AN ISOLATED PTERYGOTID RAMUS (CHELICERATA: EURYPTERIDA) FROM THE DEVONIAN BEARTOOTH BUTTE FORMATION, WYOMING

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ABSTRACT—An isolated ramus of the pterygotid eurypterid Jaekelopterus cf. howelli from the Early Devonian (Pragian) Beartooth Butte Formation (Cottonwood Canyon, north-western Wyoming) is described. Pterygotid taxonomy and synonymy is briefly discussed with the genera Pterygotus, Acutiramus and Jaekelopterus shown to be potential synonyms. The use of cheliceral denticulation patterns as a generic-level character is discouraged in light of variations within genera and its unsuitability as a major characteristic in the other eurypterid families.

INTRODUCTION

Pterygotids are a diverse group of predatory Palaeozoic eurypterids, famed for being amongst the largest arthropods ever to have lived (Braddy et al., 2008a). The Pterygotidae are characterized by the possession of enlarged raptorial chelicerae, non-spiniferous appendages III–V, undivided medial appendages, laterally expanded pretelson and a broad paddle-like telson with marginal ornamentation (Tetlie and Briggs, 2009). They originated in the late early Silurian and went extinct during the Middle Devonian (Tetlie, 2007a), possibly due to increased competition from vertebrates and the potential loss of diversity (Lamsdell and Braddy, 2010). There are currently 46 recognized species assigned to 5 genera within Pterygotidae, making them the most speciose clade of eurypterids. Pterygotids are almost certainly taxonomically over-split however (Braddy et al., 2008b): Erettopterus monroensis (Sarle, 1903) and Pterygotus impacatus Kjellesvig-Waering, 1964 were synonymized with Erettopterus osiliensis (Schmidt, 1883) by Ciurca and Tetlie (2007) while Pterygotus minor Woodward, 1864 and Pterygotus atlanticus Clarke and Ruedemann, 1912 have both been suggested to be synonyms of Pterygotus anglicus Agassiz, 1844 (Braddy, 2000; Miller, 2007).

Herein is described an isolated free ramus of a pterygotid chelicera, FMNH 6177.2, from the Early Devonian Beartooth Butte Formation of Cottonwood Canyon, north-western Wyoming. This is the same specimen as referred to by Kjellesvig-Waering (1986) in his posthumous scorpion monograph as Pterygotus mcgrewi Kjellesvig-Waering and Richardson, apparently an unpublished manuscript name that made it into the literature.

MATERIALS AND METHODS

The material described herein is deposited in the Field Museum of Natural History, Chicago (FMNH). Morphological terminology follows Tollerton (1989) with denticle terminology as used by Miller (2007). Specimens were examined using a Nikon binocular microscope and photographed immersed in alcohol using a Nikon D80 camera. Camera lucida drawings were prepared using Adobe Illustrator 10.

GEOLOGICAL SETTING

The ramus was recovered from the Cottonwood Canyon section of the Beartooth Butte Formation by Robert H. Denison and E. S. Richardson, Jr. in 1962. The Cottonwood Canyon section is situated in the Bighorn Mountains of northern Wyoming (Sandberg, 1961), roughly 100 km east of the type section of the Beartooth Butte Formation in Beartooth Butte, which is Early Devonian in age. For a more comprehensive discussion of the formation, its stratigraphy and paleoenvironment, see Tetlie (2007b). Vertebrate biostratigraphy (Elliot and Ilyes, 1996) indicates that the Cottonwood Canyon section is Pragian whereas the type section at Beartooth Butte is Emsian. Stable oxygen and isotope data (Poulson in Fiorillo, 2000) indicate that the Beartooth Butte Formation was deposited in an estuarine environment, with the Cottonwood Canyon section being slightly less saline than the type section.

The Beartooth Butte Formation is best known for its fish fauna; however, despite their lower numbers, the associated eurypterids are also of importance. The eurypterid fauna of the Beartooth Butte section were originally described by Ruedemann (1934, 1935a), Kjellesvig-Waering (1955) and Kjellesvig-Waering and Størmer (1952). Tetlie (2007b) recently redescribed the fauna, synonymizing some species and reducing the eurypterids known from the type to Dorfopterus angusticollis Kjellesvig-Waering, 1955, Jaekelopterus howelli (Kjellesvig-Waering and Størmer, 1952) and Strobilopterus princeconii (Ruedemann, 1934). He further suggested that Dorfopterus and Strobilopterus may be synonyms. The eurypterid fauna from the Cottonwood Canyon section is as yet undescribed, although Tetlie (2007b) noted that the most common eurypterid there closely resembles S. princeconii. Three scorpion specimens are also known from Cottonwood Canyon, each assigned its own monospecific genus; Hydroscorpius denisoni Kjellesvig-Waering, 1986, Acanthoscorpio mucronatus Kjellesvig-Waering, 1986 and Branchioscorpio richardsoni Kjellesvig-Waering, 1986. However, A. mucronatus, preserved on the same slab as the ramus, may in fact be a juvenile eurypterid (Legg et al., 2009).

SYSTEMATIC PALEONTOLOGY

Order Eurypterida Burmeister, 1843
Suborder Eurypterina Burmeister, 1843
Superfamily Pterygotoidae Clarke and Ruedemann, 1912
Family Pterygotidae Clarke and Ruedemann, 1912
Jaekelopterus Waterston, 1964
Jaekelopterus cf. howelli (Kjellesvig-Waering and Størmer, 1952)
Figure 1

Pterygotus mcgrewi (nomen nudum) Kjellesvig-Waering and Richardson in Kjellesvig-Waering, 1986, p. 73
reconstructed by Størmer (1936): three large principal denticles with a curved terminal denticle oriented at a right angle to the ramus. The intermediate denticle pattern of two before the anterior principal denticle and two between the anterior and primary principal denticles is identical to that described for Jaekelopterus by Waterston (1964) and seen in the large chelicera of Braddy et al. (2008a).

