The Earliest Known Venomous Animals Recognized Among Conodonts

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The earliest known venomous animals recognized among conodonts

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Conodonts, a large group of tiny extinct marine animals ranging in age from the Late Cambrian to Late Triassic (ca. 500 to 200 Mya), are usually considered as jawless vertebrates. Their only commonly occurring fossilized remains are minute, phosphatic, teeth-like elements of their feeding apparatuses. In most of the early conodonts the elements were conical and strongly elongated. Many of them are characterized by possession of a deep, longitudinal groove, usually associated with sharp edges or ridges. A comparative study of the grooved elements and venomous teeth and spines of living and extinct vertebrates strongly suggests that the groove in conodonts was also used for delivery of venom. Structural convergence of the conodont apparatus *Panderodus* with the grasping apparatus of chaetognaths, a group of extant, venomous invertebrate predators of similarly ancient origin, provides additional support for this conclusion.

Key words: Vertebrata, Conodonta, venomous animals.

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Introduction

Conodonts are well known to geologists because the fossilized elements of their feeding apparatuses are exceedingly useful for stratigraphy. The elements, usually 0.1 to 3 mm in size, occur commonly in marine rocks of Cambrian to Triassic age. Their strong morphological diversification and rapid evolution is reflected in their taxonomy. According to Sweet (1988) there are more than 200 genera of well-recognized conodonts. Morphological and chemical similarity of conodont elements to fish teeth led to early suppositions of their vertebrate origin (Pander 1856). Their inner structure and lack of other skeletal remnants in the fossil record, however, meant that for a very long time their origin was unknown. The problem presented one of the biggest paleontological mysteries of the past century. Occasional preservation of natural clusters of elements and bedding plane assemblages, as well as morphological studies and statistical analyses of co-occurring elements, resulted in recognition of numerous conodont apparatuses. All are bilaterally symmetrical and usually composed of 3 to 7 different element morphologies arranged in mirror-image pairs, with one symmetrical element unpaired. Since the discovery of conodont soft body remains (Briggs et al. 1983), which shows chordate characters such as v-shaped myomeres, the hypothesis that conodonts are related to vertebrates has become dominant (see Donoghue et al. 2000). However, the systematic position of conodonts is still under discussion (Kasatkina and Buryi 1997; Pridmore et al. 1997; Bultynck 2009). Besides, some of the microfossils considered as elements of conodonts became later identified as grasping spines of chaetognaths (Szaniawski 2002).

Wide geographic distribution shows that conodonts led a nektonic mode of life while their strong feeding apparatus suggest that they may have been swimming predators. Many of the early conodonts possessed apparatuses constructed exclusively of conical elements. Numerous of these elements have a longitudinal groove but its biological function has been hitherto unknown. The elements show similarity to the grasping spines of chaetognaths and also to the venomous fangs of vertebrates. Conodonts having grasping-like apparatuses composed of elongated, conical elements with a deep, longitudinal groove are considered herein as being venomous. A brief report of such a possibility, with reference to the family Panderodontidae Lindström, 1970, has been already published (Szaniawski 2006).

Institutional abbreviation.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Material and methods

All illustrated specimens are stored at ZPAL. The last two numerals used for the specimens in this collection indicate the number of the SEM stub and of the specimen on the stub.

For cross sections illustrated on Fig. 2A the specimen was embedded in epoxy resin, sectioned, polished with aluminum oxide (1200 grit) and etched in 2% nitric acid. The specimen

