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Title:

Morphological evidence shows that not all Velesunioninae have smooth umbos

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Short running head:

Sculpture in Velesunioninae

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Most species in the freshwater bivalve order Unionida (sensu Carter et al., 2011) display some form of shell sculpture during the early post-larval stage. These so-called ‘umbonal sculptures’, ‘beak sculptures’ or ‘rugae’ range from more or less regularly formed V- and zigzag-shapes to pseudoradial, pseudoconcentric and double-looped bars, and single-standing nodules (Modell, 1942, 1964; Watters, 1994; Zieritz, 2010). In some Unionida, this ornamentation may extend to mature ontogenetic stages (e.g. Hyriidae; Haas, 1969a, b; Watters, 1994). Others, however, are regarded as lacking sculptured umbos altogether. These include (1) the Mychetopodidae (according to descriptions by Modell, 1942, 1964; Haas, 1969a, b; Zieritz, 2010); (2) most Iridininae including Mutela rostrata (Rang, 1835), Pleiodon ovata (Swainson, 1823) and Pleiodon spekii (Woodward, 1859) (according to descriptions by Pilsbry & Bequaert, 1927; Zieritz, 2010); and (3) some Unionidae such as Actinonaias pectorosa (Conrad, 1834), Delphinonaias delphinulus (Morelet, 1849) and Pseudospatha tanganyicensis (Smith, 1880) (Zieritz, 2010). Finally, various authors, including Cotton & Gabriel (1932), Iredale (1934), Modell (1942, 1964), McMichael & Hiscock (1958) and Haas (1969a) stated that smooth umbos are also characteristic of all members of (4) the Velesunioninae, a subfamily of the Hyriidae endemic to the Australasian region (Walker et al., 2001; Walker, Jones & Klunzinger, in review). Haas (1969b), on the other hand, described beak sculpture in the subgenus “Velesunio” – comprising four of the five currently recognised velesunionine genera (except Lortiella) – as “not strong, consisting of broken, nodulose ridges curving toward each other below, generally with smooth space between”. Unfortunately, no illustration of these sculptures has been made available by this or any other author to date.

Despite the difficulties imposed by frequent abrasion and rare preservation of umbos (Ortmann, 1912; McMichael & Hiscock, 1958; Good, 1998), interspecific differences in umbonal sculpture morphology have long played an important role in species identification.
and reconstruction of phylogenetic relationships within extant and fossil Unionida (e.g. Modell, 1942, 1964; Graf, 2000; Hoeh, Bogan & Heard, 2001; Graf & Cummings, 2006). Disregarding Haas (1969b), in all phylogenetic datasets of the Unionida published to date, velesunionine taxa were coded as smooth (Table 1). This reflects the prevailing opinion that Velesunioninae lack umbonal sculpture. Graf & Cummings’ (2006) analysis, for example, recovered smooth umbos as the plesiomorphic condition for the Palaeoheterodonta (= Unionida + Trigonioida). Against this background, the non-sculptured umbos displayed by members of the family Mycetopodidae, the Iridininae (subfamily of Iridinidae) and the Velesunioninae (subfamily of Hyriidae) would represent the ancestral character state. The presence of (V-shaped or “radial”) beak sculpture in the remaining Hyriidae, on the other hand, was recovered as the single morphological synapomorphy characterising the second hyriid subfamily Hyriinae.

Here we report the discovery and provide the first photographic evidence of umbonal sculpture in two velesunionine genera and species, Westralunio carteri Iredale, 1934 and Alathyria cf. pertexta Iredale, 1934. In contrast, the umbos in two other velesunionine genera examined, i.e. Lortiella froggatti Iredale, 1934, and Velesunio [Velesunio wilsonii (Lea, 1859) and Velesunio cf. wilsonii], were smooth. Our observations suggest that refinement of current hypotheses of beak sculpture evolution within the Unionida is needed. Umbonal sculpture may have been lost in some Velesunioninae, rather than gained in their sister subfamily Hyriinae.

Sixteen specimens of Velesunioninae with well-preserved beaks (n = 2 L. froggatti, 2 V. wilsonii, 3 V. cf. wilsonii and 9 W. carteri) were analysed and photographed under a stereomicroscope (Table 2). Taxonomic identification of specimens followed McMichael & Hiscock (1958).
Despite being found in abrasive, coarse sand substrates, three juvenile *W. carteri* were recovered with little periostracal wear. These displayed, in addition to fine commarginal growth lines, elaborate oblique sculpture on the umbonal region (Fig. 1A-F). At the anterior and posterior thirds of the ornamented umbonal surface, sculpture is represented by discontinuous low ridges punctuated by a few higher nodules, running along a quasi-radial path and divaricating slightly (Fig. 1). The middle third of the ornamented surface features more prominent nodulose ridges, which merge to form V-shaped and/or W-shaped patterns. Intraspecific variation was observed mainly in the prominence of the sculptural elements and in the morphological onset and offset of ornamentation (compare Figs 1A-F).

