A TAXONOMIC AND TAPHONOMIC ANALYSIS OF LATE JURASSIC
HORSESHOE CRABS FROM A LAGERSTÄTTE IN CENTRAL POLAND

A thesis submitted to the
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in partial fulfillment of the requirements
for the degree of Master of Science

By
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A recently-discovered Late Jurassic Lagerstätte in central Poland has yielded over 100 specimens of xiphosurids within limestones representing a storm or tsunami deposit. The species, *Crenatolimulus darwinii* (Kin and Błażejowski, 2014) is reevaluated, which is the first record of the genus in Europe. The Polish specimens exhibit varying degrees of disarticulation and many are broken, which is interpreted to be a result of being tossed about during a mega-storm event; they otherwise demonstrate exceptional detail and preservation. Taphonomic experiments have been conducted on non-mineralized molts of the modern analog, *Limulus polyphemus* Müller, 1785, that were reintroduced to oxic sea water in order to determine the length of time it can take for molts to disarticulate when vigorously tumbled, simulating sea water movement during a mega-storm. Previously dried molts are analogous to those that have been washed ashore by wave activity and later returned to the sea, and these regain pliability after being reintroduced to water. Other experiments were conducted noting the length of time needed for molts to disarticulate while resting on an oxic ocean floor, excluding bioturbators and scavengers, as well as the effects of compression that lead to prosomal wrinkling. Results indicate that Polish horseshoe crab molts were likely to have disarticulated and broken before being displaced during a storm, and were not buried for days to months after molting their exoskeletons. Additionally, the presence of epibionts on horseshoe crabs is often indicative of age in modern species. Juveniles molt and burrow more frequently than adults do, and are less likely to carry epibionts. Serpulid worms were observed infesting many of the specimens from Poland, across all horseshoe crab prosomal sizes within the study sample. Although they are small in size compared to modern adult *Limulus polyphemus*, the Late Jurassic specimens are most likely mature. *Crenatolimulus darwinii* has been placed in a taxonomic context that includes all of the currently known species within the order Xiphosurida.
A summary of data regarding living horseshoe crabs and their descendants is discussed, and some taxonomic changes have been made to the classification of xiphosurids. New subordinal taxa are proposed for the genera *Lunataspis* Rudkin et al. (2008), *Bellinuroopsis* Chernyshev (1933), and *Rolfeia* Waterson (1985).
INTRODUCTION

During the Late Jurassic (upper Tithonian), central Poland was covered by a regressing shallow sea whose deposits included the calcareous sediments comprising the Kcynia Formation (Kin et al., 2011), at least some of which were deposited by a mega-storm or possibly a tsunami. Approximately 13 meters of these regressive sedimentary deposits are exposed near Sławnó, in a working quarry at Owadów-Brzezinki. Within these sediments is a highly fossiliferous *Corbulomima* horizon that contains an array of exceptionally well-preserved fossil specimens that range from non-marine pterosaurs and insects to marine fish and decapods. It also contains a large number of horseshoe crabs belonging to the genus *Crenatolimulus*, which is the subject of this study. Most of the specimens are randomly disarticulated and broken, or are covered with polychaete worm epibionts, but even these are often preserved in great detail. However, some of the limulid corpse and molt specimens collected are remarkably preserved in a *Lagerstätte*-type deposit that is somewhat similar to that of the well-known Bavarian Solnhofen *Lagerstätte* (Kin et al., 2012). Interestingly, limulids are not often found well-preserved in the fossil record as they possess unsclerotized exoskeletons, which usually makes studying the ancestors of modern species difficult.

Interpretation by Kin et al. (2013) of the deposit as a mega-storm or tsunami event that led to the *Corbulomima* horizon sediments is reinforced by the disarticulated and broken nature of the organisms preserved at Owadów-Brzezinki. Many questions arise regarding the horseshoe crabs in particular, including whether they were juvenile or adult specimens based on size and infestation of epibionts; whether the specimens were molts or corpses; and if any of the horseshoe
Crabs were molts, how much time had to pass before they disarticulated? What accounts for the breakage of many limulid specimens? Exceptional preservation of nonmineralized arthropods is dependent on rapid burial, lack of scavengers and bioturbators, the resistance of the exoskeletal chitin, and other factors (Babcock and Chang, 1997). The events leading up to the burial of broken and disarticulated horseshoe crab specimens may also be dependent on whether the corpses or molts were desiccated at any time postmortem or after being shed, respectively. Preservation may also be affected by whether these specimens were buried immediately after death or molting, or whether a long period of time passed before being buried.

Taphonomic experiments have been conducted on corpses of the modern limulid, *Limulus polyphemus*, in order to determine the length of time needed for horseshoe crabs to become fully disarticulated, which is defined by the separation of the prosoma from the opisthosoma, and the other stages of corpse disarticulation involved that include the loss of book gills and other organs and appendages, loss of movable spines, and the separation of the telson (Babcock and Chang, 1997; Babcock et al., 2000). For these studies, corpses were introduced to inoculated normal marine water and left undisturbed; others were tumbled in a lapidary tumbler, simulating near-shore or estuarine wave action, and observed for changes. The experiments originally conducted by Babcock and colleagues were mimicked using horseshoe crab molts of the modern *Limulus polyphemus*, and a lapidary tumbler to simulate wave action during a storm event in order to describe the disarticulation rates of horseshoe crabs in the Owadów-Brzezinki carbonates. From these experiments, it is possible to determine whether molts and corpses disarticulate at similar rates, and whether molts might have disarticulated before a storm, or as a result of a storm, that led to the deposition of sediments in central Poland.

Prior to the discovery of the quarry at Owadów-Brzezinki, only one horseshoe crab species had been described from the Pliensbachian Gielniów Formation in south-central Poland,
Limulitella cf. L. liasokeuperinus (Braun, 1860), and the specimen was later lost in World War II (Kin and Blażejowski, 2014). More recently, hundreds of horseshoe crabs have been excavated from Owadów-Brzezinki, and the species, Crenatolimulus darwini (Kin and Blażejowski, 2014), is reassigned herein. This is the second representative of the genus Crenatolimulus. The first, C. paluxyensis Feldmann et al. 2011, was previously described from the Lower Cretaceous of Texas, U.S.A., making C. darwini the first European member of the genus, and also the first Jurassic-aged limulid representing Crenatolimulus.

Crenatolimulus darwini has been included within a taxonomic revision of the order Xiphosurida that lists 78 currently recognized horseshoe crab species. This compilation is based on the work of Dunlop et al. (2010), but is an expansion of their original taxonomy, in that the present revision includes taxonomic descriptions to the level of genus of fossil forms, as well as modern species, and extinct species that have been described since 2010. Additionally, changes have been made to the subordinal and familial placement of several species based on phylogenetic studies performed by Anderson and Selden (1997) and Lamsdell (2013). A taxonomic analysis of this caliber allows horseshoe crab enthusiasts to appreciate the degree of morphological variation exhibited between genera and may also promote additional studies for understanding phylogenetic relationships between species-level members of Xiphosurida.
PALEOGEOGRAPHIC AND STRATIGRAPHIC SETTING