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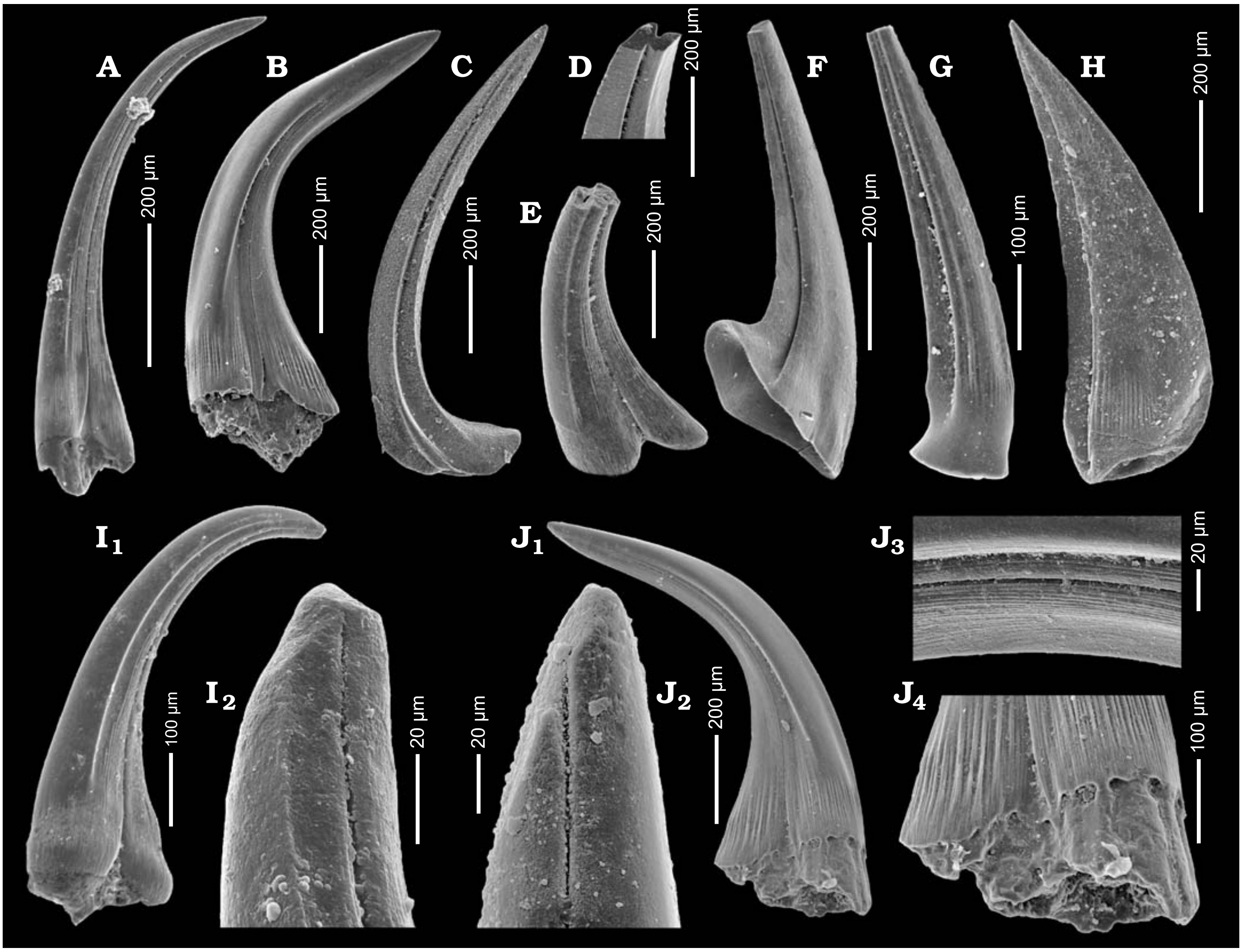

Fig. 1. Elements of venomous conodonts. **A**. *Panderodus sulcatus* (Fåhræus, 1966), Middle Ordovician, borehole Deniski, eastern Poland; ZPAL C.19/150.1. **B**. *Panderodus greenlandensis* Armstrong, 1990, Early Silurian, Jädivere, Estonia; ZPAL C.19/145.2. **C**, **D**. *Protopanderodus calceatus* Bagnoli and Stouge, 1997, Middle Ordovician, borehole Pieszkowo, north-eastern Poland. **C**. Whole element; ZPAL C.19/156.3. **D**. A fragment showing cross section; ZPAL C.19/159.19. **E**. *Panderodus sp.*, Middle Ordovician, borehole Stadniki, eastern Poland; ZPAL C.19/159.12. **F**. *Dapsilodus mutatus* (Branson and Mehl, 1933), Late Ordovician, borehole Stadniki, eastern Poland; ZPAL C.19/159.4. **G**. *Decoriconus fragilis* (Branson and Mehl, 1933), Middle Silurian, borehole Gołdap, northern Poland; ZPAL C.19/160.12. **H**. *Parapanderodus* sp., Early Silurian, Podolia, Ukraine; ZPAL C.15/1. **I**. *Panderodus* sp. Middle Silurian, borehole Gołdap, northern Poland; ZPAL C.19/149.2, whole element (I_1), distal part of the specimen showing wear of the tip (I_2). **J**. *Panderodus greenlandensis*, Early Silurian, Jädivere, Estonia; ZPAL C.19/145.1, whole specimen (J_1), distal part of the same specimen showing wear of the tip (J_2), a fragment of the specimen showing thin longitudinal ridges parallel to the groove and sharp edges delimiting the grooved surface (J_3), basal part of the specimen showing coarse ridges (J_4).

illustrated on Fig. 2B has been fractured and etched with chromium sulfate, pH 5.3.