Umbonal sculpture was also found in an adult specimen of *A. cf. pertexa* (University Museum of Zoology Cambridge, UK; CUMZ 103519; Supplementary Fig. 1). Beak sculpture in this *Alathyria* specimen differs considerably from that of *W. carteri* in that it does not consist of connected ridges but is rather composed of two radiating lines of nodules (Fig. 2). A similar beak sculpture pattern occurs, for example, in the European *Unio pictorum* (Linnaeus, 1758) and *Pseudanodonta complanata* (Rossmässler, 1835), the North American *Pleurobema sintoxia* (Rafinesque, 1820) (all species of Unionidae), and in some African Iridinidae including *Aspatharia rugifera* (Dunker, 1858) and *Chambardia nyassaensis* (Lea, 1864) (see Zieritz, 2010).

In contrast to *Westralunio* and *Alathyria*, no umbonal sculpture could be detected in the perfectly preserved specimens of *L. froggatti*, *V. wilsonii* and *V. cf. wilsonii* examined (Fig. 3). These taxa must thus remain to be considered as exhibiting smooth umbos.

The assumption that all Velesunioninae have smooth umbos as a rule can no longer be maintained. However, considering the difficulties involved, it is not particularly surprising that most previous authors have overlooked velesunionine beak sculptures. Most umbonal sculptures described in the present paper are rather faint and poorly developed. As such,
detection necessitates well preserved umbalon regions and, in some cases, the use of a microscope. Umbo wear is typical in adult Unionida, so that sculpturing as seen in the juvenile specimens presented here is not usually visible in older individuals of the same population. Small juvenile unionoids from wild populations, on the other hand, are notoriously difficult to locate (Neves & Widlak, 1987; Strayer, 2008), and rarely represented in museum collections. As a consequence, almost all velesunionine specimens depicted in previous publications (e.g. Cotton & Gabriel, 1932; Iredale, 1934; Modell, 1942; McMichael & Hiscock, 1958; Modell, 1964) and used in phylogenetic studies (Table 1) have abraded umbos, thus rendering accurate determination of their ornamentation impossible.

Our observation of the presence of beak sculpture in two velesunionine species and genera may provide an impetus to refine current hypotheses on the evolution of umbalon sculptures within the Hyriidae. As mentioned above, Graf & Cummings’ (2006) analysis retrieved the V-shaped/nodulous umbalon sculpture as the single morphological synapomorphy of the hyrid subfamily Hyriinae, discriminating it from the smooth Velesunioninae. However, beak sculptures in Alathyria and Westralunio correspond closely to those of hyriines not only in topology, but also in their mode of formation, with the generative zone of sculpture migrating along the mantle margin with growth. This complex morphogenetic pattern, which results in oblique ribs on the shell surface, has evolved only a few times within the Bivalvia (Checa & Jiménez-Jiménez, 2003), being hence strongly suggestive of homology. Rather than having evolved independently in Hyriinae and in some Velesunioninae, we gather it more likely that oblique beak sculpture is synapomorphic for a more inclusive clade than either subfamily, having been subsequently lost, perhaps iteratively, in those Velesunioninae now characterized by smooth umbos. Testing these hypotheses will require phylogenetic trees with denser taxonomic sampling than is currently available.
The fact that umbonal sculptures in Alathyria and Westralunio eluded detection for more than a century may hint at a wider problem regarding our current understanding and use of this character. In particular, we suspect that other putatively smooth, but comparatively poorly studied taxa such as the South American Mycetopodidae, African Iridininae and other Australasian hyriids, may be found to display umbonal sculptures. Field efforts and the re-examination of museum collections may be fruitful in this respect.

Acknowledgements

K.F. Walker and H.A. Jones assisted in identification of the Alathyria cf. pertexta specimen. Velesunio specimens were identified by W.F. Ponder.
References


Table 1. Velesunioninae specimens, accession numbers and literature references utilised in previous morphological phylogenetic analyses and concerning beak sculpture morphology. Note that according to Graf & Cummings (2007), the Velesunioninae comprises 16-17 species from five genera (i.e. *Velesunio*, *Alathyria*, *Lortiella*, *Microdontia* and *Westralunio*).