Late Tithonian (Middle Volgian) strata crop out in a working cement quarry near Ślawno, Poland, at Owadów-Brzezinki (Figures 1, 2). The carbonate sequences exhibited here belong to the Kcynia Formation, which yields datable specimens of the ammonite genus Zaraiskites Semenov, 1898, and can be divided into three continuous units (I, II, and III) (Kin et al., 2011; see also comparable divisions A-C in Salamon et al., 2006). These belong to the Zaraiskites zarajskensis (Michalski, 1890) Subzone, which includes the uppermost Z. regularis Kutek, 1994, Horizon and most of the Z. zarajskensis Horizon (Figure 3). The underlying Unit I (approximately 6.6 m total thickness) consists of basal thin-bedded marly limestones that grade upward into massive micritic limestones with specimens of Deltoideum delta (Smith, 1817) and Zaraiskites zarajskensis, indicative of an offshore environment (Kin et al., 2013). Unit II consists of micritic limestones that are thinly-bedded and laminated, exhibiting an abundance of calcareous polychaete worm tubes, and few specimens of Zaraiskites sp. The overlying, near-shore sediments of Unit III exhibit sedimentary structures such as low-angle cross stratification and parallel laminations, and high fossil content, with very rare occurrences of Zaraiskites Semenov, 1898. The Corbulomima limestones, known locally as the Corbulomima horizon, are exposed in the uppermost portion of Unit III; these are micritic and very fossiliferous, with $\delta^{13}$C isotope values that suggest normal, oxic marine conditions (Kin et al., 2013). Disarticulated internal molds of the small bivalve Corbulomima obscura (Sowerby, 1827) often blanket exposed areas of this horizon (up to 500 specimens per square meter), and lend the limestones their name (Kin et al., 2011). The horizon represents a very shallow depositional environment (Figure 1),
determined by truncated U-shaped burrows in the sediment, likely due to wave erosion (Kin et al., 2013). Therefore, Units I to III comprise an overall regression.

Terrestrial and near-shore vertebrate fossils are associated with Unit III, including disarticulated pycnodontiform fish bones, teeth, and scales, as well as pterosaur and sphenodont remains. Invertebrates include dragonflies, beetles, grasshoppers, decapod crustaceans, polychaete serpulid worm tubes, as well as a few articulated, and many disarticulated and broken specimens of the horseshoe crab species Crenatolimulus darwini. This represents the the first Late Jurassic limulid species described from Poland (Kin et al., 2013). Overall, the taphonomic setting of macrofossils observed in the Corbulomima limestones may be considered a Konzentrat-Lagerstätte. However, exceptional preservation of several soft-tissue specimens, including dragonflies and limulids, suggests that the limestones may locally represent a Konservat-Lagerstätte (Kin et al., 2012). There is no indication of sorting by paleocurrents of the fossils: they are randomly oriented and range considerably in size. The fossiliferous lower Corbulomima limestones grade from thinly-bedded to massive limestones with few to no fossils capped by thinly-bedded, laminated micrite with low-angle stratification and symmetrical ripple marks in the uppermost bed. Overlying these sediments are chaotic intraformational breccias and intraclasts of micritic material, approximately 80 cm thick. δ¹⁸O isotope analyses were conducted on the breccia clasts by Kin et al. (2011), and values are variable, possibly suggesting they were derived from a more evaporitic provenance, before being ripped up and deposited.

Comparisons can be made between the types of preservation and fossil assemblages evident in the late Tithonian Corbulomima horizon of Unit III and the famous Tithonian Solnhofen Konservat-Lagerstätte in Bavaria, Germany. The Polish sediments were deposited about 5 million years later than the rocks at Solnhofen, and interestingly, their fauna shows some remarkable similarities to the Solnhofen fauna, including limulids belonging to the same
subfamily Limulinae Zittel, 1885, as well as grasshoppers (family Prophalangopsidae Saussure, 1878) and dragonflies (family Eumorbaeschnidae Bechly et al., 2001), thereby allowing comparative studies of these Late Jurassic paleobiotas (Kin, in press). However, these deposits are not intertidal. Among these differences, while both deposits are Lagerstätten, soft tissue preservation is much less common in the Corbulomima limestones than it is in the Solnhofen deposits, where fossils are well-preserved and fully articulated, but fairly scarce. This is likely due to anoxic bottom conditions, and therefore sterility of the calm lagoonal waters and sediments represented by the German deposit (Barthel et al., 1978). Many specimens excavated from the Solnhofen-Eichstätt beds, specifically the horseshoe crab species *Mesolimulus walchi* (Desmarest, 1822), were discovered at the heads of erratic trackways, which likely depict failed attempts at escaping from a toxic environment, followed by asphyxiation (Lomax and Racay, 2012). Another difference is that plant fossils have not been excavated from the Polish site, but are common in Solnhofen limestones. While there have been several proposed depositional theories regarding Solnhofen-Eichstätte lithographic sediments, it is most widely accepted that carbonate muds described there were deposited in individual lagoonal basins that were isolated from the open Tethys ocean by algal-sponge and coral reefs. Many of those basins have been interpreted as potentially hypersaline back-coral reef lagoons, including the sediments observed at Solnhofen-Eichstätt, in which salinity stratification resulted in anoxic bottom waters (Munnecke et al., 2008). Fine-grained sediment was likely swept into the basins by winds from shallow areas nearby, which caused episodic mixing of oxic and anoxic bottom waters. Periods of anoxia led to the death of many organisms that eventually died and settled to the basin floor while still articulated (Barthel et al., 1978), and fine sediment floated to the bottom of the lagoon, resulting in laminated carbonate beds. Lamination does not occur in the massive *Corbulomima* sediments of Owadów-Brzezinki, and very few of its fossils are articulated. Like Solnhofen, there was
limited access to open ocean waters during the deposition of the Polish limestones, but carbon isotope values indicate normal salinity and well-oxygenated conditions. Paleogeographic reconstructions of Poland during the Late Jurassic depict the region as being submerged by a shallow epicontinental sea that received Norwegian-Greenland Seaway waters from the north, and Alpine Ocean influx from the south (Blakey, http://cpgeosystems.com/euromaps.html). It is likely that the Middle Polish Trough connected these two seaways and permitted currents to flow between them, possibly bringing organic matter into the shallow region. Phytoplankton and zooplankton may have thrived from this influx, thus supporting the high Corbulomima bivalve population, as well as bivalve feeders, such as decapods and horseshoe crabs (Kin et al., 2013).

Based on the broken, disarticulated nature and random orientation of the associated fauna, as well as sedimentary structures observed in the surrounding sediment, the Corbulomima deposit at Owadów-Brzezinki is interpreted to be the result of a late Tithonian mega-storm or tsunami event that led to rapid burial of organisms there. High-energy wave activity that is associated with mega-storms may have led to the disarticulation of organisms observed in the Corbulomima limestones, as well as the chaotic nature of intraformational breccias and rip-up clasts exhibited in the overlying beds of Unit III.
Figure 1. - Kimmeridgian-Tithonian sedimentology of Owadów-Brzezinki quarry on the margin of the Middle Polish Trough, and surrounding region (Stampili et al., 2001 in Kin et al., 2013).
Figure 2. - Road map with the location of Owadów-Brzezinki quarry (O-B) and its proximity to Tomaszów Mazowiecki in Poland (Kin et al., 2011).
Figure 3. - Stratigraphic column with idealized bedding of the *Zaraiskites zarajskensis* Subzone regressive sedimentary sequence exposed at the Owadów-Brzezinki quarry (modified from Bechly and Kin, 2013).
SYSTEMATIC PALEONTOLOGY

Order XIPHOSURIDA Latreille, 1802
Suborder LIMULINA Richter and Richter, 1929
Superfamily LIMULACEA Zittel, 1885
Family LIMULIDAE Zittel, 1885
Subfamily LIMULINAE Zittel, 1885


*Type species.* Crenatolimus paluxyensis Feldmann et al., 2011.

*Diagnosis.* Large, highly-vaulted limuline. Prosomal occipital band depressed, with anterior margin beaded. Opisthosoma small, triangular; flanks with crenulations and scalloped lateral margins. Cross-section of abdomen nearly quadrate.

*Crenatolimus darwini* (Kin and Błażejowski, 2014)

*Crenatolimus* n. sp. Kin et al., 2012, p. 92; Kin et al., 2013, p. 73-77

*Limulus* n. sp. Kin et al., 2013, p. 92; Kin et al., 2013, p. 73-77

*Limulus darwini* Kin and Błażejowski 2014

*Holotype.* ZPAL X.1/O-B/XA 1

*Type locality and horizon.* Owadów-Brzezinki Nordkalk GmbH Quarry near Sławno, central Poland; the Kcynia Formation and *Corbulomima* Horizon (Late Tithonian; Late Jurassic).

