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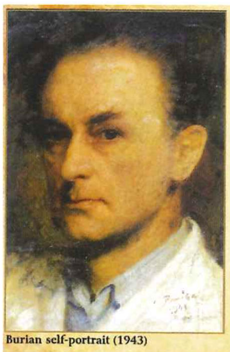
PREHISTORIC TIMES

ZDENĚK BURIAN UNDER THE SEA

GREG PAUL'S FIELD GUIDE TO DINOSAURS

TOP PALEONTOLOGY NEWS OF 2016



Burian self-portrait (1943)

Zdeněk Burian and the Golden Age of Palaeo-art

4. Palaeozoic fishes and invertebrates

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1. Introduction

Although the origins of life on Earth lay in the depths of the Precambrian, it was within the primeval oceans, lagoons and swamps of the Palaeozoic Era that invertebrates and vertebrates underwent major evolutionary radiations, with the latter eventually conquering the terrestrial realm as they followed in the wake of the land invasion by vascular plants (see PT issue 119). The celebrated palaeo-artist Zdenék Burian (1905-1981) painted an important series of monochrome and colour images of Palaeozoic aquatic life, amongst which can be found some of the most memorable reconstructions from the classical era of palaeo-art.

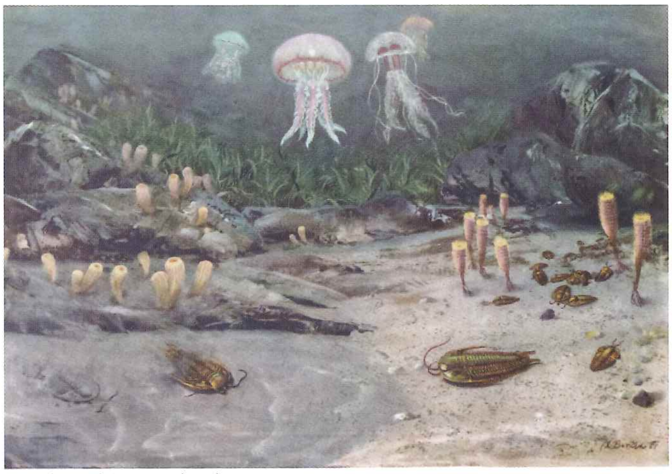


Fig. 2. The Cambrian Ocean (1951).

Readers in many countries will recall, as youngsters, being enthralled by the lucid plates in Josef Augusta's book *Prehistoric Animals* (1956) revealing Burian's portrayals of trilobites foraging like overgrown wood-lice amidst colourful tapestries of spheroid corals and sea-lilies, human-sized sea-scorpions lurking amidst the Silurian seaweed, and a giant armoured-placoderm scattering sharks from its marauding passage through the Devonian waters. This evocative imagery forms the subject of Part 4 in the ongoing series analysing Burian's palaeo-themed paintings. Once again I thank my fellow Burian enthusiasts Jan Kopecky and Paul McFarland for their assistance.

Fig. 3. The trilobites *Ellipsocephalus* and *Paradoxides* (1942).

2. Burian's collaborators

Almost all of Burian's early Palaeozoic images were completed under the supervision of the palaeontologist Dr. Josef Augusta (1903-1968) of Prague's Charles University during what I consider to be the most notable period of Burian's career (1940s - 1960s). Following Augusta's death, Burian collaborated with Augusta's successor Dr. Zdenék Špinar (1916-1995), after which his artistic flair and freestyle technique was restricted and he was directed to produce far more stylised reconstructions of greater definition and illumination. At that same time Burian also adopted brighter and less natural hues for his colour palette, a factor which is especially evident in his later Palaeozoic benthic images. While his Augustanian era Palaeozoic paintings were composed in a 'natural history'-like interpretive manner showing fauna set amidst murky backdrops and shadowy, moody silhouettes (Fig. 4), by 1970 such scenes had become a thing of the past and his benthic depictions became increasingly encyclopaedic and prescriptive in composition (Fig. 5). A curiosity associated with this change was that dorso-ventrally compressed species such as trilobites and bivalves were sometimes shown in direct dorsal aspect even when the ocean floor was at an oblique view. In addition, the organisms tended to be positioned in a somewhat contrived manner, giving the viewer the impression of observing life in a recently-cleaned and arranged aquarium.

