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SHORT COMMUNICATION

A pectinal tooth with peg sensilla from an Early Devonian scorpion

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Abstract. A cuticle fragment found in an Early Devonian (Emsian) macerate from the Strathpeffer–Struie outlier in the Northern Highlands of Scotland represents the isolated pectinal tooth of a scorpion. This remarkable find includes a distinctive field of small projections in rounded sockets consistent with the peg sensilla of extant scorpions. This is the oldest evidence for the presence of these characteristic sensory organs, which in modern scorpions play an important role in chemo- and mechanoreception. The fossil indicates that some scorpions had developed anatomically modern pectinal teeth at least 395 million years ago, suggesting that the pectines of these early scorpions played a similar role, physiologically and behaviorally, to those of living species.

Keywords: Scorpiones, fossil, Emsian, Scotland, sensory organ, pectines

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Pectines are a unique type of sensory organ found on the underside of the opisthosoma of scorpions (Arachnida: Scorpiones) and are considered one of the diagnostic synapomorphies of the order (Weygoldt & Paulus 1979; Shultz 1990, 2007). These comb-like structures are modified opisthosomal appendages, which may represent telopodites (Di et al. 2018). Each pecten comprises a segmented rachis bearing several slightly overlapping teeth. The number of teeth ranges from three to more than forty, varies inter- and intraspecifically, and often from left to right on the same individual (e.g., Brown 1996). Individual teeth bear so-called peg sensilla (Foelix & Müller Vorholt 1983; Wolf 2008), a dense aggregation of small circular pits, each containing a peg-like projection, along the proventral margin of the tooth. Studies of pectinal morphology and physiology have demonstrated that peg sensilla act as both chemo- and, to a lesser extent, mechanoreceptors (e.g., Wolf 2017; Drozd et al. 2020; Gaffin & Shakir 2021). Each peg sensilla is connected to several chemosensory neurons, but also to a neuron which responds to mechanical deflection. One of the primary functions of the pectines appears to be for courtship and mating. Pectines enable male scorpions to pick up olfactory clues about females and to assess the texture of the substrate for deposition of the spermatophore. Male scorpions have been observed actively sweeping the substrate with their pectines during courtship (Polis & Farley 1979). Pectines also assist scorpions to navigate their way back to their retreat using chemical and/or textural clues from the substrate (Gaffin & Brayfield 2017) and may be used for assessing the nature of the substrate more broadly. A mechanoreceptive role in detecting the substrate-borne vibrations of potential prey has also been suggested (Mineo & Del Claro 2006).

The first fossil scorpions date to the mid-Silurian (Dunlop & Selden 2013; Waddington et al. 2015) about 433–438 million years ago. Some of these early scorpion taxa appear not to possess pectines, although their ventral anatomy is otherwise similar to that of modern scorpions, and quite well-preserved (e.g., Dunlop et al. 2008). This led to speculation that pectines may not be part of the scorpion groundplan. If this interpretation is correct, pectines evolved within the order and are synapomorphic for a more derived scorpion grade of organization. Nevertheless, one Silurian scorpion, *Allopalaeophonus caledonicus* (Hunter, 1886), does appear to preserve pectines (Pocock 1901: p. 311, plate 19), as do some Devonian taxa such as *Branchioscorpio richardsoni* Kjellesvig-Waering, 1986; see e.g., Kjellesvig-Waering (1986: p. 227, Text-fig. 101). By the Carboniferous, several fossil scorpions, such as *Paraisobuthus dubiocarinatus* Kjellesvig-Waering, 1986, preserve relatively modern-looking pectines (e.g., Kjellesvig-Waering 1986: p. 205, Text-fig. 90) with a segmented rachis and tens of individual teeth. All these examples are compression fossils in shales or nodules, thus details of any structures on their pectinal teeth are equivocal. In the present contribution, a remarkable fossilized scorpion pectinal tooth from the Early Devonian of Scotland reveals the presence of an anatomically modern field of peg sensilla.

The sample originates from a sequence of Lower Old Red Sandstone deposits of the Strathpeffer–Struie outlier located in the Northern Highlands of Scotland. This sequence comprises a series of terrestrial-fluviatile-lacustrine deposits that accumulated in a back-tilted lacustrine basin (Dingwall-Strathpeffer Basin) within the Caledonian Mountains of southeast Laurussia. The sample is from the transition between the Strathpeffer and Moy formations collected at the locality of Wyvisdale near Strathpeffer. Here there is an interdigitating sequence of Facies 5 (red and grey mudstones) and Facies 6b (interbedded bituminous dolomitic series). These represent deposits that accumulated at the interface between a perennial lake (sheetflood and settle-out at lake margin) and a playa mudflat (sheetflood and settle-out from playa lake) in an arid to semi-arid environment. The sediment has been dated as late Emsian in age (ca. 395 Ma) based on dispersed spore assemblages (CHW, pers. obs.). Further details of the geology of the outlier and the locality are provided by Clarke & Parnell (1999). The possibility that this is a modern contaminant can be excluded, as scorpions do not occur naturally in Scotland today.