Measurements. Measurements taken on specimens of Crenatolimulus darwini are given in Table 3.

Occurrence. All specimens were collected at Owadów-Brzezinki Quarry 26-332 Sławno, Poland. Associated marine fauna includes polychaete serpulid worm tubes; bivalves including Corbulomima obscura (Sowerby, 1827), Mesosaccella sp., and Pleuromya uniformis (Sowerby, 1813); decapods, brachiopods, ostracodes, and cartilaginous and bony fish teeth and scales. Terrestrial fauna includes pterosaur bones and tooth, dragonfly remains, and beetles (Kin et al., 2013).

Diagnosis. Small- to medium-sized, weakly to moderately vaulted limuline. Prosoma semicircular with depressed occipital bands extending from ophthalmic ridges to genal spines and exhibiting beading on anterior margin. Opisthosome small, triangular with longitudinal ridges exhibiting three tubercles and framing inner margin of abdominal flanks. Moderate-sized crenulations divide flanks into sections with scalloped lateral margins. Well-defined axial ridge beaded, terminating at anterior and posterior tubercles. Muscle scars divide anterior and posterior abdomen, with beading along length of well-defined medial ridge.

Description. Overall small form. Prosoma wider than long (average length, 30.25 mm; width
55.61 mm), and weakly to moderately vaulted. Prosomal rim uniform and narrow. Compression wrinkles present along anterior prosoma. Anterior margin semicircular, with lateral margins parallel to median axis of carapace, ending posteriorly in short genal spines. Postmedial margin of genal spine forms right angle with anterolateral opisthosoma. Cardiac lobe smooth, extends 69.5% of prosoma length, terminating anteriorly at tubercle and ocelli, and bounded by grooves that widen posteriorly and become obscure anteriorly at mid-length of cardiac lobe. Large compound eyes posterior to midlength on well-defined ophthalmic ridges. Ridges terminate as tubercles posteriorly, otherwise smooth; nearly parallel to cardiac lobe, curving slightly toward axis, becoming obscure anteriorly. Depressed occipital bands extend along posterior margin from ophthalmic ridges to genal angle, broadest at mid-length; anterior rim of bands finely beaded.

Segmented opisthosoma small (average length, 28.66 mm; width, 40.68 mm), triangular, weakly to moderately vaulted in cross section. Opercular tergite VIII fused to abdomen with pleurite curved posteriorly with lateral margin not upturned. Axial ridge well-defined, beaded; terminates anteriorly and posteriorly at tubercles, and bounded by six sets of depressed pits (apodemes). Axial apodemes on anterior abdomen same width as posterior prosomal cardiac grooves, and decrease in width before terminating anterior to posterior axial ridge tubercle. Longitudinal ridges form inner margin of opisthosomal flanks that terminate at anterior tubercles, and bear one tubercle anterior to mid-length of abdomen and another tubercle at mid-length. Flanks very slightly inclined, exhibiting moderately crenulated sections and six scallops along lateral margin, from which six movable spines of equal length project and curve slightly posteriorly. Posterior to mid-length, muscle scars separate anterior abdomen from posterior area. Beading exhibited along well-defined medial ridge of posterior area between posterior axial tubercle and medial tubercle at posterior margin. Posterior margin parabolic in shape and rounded laterally, with no prolongations.
Telson styliform, triangular in cross section, and slightly longer than total body length (single specimen XAC 8.3 telson length 74.19 mm). Venter is not preserved in specimens.

*Discussion.* Kin et al. (2013, p. 75) focused on the paleoenvironment of the *Lagerstätte* from which the Polish horseshoe crab specimens were extracted, and included a figure of a specimen, ZPAL X.1/O-B/XA 1, with the caption “a nearly complete carapace of *Crenatolimus* sp. nov.” The same specimen, XA 1, was later designated the holotype of a new species, *Limulus darwini*, in Kin and Błażejowski (2014). Closer examination of specimen XA 1 reveals characters that are diagnostic of the genus *Crenatolimus*. These include depressed and beaded prosomal occipital bands; the absence of a median tubercle along the cardiac ridge; the small, triangular, and moderately vaulted opisthosoma; and scalloped margins along crenulate opisthosomal flanks. Members of the genus *Limulus* do not exhibit depressed or beaded occipital bands. Theirs do not extend to the genal angle along the posterior prosoma, but are quite short, and extend only just beyond the opercular pleurite; they exhibit a median tubercle along the cardiac ridge, and a very weakly vaulted opisthosoma, lacking crenulations or scalloped margins along the pleura. Therefore, it is determined here that specimen XA 1 is best referred to *Crenatolimus*.

Of the known limulines, only *Mesolimus* and *Crenatolimus* contain Jurassic species. The diagnostic characters of *Crenatolimus darwini* distinguish it from previously named Mesozoic limulines, including the Cretaceous *Crenatolimus paluxyensis* Feldmann et al., 2011, and additional xiphosurids that are Jurassic in age.

Members of the late Kimmeridgian genus *Mesolimus* Størmer, 1952, described from Solnhofen-Eichstätt limestones of southern Germany, are two million years younger than *Crenatolimus* specimens discovered at Owadów-Brzezinki (Kin et al., 2012). Although the two genera were collected from rocks that are stratigraphically related and nearly the same age, they
Crenatolimulus differs from Mesolimulus by having a much narrower prosomal rim, and less elongated genal angles. The anterior rims of the occipital bands of Mesolimulus are not beaded, which is diagnostic of Crenatolimulus. Additionally, the ophthalmic ridges of Mesolimulus become wider posteriorly and are obscured anteriorly, but do not curve, as they do in Crenatolimulus. The overall opisthosomal shape of Mesolimulus is broad and nearly hexagonal with a truncated posterior margin, as opposed to the small, triangular shape of that of Crenatolimulus. While the movable spines are of equal length along the lateral flanks of Crenatolimulus, the spines of Mesolimulus elongate posteriorly. Finally, the axial ridge of Mesolimulus does not extend as a medial ridge into the posterior area, anterior to the telson, as it does in members of the genus Crenatolimulus.

The new species described here has been placed in Crenatolimulus as it exhibits characters diagnostic of the genus; namely for its depressed occipital bands with beaded anterior margins, and crenulate opisthosomal flanks with scalloped lateral margins. The genus Crenatolimulus and its type species, C. paluxyensis Feldmann et al., 2011, was described from the Cretaceous in Texas, U.S.A., making C. darwini the first Late Jurassic representative of the genus to be described from Poland. Notable differences are observed between the two species C. paluxyensis and C. darwini. Overall, C. darwini is a small, weakly to moderately vaulted limuline. Limited prosomal vaultedness may be an effect of sediment compaction, indicated by wrinkling along the anterior prosoma of many specimens (Shuster, Jr. et al., 2003). Prosoma wrinkling is also exhibited on specimens of Mesolimus walchi from Solnhofen lithographic limestones, in which considerable sediment overburden affected many faunal elements, particularly collapsible shells of ammonites and bivalves (de Buisonjé, 1985). Crenatolimulus paluxyensis exhibits a tubercle at mid-length of its cardiac lobe, and large compound eyes at mid-length of its ophthalmic ridges; the cardiac lobe of C. darwini is smooth, and its compound eyes
lie posterior to midlength on the ophthalmic ridges. The opisthosomal flanks of *C. darwini* are slightly inclined and moderately crenulated compared to the more inclined flanks and pronounced crenulations of *C. paluxyensis*, which also exhibits smooth longitudinal ridges along the inner flank margins; *C. darwini* exhibits three tubercles along these ridges. Both the axial ridge and posterior area medial ridge between the posterior to midlength axial tubercle and posterior tubercle of *C. darwini* are beaded, but this beading is not exhibited in the holotype of the genus.
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Table 1. - *Crenatolimus darwini* measurements and calculations (mm). (P. = Prosoma; C. = Cardiac lobe; O. = Opisthosoma; L. = Length; W. = Width)
Plate 1. - Figs. a-e. Dorsal views of specimens of *Crenatolimus darwini* a) XAC 5n exhibits compression wrinkles along anterior prosoma, large compound eyes, depressed and beaded occipital band, tubercles on abdominal longitudinal ridges, posterior muscle scars, and beading on posterior area of opisthosoma. No telson preserved. b) XAC 8.3 B, disarticulated opisthosoma, exhibits crenulations and beading on well-defined axial ridge and medial ridge on posterior margin. c) 13.14, broken opisthosoma and prosomal genal angles; shows abdominal crenulations along flanks. d) XAC 2, no telson preserved, exhibits depressed and beaded occipital band, crenulated opisthosomal flanks, and scalloped lateral margins. e) XAC 8.3 A, movable spines and telson preserved. Scale bar = 1 cm.
METHODS