The free ramus of Pterygotus Agassiz, 1839 is also similar to that of Jaekelopterus, to the extent that Braddy et al. (2008b) considered the two genera indistinguishable by the chelicerae alone. The chelicerae of Pterygotus are highly variable; however, the free ramus does differ from Jaekelopterus in possessing seven principal denticles (Miller, 2007) and having the terminal denticle angled slightly away from the ramus (Waterston, 1964). Although a number of pterygotid species have been erected based on isolated chelicera it is felt that, given the high probability of species-level oversplitting, a single chela (or ramus thereof) is not sufficient material to warrant the description of a new species. The presence of Jaekelopterus howelli in the same formation (albeit in slightly younger strata) suggests that the ramus should be assigned to this species, however the temporal difference means such an interpretation must be treated with caution, especially given that the Strobilopterus-like species is very similar to Strobilopterus princetonii but not identical (Tetlie, 2007b). The potential for similar eurypterids between the localities to be chronospecies, as is the case in the Eurypterus Dekay, 1825 of the Berti Group in New York and Ontario (Tetlie et al., 2007), cannot currently be discounted. The chelicerae of the Beartooth Butte section Jaekelopterus are unknown and so no direct comparison between it and the Cottonwood Canyon Jaekelopterus can be made beyond the fact that they are cogenetic.

Several lines of evidence point to the Jaekelopterus being conspecific: they both have a similar projected body length (80 cm for the Beartooth Butte specimens, 100 cm for the Cottonwood Canyon specimen [Lamsdell, pers. obs.]), they both come from geographically close localities in the same formation within a relatively short geological period, the two localities have extremely similar faunal components, and there is no evidence from the Beartooth Butte section of there being more than one pterygotid species present. Nevertheless, the authors prefer to assign the specimen described herein to Jaekelopterus cf. howelli until post-cheliceral specimens are found from Cottonwood Canyon or the chelicerae of Jaekelopterus howelli are known from Beartooth Butte.

PTERYGOTID TAXONOMIC DIVERSITY

Despite the apparent differences in the chelicerae of Jaekelopterus and Pterygotus, there may be an argument for synonymizing Jaekelopterus, Pterygotus and Acutiramus Rue-demann, 1935b based on similarities in the genital appendage, reducing the recognized pterygotid genera to Pterygotus, Erettopterus Salter (in Huxley and Salter), 1859 and Cincropterus Tetlie and Briggs, 2009. It appears that Waterston (1964) had similar views on pterygotid taxonomy, considering the morphology of the chelicerae to be too dependent on mode of life and variable through ontogeny to be a suitable basis for a generic-level taxonomic framework.

Furthermore, the criteria applied to pterygotids when organizing their taxonomy differs somewhat to that applied to other eurypterid families. Of the primary characteristics defining Jaekelopterus, the marginal cuticular ornamentation of the telson is not a suitable genus-level character and while the telson shape can be used to distinguish genera, the more

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<td>Length/width at base</td>
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<td>Distance from terminal denticle</td>
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<td>35</td>
<td>14</td>
<td>53</td>
<td>6</td>
<td>9</td>
<td>25</td>
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FIGURE 1—Jaekelopterus cf. howelli (Kjellesvig-Waering and Størmer, 1952), photographs and interpretive drawings. Scale bars represent 10 mm. 1. Photograph of FMNH PE 6177.2a, comprising the free ramus of the chelicera; 2. photograph of counterpart FMNH PE 6177.2b; 3. interpretive drawing of FMNH PE 6177.2a; 4. interpretive drawing of counterpart FMNH PE 6177.2b. Abbreviations: td’—terminal denticle on free ramus, d1’–d3’—principal denticles on free ramus, d1’ indicates primary denticle, i1’–i5’—intermediate denticles on free ramus.

Discussion.—The specimen bears close comparison with the free ramus of Jaekelopterus rhenaniae (Jaekel, 1914) as
triangular telson still falls within the morphological range of the paddle-shaped telson as defined by Tollerton (1989) that is diagnostic of both *Acutiramus* and *Pterygotus*. The chelicera of pterygotids can be highly variable, as shown within *Erettopteryx* (Waterston, 1964; Ciurca & Tettie, 2007), and so their denticulation patterns should not be utilized at genus-level, although this could be acceptable for species. Adoption of this would be in keeping with the taxonomic criteria used for other eurypterid families. The other defining characteristic of *Jaekelopterus*, the morphology of the genital appendage, may vary within genera, as appears to be the case in *Acutiramus*, in which the genital appendage progressively changes from the standard spoon shape to become more bilobed until species such as *Acutiramus macrophthalmus* (Hall, 1859) approach the state found in *Jaekelopterus*.

The phylogenetic analysis presented in Braddy et al. (2008a) provided strong support for *Erettopteryx* as a genus but does not include more than a single species of *Jaekelopterus* and *Pterygotus* and so does not test whether these genera form a phylogenetic clade. It is possible that *Pterygotus* and *Acutiramus* actually represent a paraphyletic grade towards *Jaekelopterus*, and as such all three should be termed *Pterygotus*, however a more inclusive analysis with multiple species of *Pterygotus*, *Acutiramus* and *Jaekelopterus* is needed fully to resolve this issue.

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