NOTES ON THE AUTHORSHIP AND THE HOLOTYPE OF THE LATE CRETACEOUS DUROPHAGOUS SHARK *PTYCHODUS MORTONI* (CHONDРИЧТЫЕ, PTYCODONTIDAE)

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Abstract—The ptychodontid, *Ptychodus mortoni*, is a well-known species of Cretaceous durophagous shark. Many specimens assigned to the species have been collected from various Upper Cretaceous marine strata of North America. However, since the discovery of the holotype in the early 1800s in Alabama, the authorship of the species name has been unclear, or at least, inconsistent in the literature. To date, it has most often been credited to “Louis Agassiz (1839–1843)”, but assignments to “Gideon Mantell (1836)” and “Samuel Morton (1834)” have also appeared. To evaluate the true authorship of *P. mortoni*, we reviewed Morton’s and Mantell’s papers, and Agassiz’s *Recherches sur les Poissons Fossiles*, as well as other key publications, especially those published in the 1800s and the early 1900s. In addition, a reexamination of the holotypic material at the Natural History Museum in London (NHMUK PV OR 28394) is presented. Based on our review of the available information, we conclude that “Mantell (1836)” should be the authorship of the species. This investigation of the naming of *P. mortoni* also sheds light on some personal interactions between Agassiz and Mantell who were important early contributors to paleontology.

THE AUTHORSHIP PROBLEM OF *PTYCHODUS MORTONI*

The durophagous shark *Ptychodus mortoni* (Ptychodontidae) is the best known species of the genus from Upper Cretaceous marine strata in North America. The tooth morphology of this species, characterized by a large blocky-overall shape with a radially striated crown surface, can be distinguished easily from other ptychodontid sharks. Isolated teeth of *P. mortoni* are fairly common, and associated tooth sets with fully articulated jaw plates have been also discovered in Upper Cretaceous marine formations in North America (Case and Schwimmer, 1988; Everhart, 2005; Shimada and Fieltz, 2006; Hamm, 2008; Cumbaa et al., 2010; Shimada et al., 2010; Shimada, 2012). At present, however, the taxonomic criteria of *P. mortoni* are unclear with regard to: (1) the authorship (i.e., who originally named the species in publication?) and (2) the identification of the holotype (e.g., what elements exist, where it was collected, and where is it housed?). Over the last several decades, the authorship of *P. mortoni* has most often been attributed to Louis Agassiz; however, at least two other individuals, Gideon Mantell and Samuel Morton, who were closely associated with the type specimen, were cited in the literature, as well (Table 1). Nomenclature, including taxonomic authorships, should be reviewed carefully and be treated as important as classification in general (Mayr, 1954). In the present paper, we will answer the two questions based on a review of key early publications referring to the systematic of *P. mortoni* and a reexamination of the holotypic material of the species.

HISTORICAL BACKGROUND

Did Mantell Name the Taxon First in Publication?

Gideon Mantell was clearly the first author to introduce the taxonomic name ‘Mortoni’ in the literature. Mantell (1836:27) reported, “Teeth of a new species of *Ptychodus* have been discovered in the sand at New Jersey...I have named it *Ptychodus Mortonii*.” Notably, various authors after 1836 into the early 1900s gave credit to Mantell as the author (including the captions of figures 1–3 in Plate 25 of Agassiz, 1839) (Table 1). However, several other researchers did not agree with Mantell as the author or were simply unaware of his paper(s), including Agassiz’s (1843) subsequent description of the species (further explanation below). One criticism of Mantell (1836), as the taxonomic authorship, is the fact that he provided only a very brief description (or merely a statement) as opposed to a full description with figure(s), as required by the current guidelines of the International Commission on Zoological Nomenclature (ICZN) today for the naming of new taxa. However, this criticism, not providing a detailed morphological description, figures, or a proposed diagnosis for the new taxon, was not relevant in the early 1800s. Furthermore, Mantell (1836) did actually cite a previously published illustration of a tooth from Morton (1834:pl. 18, figs.1.2) (Fig.1A). This fact must have led a few researchers to refer to a combination of Mantell (1836) and Morton (1834) for the authority of the species (e.g., DeKay, 1842; Williston, 1900a,b). Notably, Mantell actually identified himself as the taxonomic author for *P. mortoni* as seen in his later publications: Mantell (1839:425, the 1st American Edition) and Mantell (1854:615, fig. 1. caption in lign. 128). Over the past several decades, Mantell has been seldom cited as the author of the species in peer-reviewed publications (e.g., Shimada et al., 2010: with the 1839 date), but his name has so appeared in a museum catalogue (Spamer et al., 1995), a comprehensive taxonomic review of *Ptychodus* (Hamm, 2008), and a reversal of a previous view (e.g., Shimada, 2012).