On the positive side however, Špinar supervised Burian to reconstruct a number of early aquatic vertebrates which had largely not been considered by Augusta, including armoured and jawless Palaeozoic fishes (placoderms and ostracoderms) and the earliest jawed-fishes (acanthodians). Several Palaeozoic amphibians were also depicted at this time, and will be reviewed in Part 5 of this series. Interestingly, Burian's Špinar era ichthyological subjects were reconstructed in a less stylised manner than were his invertebrates painted in the same period. As was the case with a number of Burian's palaeo-themed landscapes, several of his benthic images represented regional reconstructions of his native Czechoslovakia, that part of Europe having been inundated during much of the Palaeozoic.

3. Publication

Burian's first formal Palaeozoic image depicted the Permian amphibians *Archegosaurus* and *Branchiosaurus* (1935), and was also his first official palaeo-themed work. Completed before he had met Josef Augusta, it was published in the geological section of *The Great Illustrated Natural History of all Three Kingdoms*. Once their collaboration was initiated, Burian painted seven Palaeozoic images for Augusta's landmark 1942 reference text *Divy Prasveta* (*The Wonders of the Prehistoric World*), one of which was used as the frontispiece (Silurian Ocean; Fig. 4, upper). The other six images were as follows: '*Naosaurus*' (1942; colour), *Moschops* (1941; monochrome), Stegocephalian amphibians (1941; colour), *Pleurocanthus* and *Amblypterus* (Fig. 10, inset), *Meganeura* and Carboniferous forest (1942; colour), and the trilobites *Ellipsocephalus* and *Paradoxides* (1942; Fig. 3). Other than the Silurian Ocean and trilobite images, the remaining five paintings were again reproduced in Augusta's subsequent title *Prehistoric Animals*. Being a larger-format work aimed at the popular market, this book was widely translated in numerous countries including Russia, the UK, France, Italy, Germany, and Japan (amongst others).

US palaeontologist Stephen J. Gould described *Prehistoric Animals* as being amongst the three most influential popular palaeontology titles of the 20th Century but, given its distribution, I would not hesitate to rank it at the top of the list. Thirteen of Burian's 60 landscape-format plates in *Prehistoric Animals* featured Palaeozoic subjects, of which six were aquatic and seven were terrestrial. Their order of appearance was as follows: The Cambrian Ocean (Fig. 2), The Silurian Ocean (Fig. 4, lower), *Pterygotus* & *Eurypterus* (Fig. 6), *Dinichthys* & *Cladoselache* (Fig. 8, inset), The Lower Devonian landscape, The Middle Devonian landscape, The primeval Carboniferous forest, *Pleuracanthus* & *Amblypterus* (Fig. 10, upper), *Meganeura* and Carboniferous forest, The Stegocephalians, *Edaphosaurus* (which was a re-painting of '*Naosaurus*,' a genus originally incorrectly assumed to have been carnivorous), *Moschops* and *Mesosaurus*. Seven of these images would not be reprinted in editions of the later title by Špinar & Burian, *Life before Man*, although Burian updated five of the images for inclusion in those editions including three landscapes (two Devonian and one Carboniferous, see PT issue 119) and two faunal images (*Pleuracanthus* & *Amblypterus*, and *Edaphosaurus*). Burian modified the *Mesosaurus* image for *Life before Man* by painting out its intended fish prey. Interestingly, Špinar chose to include the older (1942) version of the Silurian benthos rather than the more detailed 1951 'School painting' from *Prehistoric Animals*. Both the original

1972 (hardback) version of *Life before Man* and the later 1995 (soft-cover) edition featured the same 31 aquatic and terrestrial Palaeozoic images. Of these, 25 had not appeared in *Prehistoric Animals*, the majority having been painted subsequent to that title.