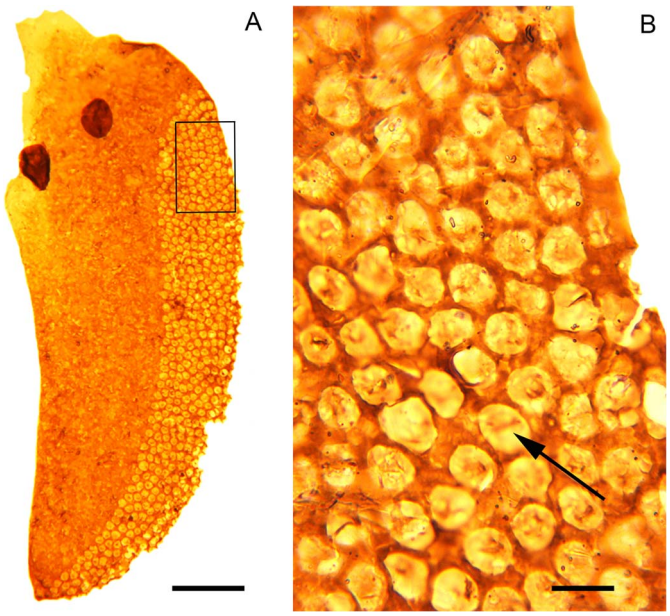

Figure 1.—(A) Pectinal tooth belonging to a fossil scorpion, acid-macerated from the Early Devonian (Emsian) Strathpeffer–Struie outlier in the Northern Highlands of Scotland. Note the angular shape and extensive ornamentation along the proventral margin. Scale bar = 0.1 mm. (B) Details of the ornament (boxed area in A) interpreted as peg sensilla with slit-like terminal openings (arrow). It is the oldest record of this chemo- and mechanoreceptive organ system. Scale bar = 15 µm.

The specimen was recovered by the second author using standard palynological processing techniques. Forty grams of rock were digested using hydrochloric (HCl) and hydrofluoric (HF) acid, followed by heavy liquid separation using zinc chloride ($ZnCl_2$). Sieving was then undertaken using a 20 µm mesh. The organic residue was mounted on glass slides/coverslips using Epoxy resin and examined by light microscopy. The slide bearing the specimen bears the repository number CSP1/3 and is housed in the collections of the Centre for Palynology of the University of Sheffield; the specimen is also located at England Finder No. G49/2.

The specimen consists of a macerated piece of arthropod cuticle representing a single, disarticulated scorpion pectinal tooth; total length ca. 0.8 mm. The entire tooth (Fig. 1A) is complete and resembles a blunt curved dagger in outline, with a distinct narrowing proximally where it articulated with the rachis of the pecten. The tooth is heavily ornamented along its proventral margin, the ornamentation occupying about a third of the width of the tooth and comprising a dense aggregation of at least 430 tiny circles, ca. 13–14 µm in diameter (Fig. 1B). These circles are interpreted as peg sensilla filling their associated sockets, although some circles towards the margins may represent empty sockets. The peg sensilla of modern scorpions bear terminal slit-like openings (Foelix & Müller Vorholt 1983; Ali et al. 2001) and these orifices may also be preserved in the fossil specimen (Fig. 1B: arrow). However, variation in the shape of the orifices in the fossil, from round to slit-like to triradiate, could also be explained by the taphonomic collapse of poorly sclerotized structures. The position of the peg sensilla field, restricted to the proventral margin of the tooth and presumably orientated ventrally towards the substrate in life, and the count of sensilla, are consistent with living scorpions, in which the counts of sensilla per tooth range from 200 to 1200 (Ali et al. 2001). Additionally, the angular shape of the tooth and the short, rounded shape of the sensilla are consistent with scorpions that inhabit arid environments today (LP, pers. obs.).

Arthropod cuticle fragments are relatively common in this sample (CHW, pers. obs.) and although other scorpion material has yet to be identified from the macerates, the significance of the specimen described here is threefold:

First, it demonstrates that anatomically modern pectinal teeth, with fields of peg sensilla, were present in at least some scorpions by the Early Devonian. This suggests that these sensory organs must be at least 395 million years old, and that pectines and their peg sensilla may have had a physiological function in these early scorpions similar to that of the pectines of living scorpions. This could in turn imply a similarity in certain behaviors such as mate location and navigation via olfactory clues (chemoreception), substrate selection for spermatophore deposition in mating, and prey detection through substrate vibrations (mechanoreception), among others.

Second, the new Early Devonian fossil predates both the oldest scorpion fossils assigned to the modern Orthosterni clade (Jeram 1994) and molecular estimates for when the scorpion crown-group evolved (e.g., Howard et al. 2019; Lozano-Fernandez et al. 2020; Santibáñez-López et al. 2022), implying that orthosterns first appeared in the Late Carboniferous.

Third, the discovery is relevant to the ongoing debate about whether the earliest scorpions were terrestrial or aquatic (e.g., Howard et al. 2019). Peg sensilla could, theoretically, function both as chemo- and mechanoreceptors in water. They have been shown to respond to experimental stimuli when immersed in oil under Knowlton & Gaffin's (2009) "mineral oil flood technique". However, peg sensilla are probably better adapted for detecting air-borne or substrate-borne molecules as well as substrate vibrations on dry land. Han et al. (2017) noted that the peg sensilla structure is more like other terrestrial sensory adaptations such as moth antennae, as opposed to the antennae of, e.g., aquatic crustaceans. On this basis, the Devonian scorpion which possessed these sense organs was probably terrestrial. Furthermore, it is noteworthy that the environment of the original habitat was reconstructed as arid to semi-arid (Clarke & Parnell 1999), consistent with the shapes of both the pectinal tooth and the sensilla. Many extant scorpions inhabit arid habitats and it is interesting to speculate whether some taxa in the Devonian were adapted to, or even preferred, such conditions as well.

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