Should Agassiz (1839 or 1843) be the Authority for the Taxon?

Agassiz described and illustrated *Ptychodus mortoni* in greater detail in his massive monograph *Recherches sur les Poissons Fossiles* (1833–1843) (Fig.IB). As a result, many early researchers credited Agassiz as the author (e.g., Giebel, 1848; Dixon, 1850; Tuomey, 1858; Mackie, 1863; Cope, 1874, 1875; Dana, 1896; Dibley, 1911) and also cited various years of publication (e.g., 1835, 1836, 1839, 1843) (Table 1). The confusion over the various years of publication is likely the result of the different dates that the separate portions of the five volumes (body texts) of Agassiz’s monograph and the five atlases (plates) were printed. To add to the confusion, not only were the five volumes printed during different years, but parts of the text and the associated plates also appeared separately (Woodward and Sherborn, 1890; Jeannet, 1928; Questedt, 1963; Lurie, 1988). For example, nearly all researchers citing the authorship to Agassiz have referred to Tome (volume) III of his monograph. This volume includes the description of *P. mortoni* (on page 158) and three illustrations (fig.1–3 on tab. (plate) 25). Notably, although the figures first appeared in April 1839, the page containing the Agassiz’s description was not printed until March 1843 (Everhart, 2013).

Besides the various publication dates, another point of confusion regarding the authorship of *Ptychodus mortoni* resides within Tome III of *Recherches sur les Poissons Fossiles*. With regard to the three illustrations of the tooth in figures 1–3 of tab. 25, Agassiz published them in 1839 with the figure caption ‘Ptychodus Mortoni Mant.’, giving credit to Mantell as the author of the species. It is also worth noting that the original illustrations were most likely drawn while Agassiz’s artist was staying at Mantell’s residence in Brighton (Dean, 1999). However, four years later in the associated text of the same volume, Agassiz (1843:158) listed ‘Ptychodus Mortoni Ag.’, indicating himself as the author. No clarification about this discrepancy has been previously addressed in the literature. However, it is possible that the authorship of *P. mortoni* was mixed with that of the other nine species of *Ptychodus* (four of which are currently valid) named by Agassiz in *Recherches sur les Poissons Fossiles*. Either and in spite of the confusing array of publication dates, this monograph likely established Agassiz as the
TABLE 1. Selected early publications of Ptychodus mortoni. The authority, illustration, holotype, and other key information of the species are summarized.