Burian's final Palaeozoic image, *Life in the Ordovician Sea* (1981) was painted shortly before his death and was the last of the Josef Vágner series to be completed (from a total of 22 large-format canvases, see PT issue 117). This image appeared in Czech language booklets but neither it nor Burian's two other Ordovician images painted in 1970 (for the Geological series) were amongst his best works. In addition to the illustrations for books authored by Augusta or Špinar, Burian painted three images of Palaeozoic invertebrates and fishes for inclusion in the multi-volume *Animal Life Encyclopaedia* (Tierleben; 1967-1972) compiled by the renowned German zoologist and conservationist Bernhard Grzimek (1909-1987). Although these were translated into English in 1975, the three supplementary volumes on prehistoric life that contained a total of 13 Burian images only appeared in the German edition. I thank Jan Kopecky for sending me scans of these images, the Palaeozoic examples of which are very highly-stylised and purely encyclopaedic in purpose.

Fig. 4. Two early depictions of the Silurian Ocean by Burian, the upper from 1942, and the lower (1951) being one of the 'School painting' educational series of canvases.

4. Cambrian Ocean

In *Prehistoric Animals* Augusta alluded to the fact that traces of the earliest Precambrian marine organisms still remained only very poorly known by the 1950s. They consisted of fragmentary evidence of algae, worms, primitive brachiopods, molluscs and possible crustaceans. By the dawning of the Palaeozoic (specifically the Cambrian Period), the oceans had witnessed an explosion of organismal diversity and an abundance of invertebrate types that were not only already advanced but also well-differentiated.

The most characteristic members of the Cambrian fauna were the trilobites, unusual segmented arthropods so named because their carapace was divided lengthwise into three parts. With ventrally-positioned mouths and a pair of compound eyes often featuring on the dorsal side, trilobites are thought to have moved over the benthic sediments feeding on minute organisms and debris, although some may have been agile swimmers.

Trilobites shared their Cambrian world with primitive brachiopods, echinoderms (especially the genus *Cystoidea*), worms, *hydrozoa*, and sponges. At this time the sea encroached into parts of Central Europe including Czechoslovakia, and Burian's 1951 painting of the Cambrian Ocean (Fig. 2) represented a typical Central Bohemian benthic scene. Large medusas are shown floating above beds of algae and siliceous sponges, while crawling about on the ocean floor is the spiny trilobite *Paradoxides gracilis* (the larger of the two) along with the smaller *Ellipsocephalus hoffi*, both of which had originally been depicted for Divy Prasvéta (Fig. 3).

As an aside, a trilobite fossil was used to 'initiate' the prehistoric adventure experienced by four boys in the popular 1955 film *Cesta do Praveku* by celebrated Czech film-maker/animator Karel Zeman (1910-1989). Burian's palaeo-artwork was used as a guide for most of the animated models used in the film's production, for which Josef Augusta was enlisted as a 'technical advisor.'

5. Silurian Ocean

By Silurian times, marine invertebrates had experienced another major evolutionary radiation compared with the fauna of the Cambrian and Ordovician oceans. In addition to trilobites and graptolites, other groups had attained a wide distribution including primitive gastropods, lamellibranchs, brachiopods and bryozoans. Crinoids were the most common echinoderms, and grew on long stems each of which carried a cup-like structure with a wreath of moveable arms. The precursors of present-day corals were also to be found forming extensive and multi-coloured colonies on the sea floor. Numerous types of early cephalopods (which were related to the present day spiral-shelled *Nautilus*), were a major faunal component, and all possessed straight or only slightly-curved shells that were often brightly patterned.

ig. 5. Burian's 1970 painting of the Silurian benthos from the Špinar era lacks the mystique, pathos and depth of earlier Augustanian scenes (Fig. 4). It shows a coastal zone abounding in spheroid *Favosites* corals (lower right & middle) and rugose corals, with a skeleton of a 'stromatoporoid' sponge (lower left) which often formed columnar tufts when alive (rear, left of the crinoids). Spherical *Ischadites* algae (mid left) flourished in the warm waters while gastropods fed amidst the corals and sponges and predatory cephalopods roamed overhead. Burian's two reconstructions of the Ordovician Sea from the same year (plus one from 1981) were largely unremarkable works showing invertebrates in unnatural dorsal aspect.