Over 100 limulid specimens have been excavated from the Sławno Nordkalk Quarry, and of these, 67 were well enough preserved to be measured for the purposes of this study. All measurements were taken using standard metric calipers with an accuracy of 0.01 mm, and each specimen was photographed using a Nikon D70s camera. Microsoft Excel was utilized for morphometric calculations and graph construction, and photographs were edited using Adobe Photoshop CS3 graphics software. SPSS 14.0 for Windows was used to perform nonparametric Mann-Whitney U tests on prosomal widths and lengths of the Polish specimens against the presence or absence of epibionts.

A tumbling experiment was completed following Babcock and Chang (1997), who originally observed the disarticulation rates of corpses of the species *Limulus polyphemus*. Dry horseshoe crab molts of the same species were reintroduced to water of normal marine salinity (34 ppt) that had been inoculated with bacteria to simulate the conditions of sea water in Late Jurassic Poland (Kin et al., 2013). Two of these molts were left undisturbed in a 20 gallon fish tank to disarticulate, and a third was crushed under a 3.69 kg weight to observe molt behavior when compressed. The smallest specimen was tumbled with inoculated marine water and no sediment in a Lortone rotary 12 pound lapidary tumbler at a rate of 1.19 kilometers per hour to simulate ocean water movement during a mega storm, and was observed daily for changes in articulation.
TAPHONOMY

The presence of epibionts, prosomal wrinkling and compression, and degree of disarticulation and breakage were recorded for each of the 67 horseshoe crabs studied from Owadów-Brzezinki.

The average size of a specimen and presence or absence of epibionts can be indicative of limulid age. One argument for this is that juvenile specimens of the modern Atlantic horseshoe crab, Limulus polyphemus, molt and actively burrow more frequently than do adults, and therefore, are rarely infested with epibionts (Tan et al., 2011 and 2012; Kin and Błażejowski, 2014); a modern limulid becomes mature at 9 or 10 years of age, when it sheds its carapace for the last time (Shuster et al., 2003). Older specimens that molt infrequently and only occasionally burrow often act as mobile substrates for organisms that include barnacles, serpulid worms, bryozoans, crepidulid gastropods, and others (Key, Jr. et al., 1996). Secondly, modern specimens are also highly variable in terms of size, and have prosomal widths that range from less than 5 mm for very young juveniles (Rudloe, A., 1981) up to 61 cm, which is the maximum female adult width. Horseshoe crabs from the Polish quarry are not this variable in size, and prosomal widths range from 24.58 mm to 86.56 mm, which is equivalent to juveniles between developmental stages (or instar ages) of 8 and 14 of the extant Limulus polyphemus (Sekiguchi et al., 1988). Kin and Błażejowski (2014) compared Owadów-Brzezinki limulid sizes to modern specimens and determined that the assemblage consisted entirely of juveniles, but did not consider epibionts, or the possibility that Mesozoic horseshoe crabs may not grow at the same rates or to the same sizes as extant species. Because the venter is infrequently preserved among excavated horseshoe crabs from Owadów-Brzezinki, it is difficult to determine whether specimens from Poland are actually
a combination of small-sized adults and juveniles, whether they represent only adults, or whether they are only juveniles with prosomal sizes that are analogous to juvenile sizes of extant species. The presence of clasper claws on the venter of mature males is indicative of adult size in modern species, but with only dorsal carapaces preserved, average prosomal size and presence of epibionts are helpful proxies when determining age. Interesting to note, descriptions of various Mesozoic species refer to the overall size of specimens, but it is difficult to determine the adult and juvenile stages of fossil horseshoe crabs without features analogous to the modern *L. polyphemus* that include the absence or presence of the clasper claws, and average size of the prosoma as it compares to associated limulids.

Another way to determine ages using the fossil record is by analyzing the types of sediment associated with the assemblage. Juveniles and adults of modern species, such as *Limulus polyphemus*, do not inhabit the same space along the inner continental shelf. Swimming larvae dwell in the intertidal zone, and older juveniles (subadults) live in the near-shore shoal areas, where sediment is coarser. In contrast, adults prefer deeper waters where fine sediment is prevalent, and they often venture to areas that average 40 meters deep along the continental shelf (Shuster et al., 2003). Adults return to the shore annually from deep waters to mate and deposit eggs, but otherwise rarely return to the intertidal or near-shore shoal areas. This is an argument that agrees with the hypothesis by Kin and Błażejowski (2014) that the sediments from Owadów-Brzezinki bear exclusively juvenile specimens, in that fossil horseshoe crabs from shallow marine sediments may exhibit more juveniles than adults based on preservation bias. This is because wave action and sediment influx resulting from near-shore storms are more likely to affect organisms in shallow environments than they would disturb animals inhabiting the outer continental shelf or deeper sea environments. However, if comparing units of the regressive sequence observed at the Polish quarry, horseshoe crabs have not been described from
sedimentary beds below the *Corbulomima* horizon that are interpreted to be a deeper water environment based on the presence of the ammonite genus *Zaraiskites* (Kin et al., 2013). Additionally, the sediments observed in all three units consist of micritic carbonates of the same grain size. Therefore, determining age of the Polish specimens based on sediment type and depositional environment is invalid.

The lack of large Late Jurassic carapaces may be related to (a) the infrequent molting of subadult horseshoe crabs that molt only once a year and (b) adults do not molt after they have matured, compared to the molting behaviors of juveniles that molt several times a year. This assumes the fossils in question are molts and not corpses (Kin and Błażejowski, 2014).
Figure 4. - Specimen ZPAL X.1/O-B/13.32, exhibiting an articulated prosoma and opisthosoma (this is broken posteriorly, and is missing the telson). Serpulid worm traces (negative relief) cover the entire specimen.

Kin and Błażejowski (2014) compared dorsal ontogenetic characters of the small-sized individuals from Owadów-Brzezinki to similarly sized Limulus polyphemus specimens, including the shape, placement, and size proportions of the compound eyes, cardiac and interophthalmic shape and proportions, prosomal width, the general marginal outline of the genal angle, opisthosomal shape and size, and movable spines of similar shape and size. They noted that without the venter this comparison is arguable, but interpreted juvenile specimens of L. polyphemus to appear to be at similar stages of ontogeny. However, serpulid worms are observed infesting the prosomas, and less frequently, the opisthosomas, of many of the Polish horseshoe crabs (Fig. 4). If these are adults, then it is assumed that those with the largest prosomas should exhibit epibions more frequently than the smallest specimens, based on what we know of modern limulids. Fifty-five of the 67 examined specimens exhibited articulated prosomas. These were numbered randomly 1-55 for graphing purposes. Specimens with both prosomal length and width preserved were analyzed. Prosomal width, length, and width-to-length ratios were compared in order to determine whether the presence of epibions was related directly to size on the Polish specimens, and whether general ages might be determined for this limulid population (see Figures 5-8).