Comparative study of grooved conodont elements

Conodont elements.—The most common of the grooved conodont elements are those of the family Panderodontidae, known from the Early Ordovician to Middle Devonian; they all have spine-like elements with a very characteristic narrow, longitudinal groove. In the type genus *Panderodus* Ethington, 1959, the groove occurs in all elements of the apparatus and is situated on their lateral, usually flattened side (Figs. 1A, B, E, I, J, 2).

The groove begins slightly beneath the apex and runs along the entire length of the element. Cross sections of the elements show that the groove was formed by infolding of the concentric lamellae rather than by a separate system of radial lamellae (Fig. 2), as supposed earlier (Barnes et al. 1973). The grooved surface is usually delimited by sharp costae. Elements of *Panderodus* and closely related genera are strongly elongated, slightly arched, and usually sub-tri-

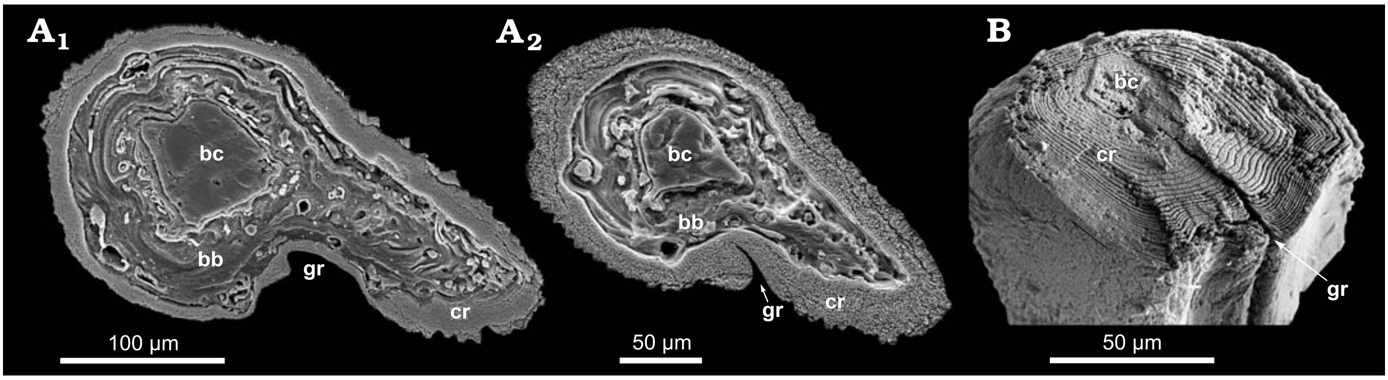

Fig. 2. Cross sections of the elements of *Panderodus*. **A**. *Panderodus greenlandensis* Armstrong, 1990, Early Silurian, Jädivere, Estonia; ZPAL C.19/137.1. Basal part (A_1) and above the basal part (A_2). **B**. Distal part of *Panderodus* sp., Middle Ordovician, borehole Deniski, eastern Poland; ZPAL C.19/19.5. Abbreviations: bb, basal body; bc, basal cavity; cr, crown; gr, groove.

angular in cross section. Most of them are longitudinally ridged or striated (Fig. 1A, I, J). Around the basal part of the element coarse ridges are usually developed (Fig. 1B, H, J).

Construction of the whole grasping apparatus of *Panderodus* is known from several natural assemblages, the most complete of which has been found in the Silurian deposits of Ukraine (Dzik and Drygant 1986; Fig. 3A). It is composed of thirteen elements differentiated mainly by size and degree of curvature. Arrangement of elements in the apparatus is not completely natural but is sufficient in order to note that originally it was very similar to the grasping apparatus of chaetognaths (Fig. 3B–D), although grasping spines of chaetognaths are organic in composition and have no grooves. Another well preserved assemblage of *Panderodus* elements occur in association with imprints of the animal soft body fragment (Smith et al. 1987).