Burian's 1951 reconstruction of the Silurian benthos (Fig. 4; lower) was one of the 'School painting' series of large-format canvases depicting life through the geological ages. From 1949 to 1967 Burian produced a total of 44 paintings for this series, in collaboration with Josef Augusta as part of a Czech state education project (sadly, only 34 are known to have survived). The School painting image is a more illuminated and detailed version of Burian's earlier (1942) depiction of the Silurian benthos (Fig. 4; upper) and represents a rocky shelf area of Central Bohemia based on fossils from the Budňany Beds at Kosor and Velká Chuchle near Prague. Amongst the beds of algae and the slender crinoid *Scyphocrinus excavatus* are loaf-like mats of extinct Tabulata corals and solitary calyces of Tetracorralla corals. Two genera of trilobites (left foreground) are the spiny *Cheirurus* and the smaller *Aulacopleura*, while to the right of them are two brightly-coloured cephalopods; the straight-shelled *Orthoceras* and *Cyrtoceras* with a slightly curved shell. The half-buried gastropod shells to the forefront are the helix-coiled *Murchisonia* (left) with the spiral-coiled *Cyclotropis* to the right. At lower right are two types of clam-like brachiopods.

Burian's 1955 monochrome canvas of the scorpion-like Merostomata arthropods that flourished in the murky Silurian ocean invokes a suitably haunting imagery that one might readily associate with that distant period (Fig. 6). Augusta's accompanying text was typically informative, and much of what he wrote at the time remains valid today. At 2 m in length, the larger genus, *Pterygotus*, was one of the most formidable predators of its day (although a similar genus *Stylonurus* grew to over 3 m) and may have preyed on the earliest vertebrates. Its body was composed of a relatively small cephalothorax attached to a long abdomen of 12 segments terminating in a spiny appendage (telson), while the two front appendages were equipped with pincers not unlike those of a lobster. The top of the cephalothorax featured compound eyes as well as separate individual eyes (ocelli) and on the underside were six pairs of appendages used for feeding and 'walking' over benthic surfaces. The smaller genus in the image (*Eurypterus*) was less than 0.3 m long and had the sixth pair of appendages modified for rowing. Augusta mentions yet another genus (*Carcinusoma*) that was even more scorpion-like in that it vanquished its unfortunate prey by stabbing it with its sword-like telson.

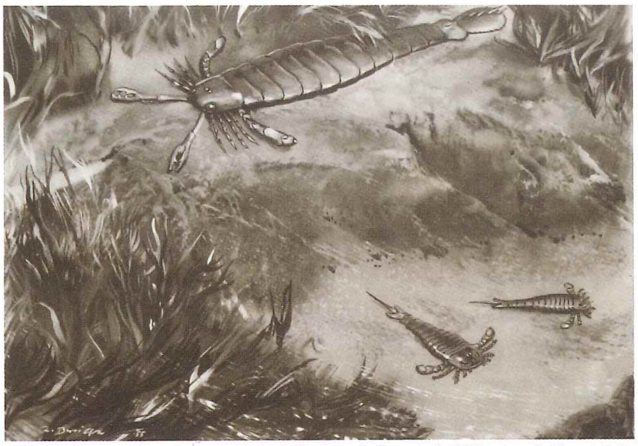
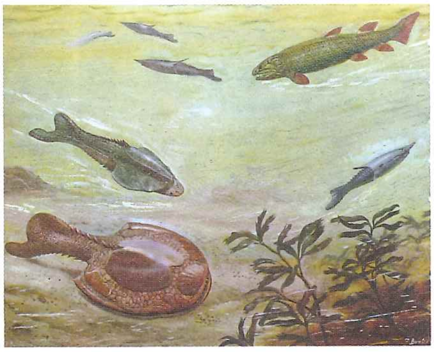