Prosomal width was measured in millimeters and plotted for each specimen, numbered 1-55 (Fig. 5). These measurements ranged from 24.58 mm to 86.56 mm, and while most of the largest specimens do not exhibit epibions, there are still large specimens (number 37, width of 75.75 mm; numbers 1 and 6, both approximately 63 mm wide) that were infested with serpulid
worms. Epibionts were not only observed on the smallest specimens, but also on medium-sized horseshoe crabs of variable widths as well. There does not appear to be a significant relationship between the presence of epibionts and larger or smaller prosomal widths among the Polish limulids overall, except that they have infested prosomas of nearly all sizes measured.

Figure 5. - Scatterplot of measured prosoma widths (mm) for each horseshoe crab from smallest to largest, which are randomly labeled (specimen number) 1-55.
Prosomal length was measured in millimeters and plotted for each specimen, numbered 1-55 (Fig. 6). These measurements ranged from 14.59 mm to 55.83 mm. Length measurements are overall much smaller than width measurements, as horseshoe crab prosomas are generally wider than they are long. Like Fig. 4, this scatterplot does not appear to show a significant relationship between the presence of epibions and prosomal length overall. However, the longest specimens (number 14, 47.24 mm; number 31, 50.48 mm; 32, 55.83 mm) did not exhibit epibions at all, which is the opposite of what one would expect, if large size represents older individuals that molt infrequently. Infested horseshoe crabs exhibit lengths between 14.59 mm and 45.25 mm, which is a wide range of size for this population.

**Figure 6.** Scatterplot of measured prosoma lengths (mm) for each horseshoe crab (numbered 1-55).

**Figure 7.** Scatterplot of prosoma length vs. width as they relate to epibiont infestation.
Fig. 7 is a scatterplot of prosoma length versus width, and shows epibiont infestation across the range of sizes excavated from Owadów-Brzezinki. The median length is 33.13 mm, and the median width is 52.23 mm. Width is increasing more rapidly than length, suggesting that prosomal width is the controlling variable. Overall, epibionts fouled specimens from the smallest horseshoe crab to one of the largest (75.75 mm wide, 45.25 mm long), although epibionts are not observed on the two widest specimens. Overall, there appears to be a higher concentration of specimens with epibionts closer to the median prosomal length and width, but horseshoe crabs with serpulids are observed within small, medium, and large sizes associated with this data set.

**PL:PW ratios and presence of epibionts**

![PL:PW ratios and presence of epibionts](image)

Figure 8. - Scatterplot of the ratio between prosoma length (PL) and prosoma width (PW), and its relationship to the presence or absence of epibionts.

A scatterplot was made to determine whether the ratio of prosoma length and prosoma width were related to the presence or absence of epibionts for each of the 55 specimens with complete
prosomas preserved (Fig. 8). Limulids with low length to width ratios exhibit larger prosomal widths than lengths, while high ratios are more equidimensional, that is, widths with measurements similar to length measurements. Epibionts fouled specimens with very wide prosomas versus length (0.499), as well as those closer to having equal length-to-width ratios. In order to determine whether epibionts preferred wider specimens to more equidimensional ones, a Mann-Whitney U test was performed using SPSS 14.0 for Windows. The variables, length and width, were tested separately against the grouping variable “epibionts (0,1)”, for which ‘0’ represented specimens with no epibionts, and ‘1’ represented those observed with them. P-values less than 0.10 were considered significant for these tests (Tables 1 and 2).

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Table 2. - Mann-Whitney U test statistics for the lengths of horseshoe crabs from Poland against the presence or absence of epibionts. P-value = 0.068.

The P-value (Asymp. Sig. [2-tailed]) was 0.068 for the tested variable ‘length’ against the grouping variable ‘epibionts’. Because the P-value is below 10% level of significance, prosomal length seems to bear significance for epibiont infestation.
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Table 3. - Mann-Whitney *U* test statistics for the widths of horseshoe crabs from Poland against the presence or absence of epibionts. P-value = 0.040.

Figure 9. - The ventral prosomal rim of specimen ZPAL X.1/O-B/13.24, completely removed from the rest of the prosoma and infested with serpulids. Note the presence of the *Corbulomima* bivalves in the surrounding sediment.
The P-value (Asymp. Sig. [2-tailed]) was 0.040 for the tested variable ‘width’ against the grouping variable ‘epibionts’, and is considered significant, as this value is less than 0.10. Although there doesn’t appear to be any significance to the trends seen on specimens 1-55 in terms of prosomal length and width overall, the Mann-Whitney $U$ test results indicate serpulid worms preferred to foul horseshoe crabs with wider prosomas than those with more equidimensional ones, because width was overall more significant than length was (0.040 for width, compared to 0.068 for length). In addition to occupying the prosoma (Fig. 9) of the Polish limulids, serpulids would often inhabit the opisthosoma (Fig. 10), and because articulated horseshoe crabs are rare in this assemblage, it is difficult to determine whether there is preferential infestation on prosomas versus opisthosomas, or whether both parts are preferred equally. As more horseshoe crabs from Owadów-Brzezinki are excavated, it may be possible to map the location of serpulid worms on articulated specimens and determine whether they favored particular locations on the cuticle.

In addition to serpulids, many of the Owadów-Brzezinki limulid fossils exhibited molds of the genus *Corbulomima*, which were likely not epibionts, but infaunal, suspension-feeding bivalves (Kin et al., 2013) (Fig. 11). It is most likely these organisms were displaced and deposited with the sediment that ended up burying the horseshoe crabs and bivalves together. This accounts for the presence of their molds on the carapaces of limulids, but they are not epibionts.

Results indicate the presence of epibionts does not seem to correlate with smaller or larger prosomal widths overall; in fact, serpulid worms seemed to infest the smallest individuals, as well as many of the larger limulids collected from Owadów-Brzezinki. They do seem to prefer wider individuals to those with prosomas that are closer to being equidimensional in length and
Figure 10. - A broken opisthosoma of specimen ZPAL X.1/O-B/13.20, disarticulated from the prosoma and covered in serpulids.

width. However, because epibionts do not correlate with prosoma size within the Polish limulid population, and epibionts infest the carapaces of small-sized individuals that would be expected to molt frequently, the horseshoe crabs in this assemblage are most likely small-sized matured adults. Kin and Błażejowski (2014) suggested the potential for comparing similarly-sized specimens of *Limulus polyphemus* to the horseshoe crabs in question, but if equal size does not correlate to similar ages between Mesozoic forms and the modern, and because ventral carapaces and information associated with fossil limulid appendages are too few or missing, it may remain difficult to determine whether small-sized epibiont-infested horseshoe crabs are adult specimens, or actually juveniles. It is also possible that the Late Jurassic limulids behaved differently than
their modern ancestors, perhaps molting and burrowing less frequently, allowing for the infestation of epibionts within younger individuals. Kin and Błażejowski also proposed that adult specimens may have retained juvenile traits during the Mesozoic, accounting for the overall small individual sizes within the population at Owadów-Brzezinki. Evidence suggests this is most likely, based on the presence of epibionts on even the smallest of limulids from the Polish quarry. Therefore, there is no reason to assume similarly-aged specimens of *Crenatolimbus darwini* and the modern *Limulus polyphemus* are the same size.