Apart from the family Panderodontidae, there are several genera of conodonts assigned to different families also possessing long, conical and grooved elements: e.g., *Dapsilodus* Cooper, 1976 (Fig. 1F), *Decoriconus* Coper, 1975 (Fig. 1G), *Colaptoconus* Kennedy, 1994, *Protopanderodus* Lindström, 1971 (Fig. 1C, D), *Striatodontus* Ji and Barnes, 1994, *Variabiloconus* Landing, Barnes, and Stevens, 1986 (Fig. 1C, D, F, G). Their groove or grooves are wider than those of the panderodontids but also run almost along their whole length from the tip to the base and in the basal part become much wider. Most of the elements are also longitudinally striated. The grooves are usually delimited by sharp cutting edges. Although constructions of the whole feeding apparatuses of most of these conodonts are known only from statistical analyses of co-occurring elements, it is suggested that their apparatuses were very similar in construction to that of *Panderodus.* Their elements, however, were morphologically more differentiated (Sansom et al. 1994; Mellgren and Eriksson 2006). In the same apparatus some elements might have one or two grooves (Fig. 1D), while others have no groove at all. All genera are not necessarily closely related to one another nor with panderodontids, but the groove apparent in their elements is very

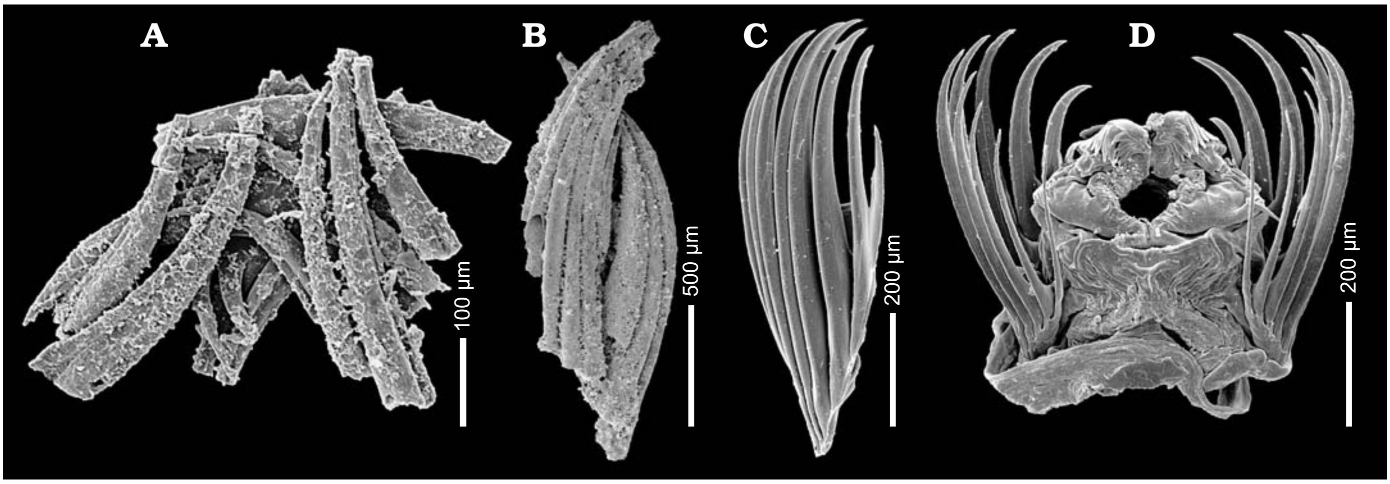

Fig. 3. Grasping apparatuses of the conodont *Panderodus* and fossil and extant chaetognaths. **A**. Partly deformed apparatus of the Silurian conodont *Panderodus unicostatus* Branson and Mehl, 1933, Ukraine, Podolia; ZPAL C.15/1 (same as Dzik and Drygant 1986: fig. 1, new photograph). **B**. Apparatus of the fossil chaetognath *Phakelodus tenuis* (Müller, 1959), subsurface Upper Cambrian of northern Poland; ZPAL C.4/6.2 (same as Szaniawski 1982: fig. 1, new photograph). **C**. Left half of the grasping spine apparatus of the extant chaetognath *Sagitta* sp., North Sea; ZPAL C.4/1.1. **D**. Head of the extant chaetognath *Sagitta* sp. with grasping spine apparatus in acting position, North Sea; ZPAL C.4/619.