Fig. 6. Burian's reconstruction of two types of eurypterid arthropods, *Pterygotus* (top) & *Eurypterus*, lurking amidst the Silurian seaweed (1955). *Pterygotus* was one of the top predators of its time.

6. Armoured fishes

Because the waters of the Devonian hosted such a significant expansion of ichthyological diversity, it is often referred to as the *Age of Fishes*. Most of Burian's Palaeozoic ichthyology images were produced during his collaboration with Zdeněk Špinar, two of which are reproduced in Fig. 7. The left image shows various armoured types including the jawless and long-snouted *Pteraspis* scattering as a primitive bony freshwater fish of the lobe-finned genus *Osteolepis* enters the scene. *Osteolepis* possessed rudimentary air sacs and was positioned at the base of the evolutionary line that would eventually lead to the tetrapod vertebrates. To the left of the painting are two ostracoderms, *Psammolepis* and the armoured and flat-bodied *Drepanaspis*.



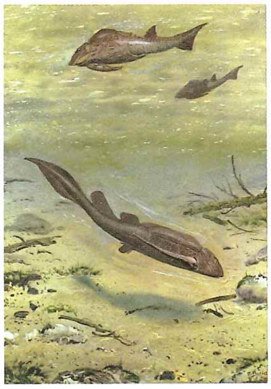


Fig. 7. Armoured Devonian fishes. The image above (1970) shows four armoured genera; the long-snouted *Pteraspis*, the lobe-finned *Osteolepis* (upper right), *Psammolepis* (middle left) and *Drepanaspis* (lower left). The image at right (1970) depicts the armoured placoderms *Pterichthyodes* (upper) and *Bothriolepis*.

Ostracoderms

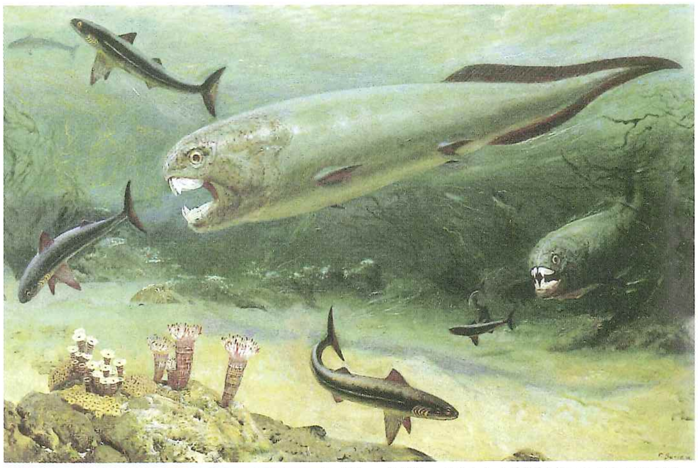
The ostracoderms were very likely the earliest types of fishes to evolve, and were the dominant vertebrates during the Silurian and part of the Devonian. They were characterised by the lack of jaws, absence of paired fins, the presence of bony armour (which was the first true bone to evolve within the vertebrate lineage), an internal cartilaginous skeleton, and what is termed a 'heterocercal' tail. All these features in combination suggest that these were benthic dwellers that fed on organic debris and small benthic invertebrates.

In 1978 fragmentary ostracoderm material was found in a North American marine deposit dated as early as the Upper Cambrian. However, it was during the Silurian Period that the group underwent significant diversification with several groups being recognised. Complete ostracoderm fossils are also known from freshwater Ordovician deposits of several parts of the world including the US, Brazil and the Baltic region. Ostracoderms all possessed a very similar body morphology which may have limited their ability to diversify ecologically, and the group eventually died out.