In addition to studying the presence or absence of epibionts and associated horseshoe crab age, the degree of disarticulation and breakage among individuals from the Polish quarry...
were analyzed. While two of the 67 specimens were preserved with the prosoma, opisthosoma, and telson intact, 43% of individuals exhibited only a prosoma and opisthosoma (no telson), and the remaining 54% were completely disarticulated. The two individuals within the study sample that were entirely articulated were also exceptionally well-preserved, with movable spines, compound eyes, and other details of the carapace intact. Kin et al. (2013) have regarded the part of the quarry containing these individuals (and others that were not in the present study sample), were excavated as a *Konservat-Lagerstätte*, locally. The remaining horseshoe crabs, though disarticulated and broken, often retain exceptional preservation and fine details as well. Some of this detailing has been obscured by the presence of serpulid worms and *Corbulomima* bivalves, but even while broken or disarticulated, many exhibit soft-tissue preservational qualities representative of *Konservat-Lagerstätten*. Due to the disarticulated nature of associated fauna, including marine and terrestrial fossils, Owadów-Brzezinki is considered a *Konzentrat-Lagerstätte*. Fossilized horseshoe crabs from Poland are thought to be molts, but it is difficult to conclude this without the ventral prosoma being preserved. Very few of the specimens from Poland are ventral, and even with these fossils, the question remains whether these are molts or carcasses. Horseshoe crabs molt from an opening at the anterior prosomal rim that closes again once the carapace is shed. Sometimes the molted carapace will close at the anterior prosoma but remain dented slightly, making it possible to identify a corpse from a molt, as corpses lack this dented feature. Additionally, the remains of corpses are more dense than molts are, even after some decay has occurred and organs and appendages have separated, essentially causing a corpse to become molt-like (Babcock and Chang, 1997). Because horseshoe crab cuticle and ventral prosomas are infrequently preserved as fossils at Owadów-Brzezinki, a molt can look very similar to a corpse. Kin and Błażejowski (2014) have concluded that the fossil individuals in question are exclusively juvenile molts. The Polish limulids are thought to have disarticulated as a result of a
mega-storm or tsunami event that caused organisms to separate and break, before becoming buried rapidly by carbonate mud (Kin et al., 2013). In order to better understand whether the Polish horseshoe crabs disarticulated as a result of a mega-storm, it is important to understand how corpses and molts behave separately post-mortem and after being shed, respectively. Previous studies have been performed on corpses of the modern *Limulus polyphemus* in order to monitor the amount of time it takes for these to disarticulate. These corpses were tumbled using an ordinary lapidary tumbler in inoculated water of normal marine salinity, and sans sediment (Babcock and Chang, 1997; Babcock et al., 2000), simulating ocean wave movement at 3 km/day. These same studies also observed the amount of time that it takes for a limulid to disarticulate while lying undisturbed in a tank of inoculated, well-oxygenated water of normal marine salinity. Their findings suggest that there are four stages of disarticulation: stage 1, book gills have detached; stage 2, opisthosomal spines and most of the legs are broken; stage 3, the telson separates from the opisthosoma; stage 4, the opisthosoma separates from the prosoma. For corpses tumbled at a rate of 3 km/day, these stages occur in order from 1 to 4 over the course of up to 40 days; undisturbed corpses reach stage 4 after 64 days. These experiments were mimicked for the purposes of the current project in order to determine whether molts disarticulate more or less quickly than carcasses, and whether separation occurs over the course of these same four stages, as the Polish horseshoe crabs exhibit degrees of disarticulation observed in each of these stages. To simulate wave action during a mega-storm (the event that is interpreted to have deposited Owadów-Brzezinki carbonates), a 12 pound Lortone lapidary tumbler was used to tumble an articulated *Limulus polyphemus* juvenile molt, at a rate of 1.16 km/hr for 24 hours/day, in inoculated water of normal marine salinity (34 ppt). Other molts of various sizes were left undisturbed in a 20 gallon tank of well-oxygenated, inoculated water of normal marine salinity. After being reintroduced to water, the molts immediately became soft, and regained pliability
within a few hours. After 11 days, the tumbling specimen started losing the tibia of its left third pedipalp, which separated from the patella on day 13. By the 26th day of tumbling, the specimen had lost all but one of the marginal spines from the left lateral opisthosoma (the loss of only left spines could be a result of the tumbler’s unidirectional flow) (equivalent of stage 2, but occurring before the separation of the book gills). After 32 days, the tibia of another left pedipalp, and the tibia and patella of a right pedipalp, had disarticulated. After 100 additional days of tumbling, the

Figure 12. - Ventral *Limulus polyphemus* molt, after being tumbled at 1.16 km/hr for 132 days. Specimen has lost 5 left movable spines (1), the tibia of two left pedipalps (2), and the tibia and patella of a right pedipalp (3). Otherwise, specimen remains fully articulated.
specimen had not disarticulated further (Fig. 12). The tumbled molt traveled approximately 3,674.88 km over the course of 132 days, yet remained nearly fully articulated. After 141 days, almost all book gills had separated from the undisturbed molts (stage 1), but one or two were attached (Fig. 13). Otherwise, these specimens were articulated, and the experiment continues.

Figure 13. - Ventral *Limulus polyphemus* molt, after being left undisturbed for 141 days in well-oxygenated water of normal marine salinity. The water was inoculated with bacteria. One book gill remains in place (1), and another book gill has almost disarticulated (2), but all others have detached. Specimen remains articulated otherwise.

Corpse and molt cuticle acts differently in these cases, likely because as corpses are exposed to
oxygen and bacteria-inoculated sea water, decay occurs, causing the breakdown of enzymes in remaining tissue that eventually leads to disarticulation in horseshoe crab carcasses (Babcock et al., 2000). Molts, however, have limited living tissue and are primarily chitinous, and therefore do not decay when exposed, making them more difficult to disarticulate. It is clear, however, that both molts and corpses disarticulate over very long periods of time, excluding scavengers and bioturbators, even after carcasses decay. One of two possibilities arise from these results: the first is that the proposed mega-storm event that has been hypothesized to have resulted in the deposition of carbonates at Owadów-Brzezinki lasted at least 40 days, presuming that the horseshoe crabs in question are, indeed, corpses, or at least 130 days, if the fossils are molts, in order for specimens to reach stage 4 of disarticulation. These storms would also have to be stagnant, in order to affect the assemblage for this extended period. However, storms of this duration are unusual; the largest Atlantic hurricane on record lasted for 47 days (Schwartz, 1992), but was a mobile storm, and did not stagnate for its duration. The second possibility, which is more likely, is that the limulid specimens, consisting of either corpses or molts, were disarticulated well before being buried by the proposed Late Jurassic storm event that led to the deposition of the Polish carbonates.

Breakage is also apparent in the cuticle of both articulated and disarticulated specimens, which seems strange at first, given the pliability of molt and corpse cuticle even after being reintroduced to water. In fact, 81% of the limulids analyzed for this study are broken in some fashion, which is even observed on otherwise exceptionally well-preserved individuals (Fig. 14). The Polish fossils are representatives of a near-shore environment; it is very possible that broken specimens are corpses, molts, or a combination of corpses and molts, that were washed to shore and desiccated. Dried molts and corpses alike become brittle and easily broken, which may have occurred as a result of storm wave disturbance. Carbonate rip-up clasts of an evaporitic nature are
indicative of a storm disturbing non-marine deposits near the seashore. Breakage of some individuals might also be a result of anthropogenic influence as a result of fossil extraction. Other types of post-mortem distortion are apparent within limulid specimens at Owadów-Brzezinki, in the forms of prosomal wrinkling and compression. Wrinkling occurs primarily along the prosomal rim, and has been documented in Paleozoic limulines (Babcock et al., 2000), as well as

Figure 14. - Broken prosoma of the horseshoe crab specimen ZPAL X.1/O-B/12. Prosomal details (cardiac lobe and ophthalmic ridges) are otherwise well-preserved.