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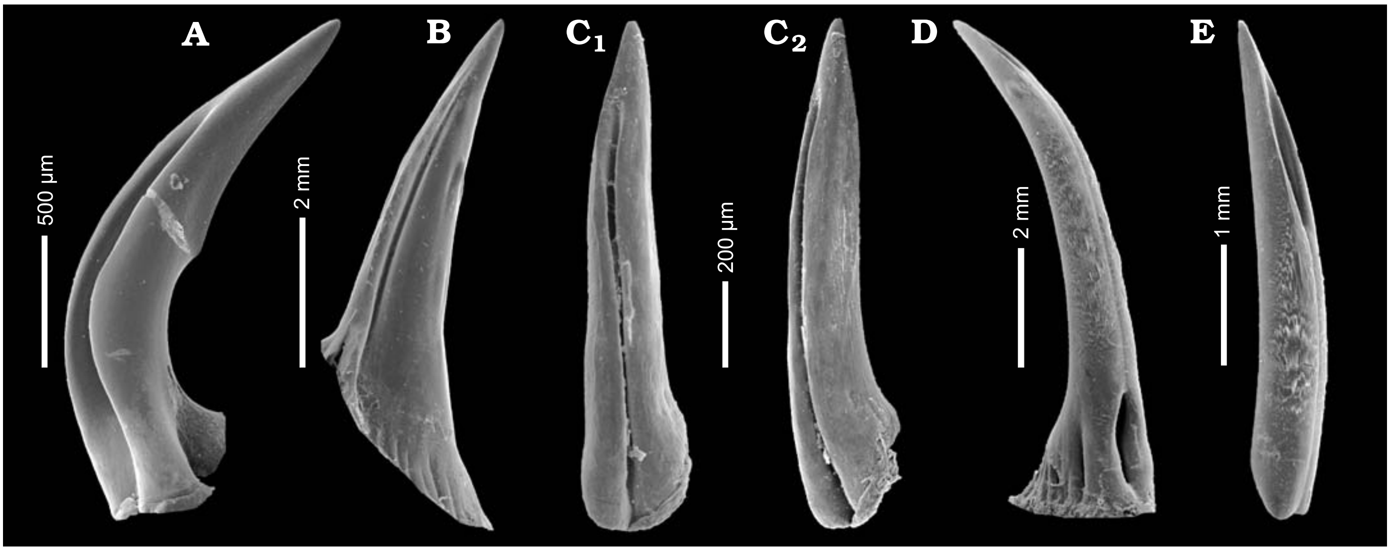

Fig. 4. Venomous teeth of some extant vertebrates. **A**. Fang from the lower jaw of the fish *Meiacanthus grammistes* (Valenciennes, 1836), family Blenniidae, Indonesia; ZPAL C.19/153.2. **B**. Tooth from the lower jaw of the lizard *Heloderma suspectum* Cope, 1869, North America; ZPAL C.19/165.1. **C**. Posterior maxillary tooth of the snake *Psammophis* cf. *shokari* Forskal, 1775, family Colubridae; ZPAL C.19/155.1, in dorsal (C_1) and oblique (C_2) views. **D**, **E**. Fangs of the snake *Trimeresurus gramineus* (Shaw, 1802), family Viperidae, India.1 **D**. ZPAL C.19/164, Mature form in lateral view. **E**. ZPAL C.19/164.2, replacement fang of the same snake in oblique view.

characteristic. The groove is very deep and comparatively narrow. However, conodont elements grew by addition of new lamellae from the outside, and most probably only the outer, wider part of the groove was used for conduction of venom. In some other panderodontids, the groove is much wider, especially in their basal part. Generally, the groove of the earlier conodonts, such as the Ordovician *Decoriconus*, *Parapanderodus* or *Striatodontus* (Fig. 1G, H) was much wider than that of the later genera, like the Devonian *Neopanderodus* Ziegler and Lindström, 1971. There were also long-lived genera (*Panderodus* and *Protopanderodus*, for example) that were conservative in this respect. The groove was constructed by many growing lamellae. It must have occurred early in the ontogeny of the elements and likely had an important biological function. According to the hypothesis of Lindström and Ziegler (1971) the groove of panderodontids served for muscle attachment. However, in the early 1970s when their paper was published, many paleontologists were convinced that conodont elements were constantly embedded in soft tissue. Since then we have learned that at least some of them were partly exposed and could be used for grasping, biting or grinding food, thereby refuting, in this case, the presence of soft tissues such as a keratinous sheath (Bengtson 1976; Jeppson 1979; Purnell 1995; Donoghue and Purnell 1999; see also Fig. 1I, J which show wear at the tips of some elements). The supposition that they served only the muscles seems presently improbable. Besides, many other apparatuses of conodonts are constructed of similar, conical elements but have no grooves at all.