The origin of the ostracoderms impacts on major questions surrounding the earliest evolution of fishes. It is assumed that the chordate ancestors of fishes (and therefore of all vertebrates) were sessile forms that had a free-swimming larval stage upon which they depended for dispersal. Eventually, larvae capable of reproduction evolved (= neoteny) leading to the loss of the sessile adult stage altogether. Whether this evolutionary significant process occurred in marine or freshwater habitats is unknown, although some ichthyologists believe it might have eventuated in both environments, the early stages within the oceans with the later stages in freshwater.

7. Jawed-fishes - Placoderms

The placoderms (= 'plate-skinned') made up another major fish group that evolved after the ostracoderms. It has been suggested that the recognised list of genera may possibly represent an artificial grouping of different types that are poorly-known from the fossil record. Having said that, most assumed placoderms exhibit similar features including true jaws, an internal ossified bony skeleton, paired fins, and a dorso-ventrally compressed body sheathed in ossified dermal plates. The first three of these features were also characteristic of the bony fishes that would later replace the placoderms. Nonetheless the placoderms' compressed bodies and dermal plates probably limited them to a largely benthic existence (although there may have been some exceptions). Within that role, they were very successful, and became far more ecologically diverse than the ostracoderms. In addition their jaws permitted them to adopt predatory habits and reach very large sizes.



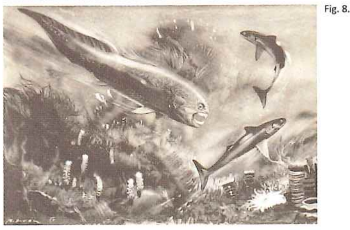


Fig. 8. Above: *Dinichthys* and *Cladoselache* (1967). This canvas is one of the later examples from Burian's 'School painting' series, and is very similar to his original monochrome version (1955; left) painted for inclusion in Augusta's 1956 book *Prehistoric Animals*.

Dinichthys is one of the largest known arthrodire placoderms and may have reached 6 m in length with a weight of over a tonne. Thought to have dwelt in inshore waters, this top trophic-level predator is mostly known from skull remains (in place of teeth it possessed two pairs of sharp bony plates which formed the beak-like jaws). The rest of the body shown in these paintings is partly speculative.
The smaller fish in the images is *Cladoselache*, an early genus of shark that grew to 1.8 m (6 ft) and possessed a mouth positioned at the front of the skull as opposed to the ventral position as in modern genera. Some *Cladoselache* fossil remains are so complete that in addition to teeth and fin spines, other preserved features include crania, jaws, vertebrae, muscle fibres and even kidney tubules.

The right image in Fig. 7 shows two types of heavily-armoured Devonian placoderms, *Pterichthyodes* and *Bothriolepis*. Both genera, which had been contemporaries of the ostracoderms, possessed armour plates over the head and body and are believed to have been benthic dwellers, propelling themselves with thick paddle-like limbs.

Placoderm remains were first discovered by the Scottish quarryman Hugh Miller and were originally distinguished by whether their pectoral fins were composed of one segment (Arthrodira) or several (Antiarcha). The earliest representatives of the Arthrodira were characterised by very large heads with anterior bodies encased in regularly-arranged bony plates, and are thought to have inhabited brackish Devonian lagoons of Europe, North America and Australia. Burian's rarely-reproduced

1967 School painting (Fig. 8) depicts one such giant Arthrodiran genus, *Dinichthys*, whose head alone was over a metre in length. The smaller fish in the image is a contemporary shark *Cladoselache*. Having earlier painted a very similar scene in monochrome in 1955 (inset) for inclusion in *Prehistoric Animals*, Burian's coloured *Dinichthys* displays a more torpedo-like morphology, with a second marauding example bursting out from amongst the sea-weed. This image was one of the very few times that Burian managed to infuse almost as much pathos and drama into a re-painted colour version of an existing monochrome image.