other Mesozoic forms, including *Mesolimulus walchi* (Desmarest, 1822) (Fig. 15). The location of wrinkles along the anterior prosomal margin is indicative of pliability of horseshoe crab exocuticle after burial. It is possible that enough weight pressed down upon these pliable individuals from overlying sediment to result in wrinkling along the prosoma; however, there was not enough force to crush these specimens. Others have been crushed completely, perhaps due to
the overlying weight being too great. Alternatively, these were not pliable enough to wrinkle, and were perhaps partly desiccated before being buried and collapsing (Babcock et al., 2000) (Fig. 16). A compression experiment was conducted for the purposes of the present study that used a single 3.69 kg weight on a *Limulus polyphemus* molt in water of normal marine salinity and inoculated with bacteria. The specimen had neither been sitting in sediment, nor filled with sediment. Horseshoe crab exuviae are hollow and after being molted, may be subsequently filled with sediment. The cardiac lobe and interophthalmic region of the specimen eventually

![Figure 15.](image)

Figure 15. - Compression wrinkling exhibited along the prosomal rim of A) ZPAL X.1/O-B/14.4; B) CMNH 2348, *Mesolimulus walchi* from the Solnhofen *Lagersätte* in Bavaria, Germany.

compressed, similar to that seen in Fig. 16, but including the entire cardiac lobe. Prosomal
wringling was not observed. A future study will be performed that will monitor the effects of compression using varying weights on a horseshoe crab molt that is surrounded by, and filled with, clay-sized sediment to simulate lagoonal muds from which the Polish horseshoe crabs were excavated. Other similar tests will be performed on carcasses in order to compare whether prosomal wrinkling occurs more or less frequently in molts than corpses, and whether compression that leads to crushing can occur together with prosomal wrinkling. Future testing will help determine the amount of weight and/or shear stress that is necessary to promote wrinkling along the anterior prosomal margin as observed in specimens from Owadów-Brzezinki and Solnhofen.

Figure 16. - Disarticulated prosoma of specimen ZPAL X.1/O-B/13.21 A. Partly crushed interophthalmic region of medial prosoma and distorted right ophthalmic ridge.

Because molts and corpses behave similarly when dessicated, and both disarticulate very
slowly through comparable stages of exoskeletal separation when rigorously tumbled, it is difficult to say whether the Late Jurassic specimens at Owadów-Brzezinki are exclusively corpses or molts. While Kin and Błażejowski (2014) interpreted the quarry sediments as consisting strictly of molts, it is possible that the assemblage represents a combination of both molts and corpses. A near-shore environment consisting exclusively of hundreds of limulid molts but no living specimens seems unlikely, but a study on living and molting behaviors of extant horseshoe crabs should be conducted to explain this. Horseshoe crab molts being washed up on beaches due to seasonal storms may be an interesting topic, and could lead to seasonal studies for ancient beach environments. Additionally, energy-dispersive X-ray analyses using a scanning electron microscope should be performed to compare carcass and molt cuticle microstructure, in order to conclude whether differences can be seen among fossil forms. Finally, a continuation of compression experiments may lead to a better understanding of how carcass and molt cuticle behaves under varying weights, and may help determine whether compressed Polish specimens represent once-living organisms or shed exuviae.

Other taphonomic experiments will be conducted in the future. Previous tumbling experiments on limulid corpses (Babcock and Chang, 1997) and molts have excluded sediment as a variable that might affect disarticulation. Wave activity that displaced the Polish specimens would have mixed with very fine carbonate muds; modern *Limulus polyphemus*, in contrast, thrives on the North American Atlantic coast, where medium sand to silt-sized siliciclastic material extends to the edge of the continental shelf. In order to determine whether different nearshore sediment types and grain sizes have varying effects on horseshoe crab molts and corpses, clay, silt, fine sand, medium sand, and coarse sand sizes, will individually be added with normal marine water and horseshoe crab corpse and molt specimens to a lapidary tumbler. These specimens will be monitored over time and changes will be recorded, noting the time it takes for
mols and corpses to disarticulate, and whether added sediment might lead to molt breakage, as well as general wear on the chitin of each specimen.

Finally, it is often difficult to determine whether articulated horseshoe crab fossils are molted exuviae or carcasses. Horseshoe crabs shed their exoskeletons by crawling out a single opening at the anterior prosoma, which is visible on the ventral side of molts, but because ventral horseshoe crab fossils are rare from Owadów-Brzezinki, quantifying the number of molts and corpses is problematic. Additionally, Babcock et al. (2000) observed that after just seven days of being tumbled in an ordinary lapidary tumbler to simulate wave movement, the organ tissues of a horseshoe crab corpse will decay and book gills will be lost, in which case the corpse becomes essentially molt-like. It is important to note that a rubber stopper is required to seal the barrel of a Lortone lapidary tumbler. When tumbling horseshoe crab corpses, the stopper does not allow oxygen to enter the barrel, and therefore, potentially slows the decay of a horseshoe crab corpse while it is being tumbled. Therefore, it is possible that the length of time needed for a tumbling corpse to decay in well-oxygenated ocean water of normal salinity may take less time than described, and therefore, become molt-like in less than seven days. In order to determine whether morphological or structural differences are exhibited between molt and corpse cuticle in the fossil record, molds will be taken of modern Limulus polyphemus carapace and carcass exocuticle and endocuticle on the dorsal exterior and ventral interior of the prosoma. Molds will be analogous to sediment interior and exterior molds exhibited in the fossil record, and may help determine whether morphological or structural differences can be observed by comparing molds of exuviae and corpse epicuticle and endocuticle.
GLOSSARY OF MORPHOLOGICAL TERMS

The following morphological terms are arranged alphabetically and can be applied to members of the order Xiphosurida. These terms are included within the taxonomic descriptions following this section and are listed here for convenience, and many can be referenced in Figure 17. The following definitions are adapted from Størmer, 1952, and Lamsdell, 2013.

Apodeme. Inward deflection of sclerite that corresponds to muscle attachment.

Axial Furrow. Longitudinal groove that separates the opisthosomal cardiac lobe from the pleura.

Axial Ridge. Longitudinal crest of opisthosomal cardiac lobe.

Book Gills. Flattened ventral opercula that bear respiratory organs.

Cardiac Lobe. Median section of prosoma and opisthosoma; also referred to as the axial lobe on opisthosoma.

Cardiac Ridge. Longitudinal crest of the prosomal cardiac lobe.

Cardiophthalmic Region. Space on the prosoma between ophthalmic ridges.

Cardiophthalmic Ridge. See interophthalmic ridge.

Chilaria. Postmedial appendage of pregenital segment.

Chelicera. Preoral appendage with chelate distal joint that is modified for biting or piercing.

Compound Eye. Composed of units that each work as an individual visual receptor; located on ophthalmic ridges.

Genal Angle. Posterolateral margin of the prosoma, also referred to as the genal spine.

Intercardiophthalmic Region. Rectangular portion of prosoma that includes the cardiac lobe and minor part of interophthalmic region.

Interophthalmic Region. Space between prosomal cardiac lobe and ophthalmic ridges.
Interophthalmic Ridge. Located within the area bounded by ophthalmic ridges, may correspond to apodemes for ventral limb musculature; also referred to as the cardiophthalmic ridge.

Ocelli. Rudimentary photoreceptors located on the anteromedial prosoma, near the anterior cardiac lobe.

Occipital Band. Posterior prosomal margin, extends the length of the posterior genal angle.

Opercular Pleurite. The pleurite of somite VIII.

Opercular Tergite. The tergite of somite VIII.

Ophthalmic Ridges. Parallel prosomal crests extending posteriorly and anteriorly from each compound eye, located between the cardiac lobe and lateral margins of the prosoma.

Opisthosoma. Portion of body posterior to prosoma.

Pleura. Lateral portion of opisthosoma. Also referred to as the abdominal or opisthosomal rim.

Pleural Ridge. Transverse or longitudinal crest along the pleura.

Pleurite. Sclerite of the abdominal pleura.

Prosoma. Part of body that includes the dorsal carapace and prosomal appendages, anterior to opisthosoma.