Venom delivery structures of vertebrates.—Most of the venomous representatives of vertebrates use long, arched, coniform teeth or straight spines for envenomation (Halstead 1970a, b; Smith and Wheeler 2006; Jackson 2007). The teeth and spines usually have one or more longitudinal grooves or, in some cases, a central canal (Figs. 4, 5). Fangs of most of the venomous snakes (viperids and elapids) bear a canal that, from study of their early development stages, appears to have originated from grooved forms (Fig. 4E). This traditional opinion (see Kardong 1982) is consistent with recently published results of molecular and embryological studies of the origin and evolution of snake fangs (Vonk 2008).

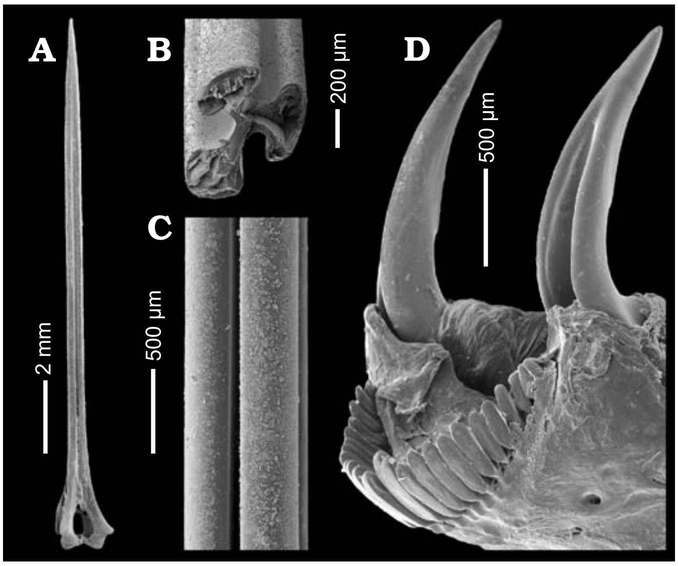

Fig. 5. Venom delivery structures of extant fish. **A**–**C**. Dorsal spines of *Pterois volitans* Linnaeus, 1758, family Scorpaenidae. **A**. Whole spine; ZPAL C.19/165.1. **B**. Distal portion of another spine, fractured to show cross-section; ZPAL C.19/165.2. **C**. Magnification of a fragment; ZPAL C.19/165.3. **D**. Anterior part of the lower jaw of *Meiacanthus grammistes* (Valenciennes), 1836, family Blenniidae, Indonesia; ZPAL C.19/2.1.

Structural comparison of grooved elements of conodonts with venomous teeth and spines of living and extinct vertebrates strongly suggest that the grooves were used for delivery of venom. Although grooved teeth do also occur in non-venomous vertebrates (especially among mammals, see Folinsbee et al. 2007; Orr et al. 2007), the groove of conodont elements are more similar to those of the typical venomous structures of colubrid snakes and helodermatid lizards, which are usually narrow, long and deep (Meier 1981; Nydam 2000; see also Fig. 4B, C). There are other arguments which lend support to the hypothesis—cutting edges or sharp ridges parallel to the grooves, in addition to the coarse ridges in their basal part (Fig. 1B, H, J), are common also in venomous fangs (Young and Kardong 1996; Beck 2005).

Although somewhat indirect, another argument supporting the venom hypothesis is the high degree of similarity between the *Panderodus* apparatus and the grasping apparatus of chaetognaths (Fig. 3). Although Sansom et al. (1994) pointed out some differences in structure of the apparatuses but did not question the earlier hypothesis of their similar function (Dzik and Drygant 1986). This similarity, probably the result of functional convergence, strongly suggests that apparatuses of the *Panderodus*-like conodonts, similarly to those of chaetognaths, were used for grasping. Extant chaetognaths paralyse their victims with toxins to facilitate their swallowing (Thuesen 1991). Such capability would undoubtedly also have been very useful for conodonts, so it is possible this apparatus functioned in the same way. Chaetognaths, commonly known as arrow worms, have been extremely conservative in evolution. Their paleontological record extends to the Early Cambrian and already at that time their grasping apparatus was very similar to the extant forms (Chen et al. 2002; Chen and Huang 2002; Hu et al. 2007). However the spines were usually considered as "protoconodonts" (see Szaniawski 1982, 2002). It is not known when some of chaetognaths first became venomous.

