyocaris* specimens were originally thought to be fragments of large arthropod carapaces, with the holes as parasitic injuries from *Jamoytius* mouths [30]. *Dictyocaris* is, however, never found even partially articulated, despite its association with articulated *Ceratiocaris* specimens which have no similar holes. And the large number of holes on the illustrated specimen also seems too many to be the results of parasitism, considering the size of *Jamoytius* (14–18 cm). *Dictyocaris* thus is likely a plant [30].



**Figure 9.** *Dictyocaris*: (A) thallus with holes; (B) drawing showing holes of varying sizes and raised rims (both from van der Bruggen, 1995 [76]).

The morphologies of the rare eurypterids in the *Jamoytius* bed are more easily interpreted as those of nektonic scavengers, because they have none of the specialized adaptations for catching prey found in eurypterids in higher fish beds at Lesmahagow, such as the large spiny grasping arms of the mixopterid *Lanarkopterus dolichoschelus* [77,78] (Figure 10A). For example, *Erettopterus* with its small pincers and compound eyes was probably a predator/scavenger with high visual acuity, but it was not as highly specialized or active as other eurypterids [79]. Similarly, *Ainiktozoon* had likely neither the speed, nor the appendages, to catch a fast-moving *Loganellia* (Figure 10B).



**Figure 10.** (A) Reconstruction of *Lanarkopterus dolichoschelus* Ritchie 1968 (after Ritchie, 1968b [2]); (B) *Ainiktozoon* chasing a *Loganellia* (with permission from Nobu Tamura).

Of the rare molluscs and the small orthocone cephalopod recorded by Ritchie [30] in the *Jamoytius* horizon, the bivalve *Pterinea* is a byssally attached suspension feeder. Small clusters of *Pterinea* occur with carbonaceous patches, which may be floating plants to which they attached [30] (p. 149); such Pteriniids often attach to floating vegetation [80]. The low-spined gastropod *Platyschisma* is most likely a grazing or scavenging form [81]. The small orthocones are not part of the *Jamoytius* bed biota, and were transported in from another shallower water environment, as they occur in the turbidite sandstones interbedded with the laminated siltstones that have the vertebrates and the eurypterids (personal observations in 2022).

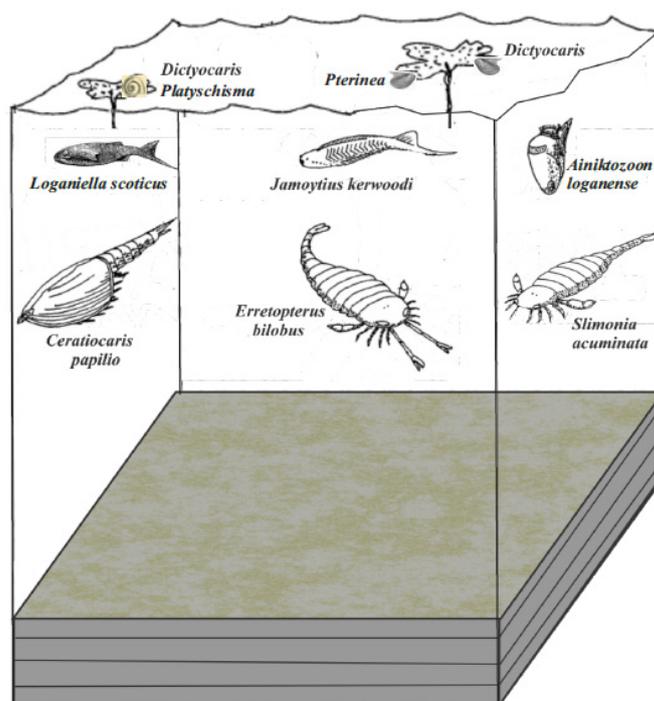
## 6. Discussion

The *Jamoytius* association is dominated by supposed omnivores and herbivore/detritus feeders, with primary production represented by phytoplankton and land plant spores and? algal thalluses (? *Dictyocaris*) that contribute the dark laminae within the siltstone beds (Figure 8B). There is no evidence for large scale transportation of the fossils after death: they simply settled into the anoxic bottom.

The *Jamoytius* reconstructions with a terminal mouth suggest a filter-feeder or a detritus-feeder, analogous to larval lampreys [82] (Figure 1C,E) and possibly to the Loganelliform thelodonts with which it is associated [83,84]: the latter are interpreted as pelagic slow swimmers in open water [85]. Larval lampreys can feed on highly concentrated food suspensions so thick that they border on organic deposits [86,87]. *Jamoytius*, however, lacks any obvious adaptations to suspension feeding [88], and the more likely anterior ventral position of the mouth indicates particulate feeding or grazing [47]. The mouth-sized holes in the possible plant *Dictyocaris* suggest its soft tissues (there are no signs of cuticles) was grazed by *Jamoytius* without teeth, which may have been later evolved in younger forms like the Devonian *Priscomyzon*.

A bottom detritus feeding life style proposed by Parrington (1958) [89] is unlikely given the anoxic bottom inferred from sedimentology, and the hypocercal tail which would give lift to a fish whose morphology also suggests an active lifestyle, like the related euphaneropids [90]. Like euphaneropids, *Jamoytius* resembles elongate arrow-like bony fish, like pike (*Esox* spp.) and barracuda (*Sphyraena* spp.), with posterior dorsal and anal fins, which assist the tail in bursts of rapid acceleration, but are inefficient at steady swimming [91]. Ritchie (1968) considered that its highly developed metamerism (a linear series of body segments fundamentally similar in structure) and large eyes of *Jamoytius* indicated a very active, fast-swimming vertebrate.

Sedimentological and palaeoecological characteristics of the *Jamoytius*-associated organisms indicate that *Jamoytius* lived in a brackish water environment in which the bottom waters and sediments were anoxic, and inhospitable to benthos and a predominantly planktonic and nektonic biota lived only in the overlying oxic waters (Figure 11). A benthonic mode of life for any of the *Jamoytius* association organisms is unlikely. *Jamoytius* and its likely euphaneropid sister taxa, despite the latter's autapomorphic, elongated branchial basket, could plausibly be stem lampreys [5], especially considering that the earliest lampreys are interpreted as non-parasitic [32]. Lampreys may initially have evolved as herbivorous organisms and only later developed ectoparasitic modes of life [34,86,92]. The tiny preserved dentition in Devonian *Priscomyzon riniensis* might be an evolutionary advance for algal grazing from inefficient toothless *Jamoytius*.



**Figure 11.** Palaeoecological sketch of the *Jamoytius* association living over an anoxic bottom (modified from Lovelock, 1998, [22], Figure 4.3).

## 7. Conclusions

*Jamoytius* is associated with a low-diversity dominantly nektonic detritus and herbivorous fauna living over an anoxic bottom, at the transition from a marine-influenced, probably brackish-water and deep-water basin to a shallower-water, less saline and likely freshwater basin. *Jamoytius* was likely a free-living surface feeding detritivore/herbivore.

**Funding:** This research received no external funding.

**Data Availability Statement:** Data is contained within the article.

**Acknowledgments:** This study is part of an ongoing study on the palaeoenvironments and ages of the Silurian inliers of the Midland Valley of Scotland. I thank my colleagues, Elizabeth Catlos and Hector Garza for help during joint field and Susan Turner for a detailed review. I also thank Reviewer 3 for an outstandingly helpful and constructive review. This paper is dedicated to Alex Ritchie, who sadly died on 16 November 2023 at the age of 88.

**Conflicts of Interest:** The author declares no conflicts of interest.

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