<table>
<thead>
<tr>
<th>Publication</th>
<th>Velesunioninae specimens analysed</th>
<th>Notes on umbonal erosion status of specimen(s)</th>
<th>Supporting references</th>
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<tbody>
<tr>
<td>Hoeh et al. (2001)</td>
<td><em>Lortiella rugata</em> <em>Velesunio angasi</em></td>
<td>Unknown</td>
<td>Modell (1942, 1964)</td>
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</table>
Table 2. Specimens with intact umbos examined for sculpturing. Abbreviations: CUMZ = University Museum of Zoology Cambridge, UK; DEC = Department of Environment and Conservation, Government of Western Australia, Woodvale, Australia; WA = Western Australia; WAM = Western Australian Museum (Perth).

<table>
<thead>
<tr>
<th>Lot ID</th>
<th>Species</th>
<th>N</th>
<th>Name of water body</th>
<th>Site</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Collection date</th>
<th>Source</th>
</tr>
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<tr>
<td>CUMZ_103519</td>
<td><em>Alathyria</em> cf. <em>pertexta</em> Iredale, 1934</td>
<td>1</td>
<td>Unknown</td>
<td>‘New South Wales’</td>
<td>Unknown</td>
<td>Unknown</td>
<td>1873</td>
<td>MacAndrew Collection</td>
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<td>CUMZ²</td>
<td><em>Lortiella</em> froggatti Iredale, 1934</td>
<td>2</td>
<td>Snake Creek</td>
<td>Durack Pool, West Kimberleys, WA</td>
<td>17°34’60&quot;S</td>
<td>124°09’14&quot;E</td>
<td>13 Nov 2009</td>
<td>Klunzinger <em>et al.</em> (in press)</td>
</tr>
<tr>
<td>DEC_PSW067</td>
<td>&quot;</td>
<td>1</td>
<td>Brumby Creek</td>
<td>Wannagunna Spring Pool</td>
<td>24°18’04&quot;S</td>
<td>118°52’26&quot;E</td>
<td>20 April 2005</td>
<td>Pinder <em>et al.</em> (2010)</td>
</tr>
<tr>
<td>CUMZ¹</td>
<td><em>Westralunio</em> carteri Iredale, 1934</td>
<td>3</td>
<td>Collie River</td>
<td>100 m downstream from Southwest Hwy, WA</td>
<td>32°18’08&quot;S</td>
<td>115°49’03&quot;E</td>
<td>18 Feb 2010; 26 Jan 2010; 3 Nov 2010; 17 Oct 2011</td>
<td>Klunzinger <em>et al.</em> (2012)</td>
</tr>
<tr>
<td>CUMZ¹, WAM¹</td>
<td>&quot;</td>
<td>3</td>
<td>Yeagarup Lake</td>
<td>Warren State Forest, WA</td>
<td>34°32’35&quot;S</td>
<td>115°52’25&quot;E</td>
<td>14 March 2011</td>
<td>Klunzinger (2013)</td>
</tr>
<tr>
<td>CUMZ¹</td>
<td>&quot;</td>
<td>3</td>
<td>Yule Brook</td>
<td>Beckenham, WA</td>
<td>32°01’58&quot;S</td>
<td>115°57’25&quot;E</td>
<td>22 March 2012</td>
<td>Klunzinger (2013)</td>
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¹Accession number will be provided after acceptance of manuscript.
Figure captions

Figure 1. Left (A,C,E) and right (B,D,F) umbos of *Westralunio carteri* from Yule Brook (A,B), Yeagarup Lake (C,D) and Collie River (E,F). Scale bars: A,B,E,F = 2 mm; C,D = 1 mm.

Figure 2. Left (A) and right (B) umbos of *Alathyria cf. pertexta* from New South Wales, Australia (CUMZ_103519). Scale bar: 1 mm.

Figure 3. Velesunioninae with smooth umbos (left valves towards the top). A, *Lortiella froggatti* from Snake Creek, Western Australia; B, *Velesunio wilsonii* from Tunnel Creek; C, *Velesunio cf. wilsonii* from Red Hill Creek. Scale bars: A,C = 2 mm; B = 0.5 mm.

Supplementary Figure 1. External and internal views of the left (A,C) and right (B,D) valves of *Alathyria cf. pertexta* (CUMZ_103519). Scale bar: 1 cm.
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