Short review of extant and fossil venomous vertebrates

Fish.—According to recent estimates, the number of extant species of bony fishes using toxins exceeds 1200, making up about 50% of all venomous vertebrates (Smith and Wheeler 2006). Most of them belong either to spiny-rayed fish (Acanthomorpha) or to catfish (Siluriformes). Most of the fishes use venom for defense. For envenomation they usually use fin spines with distinct longitudinal grooves (Fig. 5A–C).

However, there are also fish with "hollow" spines that inject venom in a similar way to fangs of most venomous snakes. Only one genus of small reef-associated fishes—*Meiacanthus* Norman, 1944, family Blenniidae—is known to possess specialized venomous canine teeth (Figs. 4A, 5D). The teeth are situated on both sides of the lower jaw, are very large, recurved, and deeply grooved. They are directly connected with glands that produce a toxic secretion. Biting combined with injection of the secretion take place when the venomous fish is already swallowed by a predator, and usually results in rejection of the fish alive (Fishelson 1974). This unique strategy of defense must be very efficient because some of the non-venomous blenniids developed mimicking similarity to the venomous forms (Randall 2005). Venomous fangs of fossil fish are not known but that is understandable if one takes into consideration that even the "sabre teeth" of the extant genus *Meiacanthus* were not recognized as venomous until monograph of Springer (1968).

Venomous representatives are common not only among bony fishes but also among the cartilaginous fishes. The venomous spike possessed by some sharks is situated in the dorsal fin and at the tail in rays and chimaeras. The spikes have one or two longitudinal grooves filled with soft tissue containing toxins. Compared to the bony fishes, the spines of cartilaginous fishes are usually shorter and stouter.

The oldest scales of fishes are known from the Late Cambrian (Smith et al. 2006). Scales of shark-like fishes are reported from the Late Ordovician (Sansom et al. 1996), but as their cartilaginous skeleton has very low fossilization potential, the oldest articulated shark is known only from the Early Devonian (Miller et al. 2003). Typical venomous spines are documented in the extinct elasmobranchs of genera known since the late Permian (Muir Evans 1923). Along the concave side of the fossil spines runs a median ridge with two wide grooves on each side. The spines are very similar to those of the extant venomous sharks and rays. Chondrichthans were extremely conservative in evolution and because of that it is quite probable that their venom capability originated even earlier than the Permian.

Reptiles.—About one-third of presently living species of reptiles produce toxins (Gans 1978). The most diversified and sophisticated venomous system is that of snakes. Two families of exclusively venomous snakes, Elapidae and Viperidae, have long frontal fangs (Fig. 4D) to conduct venom through a hollow tube and inject it under pressure. Early developmental forms, which are well represented by a series of replacement fangs, are more similar to grooved fangs: their orifice is strongly elongated and the whole tube is not completely enclosed (Fig. 4E). Venomous snakes of the family Colubridae retain an open and usually deep groove, or rarely two grooves, in both the functioning and the replacement fangs (Fig. 4C). Contrary to elapids and viperids the fangs are situated in the posterior part of the maxilla (opisthoglyph). The grooved fangs are evidently less efficient in delivery of venom and most of the venomous colubrid snakes are harmless to humans.

Until recently, apart from snakes, only two species of lizards were known among extant reptiles to be venomous—the only representatives of the primitive family Helodermatidae. Both of the species have numerous teeth and most of them

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are grooved. The teeth usually have two grooves, one much longer and deeper than the other (Fig. 4B). According to (Beck 2005: 43) "Each groove is flanked by a cutting flange, which makes the tooth better adapted for piercing flesh ...". At the basal part of the teeth there is a series of short and shallow grooves. Similar cutting edges and basal grooves occur in some elements of the postulated venomous conodonts and in some fangs of the venomous snakes (Figs. 1B, H, J, 4D). Recently, members of two other lineages of lizards—iguanians and varanoids—have been recognized as venomous (Fry et al. 2006).