Acanthodians

The freshwater rivers and lakes of the Palaeozoic were inhabited by other types of primitive bony fishes; the acanthodians (sometimes referred to as 'spiny-sharks'). Acanthodians arose in the mid Silurian, diversified greatly in the Devonian, and died out in the mid Permian. They are believed to be the oldest known jawed-vertebrates, having an origin that likely pre-dates that of the placoderms. The origin of vertebrate jaws remains a mystery but studies of the embryological stages of modern fishes suggests one possibility. Fish possess thin rods of bone or cartilage that support the gill slits and these occur in hinged pairs (each with an upper and a lower element). At some stage the front gill support may have become attached to the skull, the upper and lower sections giving rise to the upper and lower jaw sections, respectively.

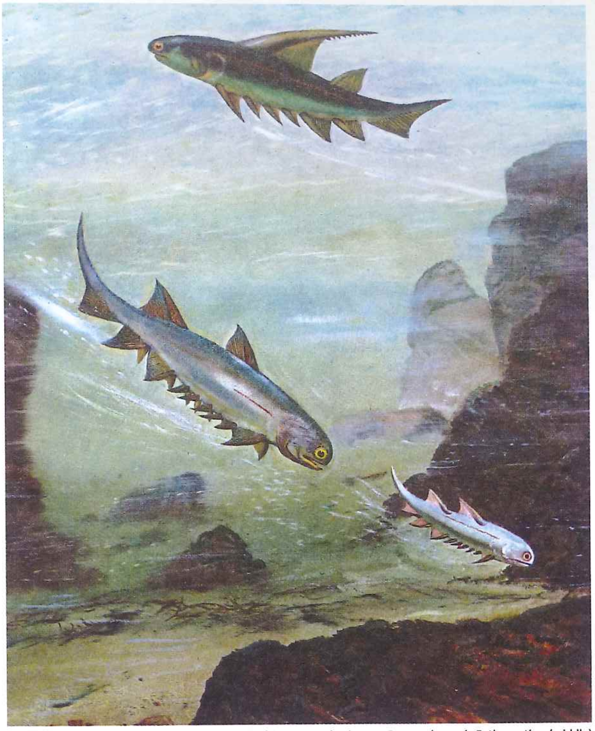


Fig. 9. Three acanthodian genera are depicted in this 1970 Burian image: *Parexus* (upper), *Euthacanthus* (middle) and *Climatius* (lower).

Acanthodians are known from many parts of the globe and most were no more than 10-15 cm in length, although species that migrated to the oceans were far larger. They had large eyes, internal skeletons that were partially ossified, and flexible streamlined bodies protected by scale-like bony plates (Fig. 9). Their most distinctive features, however, were rows of ventral paired 'fins', each of which was preceded by a stout spine. In *Life before Man* Špinar commented that for a predator to dare to try and consume such a fish would be akin to swallowing an open Swiss army knife. One theory holds that acanthodian 'fins' represented an intermediate stage between the less developed lateral folds that were likely used as stabilisers on tadpole-like primeval fish types, and the paired fins that are typical of today's fishes.