<table>
<thead>
<tr>
<th>Author</th>
<th>Authority</th>
<th>Holotype Information</th>
<th>Illustrations</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morton (1834)</td>
<td>NA</td>
<td>Not specified</td>
<td>Plate 18 (figs. 1 &amp; 2)</td>
<td>Referring Morton 1834</td>
</tr>
<tr>
<td>Mantell (1836)</td>
<td>NA</td>
<td>Not specified; from NJ Greensand? (likely, error)</td>
<td>None</td>
<td>The taxonomic name first appeared</td>
</tr>
<tr>
<td>Agassiz (1839, 1843)</td>
<td>Manuell (or Agassiz?)</td>
<td>Not specified</td>
<td>fig. 1–3 on plate 25</td>
<td>&quot;Ag.&quot; in the figure (1839) and &quot;Mant.&quot; in the body text (1843)</td>
</tr>
<tr>
<td>Morton (1842)</td>
<td>Manuell</td>
<td>Not specified; from Prairie Bluff, AL</td>
<td>None</td>
<td>Found by ‘Mr. Conrad’</td>
</tr>
<tr>
<td>DeKay (1842)</td>
<td>Manuell &amp; Morton Agassiz</td>
<td>Not specified</td>
<td>None</td>
<td>The author seems to be a combination of the three</td>
</tr>
<tr>
<td>Giebel (1842)</td>
<td>Agassiz</td>
<td>Not specified</td>
<td>XXXL, figs. 6 &amp; 7</td>
<td>Found from Bedding chalk pit of Greensand in Shoreham, N. America?</td>
</tr>
<tr>
<td>Dixon (1850)</td>
<td>Agassiz (vol. III, p. 158)</td>
<td>Mr. Cat's collection (p. 384)</td>
<td>Lign 128, fig. 1</td>
<td>Same tooth illustrated in Morton (1842)—perhaps redrawn; from ‘New Jersey’</td>
</tr>
<tr>
<td>Mantell (1854)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>Fig. 114 (p. 220)</td>
<td>Redrawn from Agassiz?; from ‘New Jersey’</td>
</tr>
<tr>
<td>Gray &amp; Adams (1857)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td>Single tooth illustrated in a plate; From ‘White Chalk of Kent, UK’</td>
</tr>
<tr>
<td>Tuomey (1858)</td>
<td>Agassiz</td>
<td>Not specified</td>
<td>Plate IX</td>
<td>12 teeth in YPM collection and a number of ANSP specimens from Alabama and Mississippi</td>
</tr>
<tr>
<td>Hilgard (1860)</td>
<td>Not specified</td>
<td>Not specified</td>
<td>None</td>
<td>Mentioning USNM specimens, UK specimens</td>
</tr>
<tr>
<td>Mackie (1863)</td>
<td>Agassiz</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Dana (1863)</td>
<td>Not specified</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Leidy (1868)</td>
<td>Both Agassiz and Morton (?)</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Meck (1870)</td>
<td>Not specified</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Dixon (1872)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Leidy (1873)</td>
<td>Not specified</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Cope (1874, 1875)</td>
<td>Agassiz</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Woodward (1887)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Woodward (1889)</td>
<td>Manuell 1836</td>
<td>28394 Mantell Collection</td>
<td>None</td>
<td>From Cretaceous of Alabama</td>
</tr>
<tr>
<td>Woodward &amp; Sherborn (1890)</td>
<td>Manuell 1836</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Jackel (1894)</td>
<td>Leidy</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Dumble (1895)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Dana (1896)</td>
<td>‘Ag.’ (= Agassiz)</td>
<td>Not specified</td>
<td>Fig. 772</td>
<td></td>
</tr>
<tr>
<td>Williston (1900a,b)</td>
<td>‘Mantell (plus Morton)’</td>
<td>Various (Kansas specimens, but not the holotype)</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Hay (1902)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Leriche (1902)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Merrill (1907)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Dibley (1911)</td>
<td>‘Ag.’ (= Agassiz)</td>
<td>Oxford Museum specimen(s) (# No not specified)</td>
<td>Plate 22, figs. 7.8 (pictures)</td>
<td>One from Kansas; another from the Chalk near Winchester, UK?</td>
</tr>
<tr>
<td>Woodward (1912)</td>
<td>Manuell (1912?)</td>
<td>Detached tooth (indicating single element); Unspecified British Museum specimen</td>
<td>Plate LIV, fig.1</td>
<td>Illustrated tooth from UK (Oxford Museum specimen); from Upper Cretaceous of Alabama</td>
</tr>
<tr>
<td>Stephenson (1914)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td></td>
</tr>
<tr>
<td>Willis (1912)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td>NA</td>
</tr>
<tr>
<td>Jordan (1919)</td>
<td>Manuell</td>
<td>Not specified</td>
<td>None</td>
<td>NA</td>
</tr>
</tbody>
</table>

authority figure for Ptychodus in the eyes of many early and recent paleontologists.