The oldest skeletal remains and tracks of reptiles (amniotans) are known from early in the Pennsylvanian (Falcon-Lang et al. 2007), whereas the earliest known fossil reptile with a comparatively well documented venomous apparatus is the Upper Permian therocephalian therapsid *Euchambersia mirabilis* Broom, 1931 from the Karoo Basin in South Africa (Mendrez 1975). Preserved are not only the large grooved canine teeth, but also recesses in the maxilla, which, in extant venomous reptiles, house venom glands. Taking into account the paucity of the paleontological record of non-marine vertebrates, it seems probable that the venom delivery system of reptiles originated much earlier.

Isolated, laterally compressed reptilian teeth with serrated margins and deep longitudinal grooves on both lateral sides have been described from the Upper Triassic of Virginia and Arizona (Sues 1991, 1996). According to the author of the papers they show "Close similarities to the teeth of many carnivorous archosauromorph reptiles" that "possibly indicate affinities to that group" (Sues 1996: 571). From the Middle Jurassic of Mexico there is known a right lower jaw of a probably venomous sphenodontian (Reynoso 2005). The jaw has two anterior caniniform teeth with single groove on their anteromedial surface. Described from the Upper Cretaceous of Mongolia is an almost complete skull of the varanoid lizard *Estesia mongoliensis* (Norel et al. 1992). Its longitudinally grooved teeth are very similar to the venomous teeth of extant helodermatids. Fossil helodermatids are known from the late Eocene of France and possibly from the Late Cretaceous but certainly from the late Paleocene to Recent of North America (Pregil et al. 1986). The paleontological records and molecular investigations suggest that varanoids, iguanians, and snakes belong to the same clade originating in the Early Jurassic (Fry et al. 2006). According to the authors it seems probable that venom capabilities of the whole clade developed around the same time. However, the oldest well preserved fangs of snakes are known from the early Miocene of Germany. Some of them have structures indistinguishable from the fangs of modern viperids or elapids. This suggests that "… the evolution of the most efficient venom-delivery systems was already completed at the Oligocene–Miocene transition" (Kuch et al. 2006: 86).

Mammals.—Extant venomous mammals are not common. Some insectivores—a few species of shrews and two nearly extinct species of *Solenodon*—have poisonous saliva. The male duck-billed platypus, one of the 5 species of extant monotremes, has a venomous spur on its hind leg. However, across the gamut of mammals, well developed grooves for delivery of venom are known only in the second lower incisor of the *Solenodon*. The two groups of living mammals with venomous members (Soricomorpha and Monotremata) are regarded as being very primitive.

Paleontological records of venomous mammals are rare. Teeth with possible venom-conducting grooves are known in two species of shrews from the early Pleistocene of Spain (Cuenca-Bescós and Rofes 2007), and in the pantolestid *Bisonalveus browni* Gazin, 1956 as well as several undetermined isolated teeth from the late Paleocene of Canada (Fox and Scott 2005). It is not certain if they functioned for delivery of venom because grooved teeth are known also in non-venomous extant mammalian species (such as some primates; Orr et al. 2007, Folinsbee et al. 2007). Nevertheless, there are some convincing arguments that use of the salivary venom among extinct mammals was much more common (Cuenca-Bescós and Rofes 2007).

Fossilized mammalian spurs, similar to those of the platypus but not necessarily venomous, are known from the Lower Cretaceous of Montana and China (Jenkins and Schaff 1988; Hu et al. 1997). The basal component of the spur, the os calcaris, is known also from several Upper Cretaceous specimens of multituberculate mammals from Mongolia (Hurum et al. 2006). A very convincing hypothesis assumes that the extratarsal spur, such as the venomous spur of the duckbilled platypus is "a basic feature of Mammalia" (Hurum et al. 2006: 9).

Birds and amphibians.—Some extant amphibians and birds use toxic liquids for protection but probably never developed any special venom delivery system which could be fossilized (Dumbacher et al. 2000; Chen et al. 2003).

Conclusions

The main results of the paper can be stressed in the following conclusions:

- Conical, grooved elements of conodont feeding apparatuses have structural features characteristic for venom-conducting structures of living and fossil vertebrates. They appear to have functioned as grasping spines, similarly to those of chaetognaths.
- In the early stage of conodont evolution, one or some of their lineages developed features consistent with the capability to produce and deliver venom. Based on the short review of the fossil and living venomous vertebrates, one can presume that this also happened during the early evolution of fishes, reptiles and probably mammals.
- Conodonts with grooved elements are known from the Early Ordovician and were represented by many taxa until the Early Devonian. If the venom hypothesis proves to be correct they are therefore the earliest known venomous animals documented to date.

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