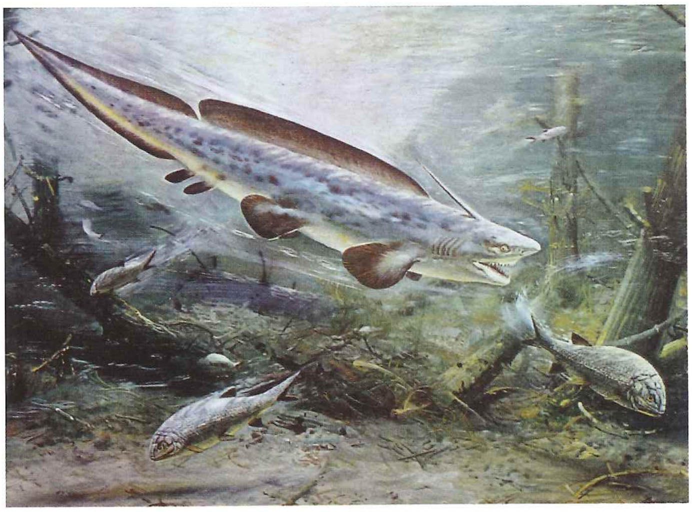


Fig. 10. Above: *Pleuracanthus* and *Amblypterus* (1964). In spite of its small size, *Pleuracanthus* was one of the principal freshwater predators of the Carboniferous, the larger placoderm predators of the preceding Devonian waters having had almost all since become extinct.

This image is unusual in that it is a largely unmodified coloured version of his earlier monochrome gouache from 1941 (left). Although Burian frequently re-painted palaeo-subjects, they rarely resulted in such a close copy. As was the case with a number of his other Palaeozoic images (especially benthic scenes), this reconstruction was based on fossils from Czechoslovakia.

8. Carboniferous sharks

The rivers and pools of the dense Carboniferous forests hosted a rich fauna; worms and lamellibranchs inhabited the muddy benthos, while gastropods and crustaceans crawled amongst the sunken, tangled vegetation, between which flitted the larvae of numerous insects. Unlike the preceding Devonian waters where the top predators had been giant placoderms, with sharks assigned to a subordinate role, the placoderms had almost all died out by the end of the Devonian. Thus the main predators of Carboniferous freshwaters were small sharks that included the genus *Pleuracanthus* (Fig. 10). Remains of this fish are particularly well known from Upper Carboniferous and Lower Permian Czech strata (at Nýrany and Broumov, respectively) and much of what is known of this unusual fish comes from the work of the zoologist/palaeontologist Antonin Jan Friç (1832 – 1913) who specialised in studying Carboniferous and Permian ecosystems.

Pleuracanthus had a cartilaginous skull and endoskeleton (the latter studded with irregular calcareous prisms), five gill arches, many small needle-like teeth, a long dorsal fin extending along most of the body's length (up to 71 cm), and paired pectoral and pelvic fins. The most unusual feature was an aerial-like spine with ridged sides that protruded from the top of the skull. These diminutive sharks shared their world with shoals of smaller fishes from the families Palaeoniscidae and Platysomidae, both of which possessed markedly laterally-compressed bodies clad with large rhombic scales. The most common genus known from Czech deposits was *Amblyterus* which was represented by many species. Burian's monochrome image of *Pleuracanthus* and *Amblypterus* (1941) first appeared in Divy Prasvéta and was re-painted in colour in 1964.

9. Conclusions

Burian's reconstructions of Palaeozoic fishes and marine invertebrates formed an important component of his palaeo-themed collections. Five of these images were part of the Geological Series and at least two were School paintings. As was the case with many of his palaeo-themed subjects, the most accomplished and memorable examples of his Palaeozoic scenes date from the Augustanian era. At this time Burian was still employing his special technique of b & w gouache rendering, which proved an ideal medium for depicting underwater scenes as it conveyed an impression of translucent depth and blurred movement (as evident in figures 3, 6 and 8; inset). Burian also used this technique to good effect in reconstructions of marine reptiles (to be considered in a future instalment of this series), as well as numerous illustrations for popular adventure novels set on the high seas.

As mentioned in Burian's biography (PT 116), several years after *Prehistoric Animals* was published he largely abandoned monochrome as a medium for palaeo-subjects, most likely due to contemporary publishers' preference for colour printing. Following Augusta's death, Burian's style soon changed again and the rather formal and more systematic format in which he painted his Špinar era images is particularly discernible in his Palaeozoic benthic canvases. In comparison, his Palaeozoic ichthyological reconstructions from the same period managed to retain an Augustanian aura (particularly if converted to monochrome). In spite of these stylistic variations during his career, Burian's Palaeozoic reconstructions convincingly portray the primeval Earth in imagery that is not only scientifically accurate but also aesthetically pleasing.