Mantell (1836) as the Author of Ptychodus mortoni

Based on a review of those early publications above, we conclude that Mantell (1836) should have the sole authorship for Ptychodus mortoni and that Morton’s (1834) illustrations (Fig. 1A) should be considered as part of Mantell’s description (under the ICZN articles 12.2.1 and 12.2.7: “Names published before 1930”). In addition, Morton should be excluded from the authorship of the species, and the combination of “Mantell and Morton” (e.g., DeKay, 1842) is incorrect. Although Agassiz was cited as the author of P. mortoni shortly after the publication of Recherches sur les Poissons Fossiles was completed (e.g., Giebel, 1848; Dixon, 1850) (Table 1), Agassiz himself did not seem to disagree with Mantell’s assertion of authorship (e.g., Mantell, 1836, 1839) for the species (or at least not so in the literature). Furthermore, Mantell (1836) was subsequently cited as the author of the species by other researchers (Table 1). This fact should be considered as the criteria to claim the taxonomic authorship under the ICZN Article 51A: “The original author and date of a name should be cited at least once in each work dealing with the taxon denoted by that name.”

HISTORY AND CLARIFICATION OF THE HOLOTYPE

Reexamination of the Holotypic Material

The exact current specimen number and existing element(s) of the holotype of Ptychodus mortoni have not been appeared precisely in the literature. One of the reasons may be due to Mantell (1836, 1839, 1854) and Agassiz (1833–1843). These key publications did not specify
this information, and their illustrations do not clarify if they really examined the same specimen and/or if any additional elements were associated with the holotype. Woodward (1889:150) reported a single tooth described in *Recherches sur les Poissons Fossiles* with a catalog number ‘28394’ for the specimen as part of the Mantell Collection at the British Museum of Natural History. The name of the institution published by Woodward for this specimen, however, is not valid today due to changing the institutional name into the Natural History Museum in London (NMHUK).

To clarify these points, we recently had the opportunity to investigate the original material. The holotype is currently curated as a specimen number, NHMUK PV OR 28394, at the Natural History Museum in London, UK (Martha Richter, pers. comm., August, 2012) (Fig. 2). Only a single tooth is curated with that specimen number in the collection. Based on photographs of the tooth provided by Christopher Duffin, we are able to confirm that this tooth is clearly the same specimen illustrated in Morton (1834). Moreover, the three illustrations in Agassiz (1843), which may look like two or three different teeth at first sight, are certainly based on the same single tooth drawn in three different views (occlusal, left lateral, and posterior in his figs. 1–3 of tab. 25, respectively). Unfortunately, the exact fossil locality is still unclear. Mantell (1836, p. 27) noted it was “discovered in the sand at New Jersey”, but we suggest this was a factual error. Mantell assumed that this published locality information from Morton (1834: 29–30), who was making reference to a New Jersey specimen of a different fish (*Saurodon*) in the paragraph just above the one describing the specimen of *P. mortoni*, was correct. Morton (1834), in fact, did not actually report the location (i.e., New Jersey) of *P. mortoni*. Later in 1842, Morton (1842:215), however, corrected the locality of the holotype as “*P. Mortoni*, (Mantell.)…were found by Mr. Conrad in the older cretaceous strata at Prairie Bluff, Alabama.” Referring to a paleontologist and artist, Timothy A. Conrad in New York, Morton (1842) alludes to the fact that Conrad collected the holotype from the exposed Cretaceous strata (stratigraphic unit unspecified) near the town of Prairie Bluff in 1832 which is an abandoned townsite along the Alabama River in Wilcox County, southwestern Alabama (more

FIGURE 1. Illustrations referred to holotype of *Ptychodus mortoni* in early publications. A, Morton (1834, plate 18); B, Agassiz (1839, fig.1–3 on plate 25); C, Dana (1863, fig. 772); D, Mantell (1854, lign 128, fig. 1). Mantell (1836) referred the Morton’s illustration while describing the taxon. Note that specimen number(s) was never be specified in those publications, and there is an uncertainty if a single specimen (tooth) has appeared or multiple specimens were shown (see further explanation in text).
detailed information about Conrad’s visit to Alabama is in Wheeler, 1935 and Ebersole and Dean, 2013. Notably, the locality information of the holotype reported by Morton (1842) might also contain some errors. According to Ikaji et al. (2013), surface exposures of stratigraphic units of the right geologic ages (Santonian-early Campanian) for *Psychodus* are extremely rare in Wilcox County (i.e., only upper Maastrichtian strata are exposed), and no other specimens of *P. mortoni* have been recorded from the vicinity of the area of Prairie Bluff. The authors also reported that specimens of *Psychodus* (three species including *P. mortoni*) have been known only from Santonian strata (e.g., the Eutaw Formation) and lower Campanian units (e.g., Mooresville Chalk) in Alabama. Furthermore, the type specimen of *P. mortoni* collected by Conrad was shipped, with many other vertebrate and invertebrate fossils, to Morton at the Academy of National Sciences in Philadelphia (Morton, 1834, 1842; Wheeler, 1935; Ebersole and Dean, 2013). The specimen was later sent to Mantell in the UK for his scientific examination. During this series of transfers, we speculate that the correct locality information of the holotype was likely misplaced or confused with that of other specimens. Further investigation may eventually verify the locality and stratigraphic unit of the holotype.

**SYSTEMATIC PALEONTOLOGY**

Chondrichthyes Huxley, 1880

Euselachii Hay, 1902

Ptychodonta Jaeckel, 1898

*Psychodus* Agassiz, 1835

*Psychodus mortoni* Mantell, 1836

Holotype—NHMUK PV OR 28394. The type was previously reported as part of the Mantell Collection (28394) at the British Museum of Natural History (Woodward, 1889). The holotype consists of a single, medial-row tooth (Fig. 2) that was reported to be collected from Upper Cretaceous strata (stratigraphic unit not specified) near the town of Prairie Bluff in Wilcox County, Alabama (Morton, 1842; Leidy, 1873).

**Notes on the Interaction between Agassiz and Mantell**

In late October–early November of 1835, Agassiz visited Mantell’s home in Brighton to examine fossil fish specimens in Mantell’s collections. At this time, Agassiz, at age 28, had just started his brilliant career as a paleontologist. In contrast, Mantell (at age 45) had already published two books and several articles on English geology and paleontology, and had been elected as a fellow of the Linnean Society of London, receiving broad recognition from the established paleontological community. Based on circumstantial evidence of Agassiz’s visit from Silliman (1835) and Lurie (1898), the two researchers must have agreed that Mantell was going to name *Psychodus mortoni* (at least, we do not see any evidence indicating that Agassiz was assuming the authorship of the species). For years after *Recherches sur les Poissons Fossiles* was published, some researchers appeared to have missed Mantell’s papers and “incorrectly” cited Agassiz as the author. With all due respect to Agassiz and his contributions to paleontology, we would like to take this opportunity to clarify this matter between these two giants in vertebrate paleontology. Mantell (1836) should have the authorship for *P. mortoni*, no others!

**ACKNOWLEDGMENTS**

We thank Martha Richter (NHMUK) for information of the holotype. Christopher Duffin kindly provided photos of the holotype for us to study. Alvaro Mones kindly provided a copy of Jeanne (1928) to one of us (MJE). Jun Ebersole provided useful comments on the original manuscript. We also thank Shawn Hamm and Spencer Lucas for reviewing this paper.

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87–101, pls. 1–2.
Williston, S.W., 1900b, Some fish teeth from the Kansas Cretaceous: Kansas University Quarterly, v. 9(1), p. 27–42, pls. 11–14.