Prosomal Rim. Distal margin of prosoma, extends anteriorly from both genal angles and meets at the anteromedial margin.

Sclerite. The chitinized cover of exoskeletal body segments.

Segment. Differentiated section of external carapace, may comprise multiple somites.

Somite. Fundamental division of the body, numbered 0 to XVII in xiphosurans (Figure 18).

Spines. Lateral projections of the opisthosoma; movability and curvature are species dependent.

Sternite. The ventral sclerite of each segment.

Telson. Postanal spine, posterior to opisthosoma.

Tergite. The dorsal sclerite of each segment.
Thoraceton. Fully fused dorsal opisthosomal shield (Figure 18).

Figure 17. - Diagram of morphological features exhibited on the dorsal carapace of

*Crenatolimulus darwini*. Not observed on the holotype XA 1 are the telson and opisthosomal spines.
Figure 18. - Diagram of somites numbered 0-XVII; ‘tl’ indicates the telson (modified after Lamsdell, 2013).

*Limulus polyphemus* Linnaeus, 1758

*Left Dorsal View*
SYSTEMATIC ARRANGEMENT WITHIN XIPHOSURIDA

The order Xiphosurida includes modern species of horseshoe crabs and all of their fossil relatives. While there are only four living horseshoe crab species today, the fossil record exhibits impressive variation among forms ranging from the Early Ordovician to recent times, and there are eighty-one morphologically distinct species of horseshoe crabs that have been described. Overall, the basic morphology of xiphosurids has changed very little, as each species exhibits a prosomal head-shield, opisthosoma, and styliform telson. Many may inappropriately refer to horseshoe crabs as “living fossils” because the group as a whole has been generally morphologically stable during the last 380 million years. However, there is great morphological diversity as characters become more derived in increasingly modern forms.

A comprehensive list of the systematic positions of horseshoe crabs has not been assembled since Dunlop et al. (2010) summarized the subphylum Chelicerata. Their list focuses primarily on fossil forms of all spider relatives, and does not include extant species. The present revision places emphasis on horseshoe crab species described within the order Xiphosurida, and includes extant species (*Limulus polyphemus* Müller, 1785; *Carcinoscorpius rotundicauda* Pocock, 1902; *Tachypleus gigas* Müller, 1785; *T. tridentatus* Leach, 1819). Annotated systematic descriptions to the generic level are provided. The descriptions are based on those written by the original authors or are from subsequent papers regarding the taxa in question. It is important to note that only current names are incorporated.

Taxonomic changes and additions have been made to Dunlop et al. (2010). The Late Ordovician xiphosurid, *Lunataspis aurora* Rudkin et al., 2008, is older than species of more
primitive groups. Placement of *L. aurora* by its designating authors was previously uncertain due to its bipartite thoracetron, which is a character not exhibited on other limulines. However, phylogenetic analysis of xiphosurans by Lamsdell (2013) revealed this horseshoe crab to be a member of a sister group to a clade that includes bellinurines and limulines. Supporting this relationship, *Lunataspina* n. subord. and *Lunataspidae* n. fam., have been erected to accommodate those xiphosurids that exhibit three segments on a fused thoracetron; the suborders *Bellinurina* Zittel and Eastman, 1913, and *Limulina* Richter and Richter, 1929 consist of all other xiphosurids observed with a thoracetron exhibiting a single segment. Another major change is based on the phylogenetic analysis of *Bellinuroopsis* Chernyshev, 1933, and the family Rolfeiidae Selden and Siveter, 1987, and its only included genus *Rolfeia* Waterson, 1985, by Anderson and Selden (1997). Neither *Bellinuroopsis* nor *Rolfeia* belong within the previous suborders *Bellinurina* or *Limulina*, as Anderson and Selden determined the two species to be plesiomorphic and ancestral to the limulines. A new suborder, *Bellinuroopina*, which contains the *Bellinuroopoidea* n. superfam. and *Rolfeoidea* n. superfam., has been erected to accommodate these species. Additionally, with respect to the unpublished work of Anderson (1996), the family name *Bellinuroopsidae* n. fam. is included herein. The phylogenetic work of Anderson and Selden (1997) and Lamsdell (2013) has been adopted in this current summary, but should be verified by further research on the phylogenetic relationships of all species that comprise the order Xiphosurida.

Other revisions to Dunlop et al. (2010) have been made. Included in *Rolfeia* is the species previously referred to as *Paleolimulus longispinus* Schram, 1979, now *R. longispinus*, based on observations by Anderson (1996). The species bears a distinct opercular pleurite, six fixed spines, and five shorter, movable spines. *Belinurus’ alleghenyensis* Eller, 1938a, was interpreted by Pickett (1993) to be more closely related to species in the Kasibelinuridae than to bellinurids, due
to its fusion of the posterior three opisthosomal tergites. Dunlop et al. (2010) also regarded the species to be a possible kasibelinurid. However, ‘B.’ allehenyensis was reexamined by Anderson and Selden (1997), who determined that all members of the Bellinuroidea, including the species in question, exhibit full fusion of opisthosomal tergites into a thoracetron. Therefore, ‘B.’ allehenyensis has been included herein with its original misspelling in the genus Bellinurus.

There has also been confusion regarding the correct generic placement of Limulus woodwardi Watson, 1909, and Limulus syriacus Woodward, 1879. Størmer (1952) observed both species as possibly belonging to a different genus, specifically Mesolimulus. Limulus woodwardi is known only from its prosomal shield (Romano and Whyte, 1987), and the specimen exhibits features that are much smaller than others in Mesolimulus (Vía, 1987), yet the species is referred to in the literature as Mesolimulus (?) woodwardi (Romano and Whyte, 1987; Vía, 1987). Similarly, Limulus syriacus exhibits a short opisthosoma with only five moveable spines (Størmer, 1952; Feldmann et al., 2011), and the only specimen of the species is imperfectly preserved, which explains its puzzling generic placement. However, L. syriacus is also referred to in the literature as Mesolimulus (?) syriacus (Dunlop et al., 2010). The species are therefore referred to as Mesolimulus (?) woodwardi and Mesolimulus (?) syriacus herein to recognize that both should be reexamined. Other taxonomic changes have been made based on the original descriptions of the taxa in question. Alanops Racheboeuf, 1992 is now placed in the family Euproopidae, based on Racheboeuf’s description and original placement of the genus, instead of the superfamily Limulacea as in Dunlop et al. (2010). Similarly, Panduralimulus has been revisited by Feldmann and Allen (2005) who observed that morphological features of the genus indicate its better placement within the superfamily Paleolimuloidea (and Paleolimulidae), as opposed to the superfamily Limulacea. Valloisella Racheboeuf 1992 was originally assigned to Euproopidae; however, Anderson and Selden (1997) suggested it would be better placed in the Limulacea based
on phylogenetic observations. The genus is currently a member of the Paleolimulidae (Anderson and Horrocks, 1995), as its opisthosomal axial ridge is carinate, a character shared by members of the same family. For this summary, Valloisella is included in the Paleolimulidae. Casterolimulus Holland et al. 1975, was described by Feldmann et al. (2011) as belonging in Limulidae, as opposed to its original placement within the Tachyleinae. Carcinoscorpius rotundicauda Pocock, 1902, has been observed by Yamasaki (1988), to be morphologically similar to members of the genus Tachyleus (Shuster, Jr. et al., 2003), and is considered better placed as a member of that genus. Action has yet to be taken on the reclassification of the extant species; therefore, for the purposes of this summary, the species remains C. rotundicauda. Additionally, the genus Heterolimulus Boada and Villalta, 1966, has been included in the Heterolimulidae that had previously been placed in the superfamily Limulacea. Other taxa that were not considered by Dunlop et al. 2010 include those species that have been described since 2010, specifically Crenatolimulus darwini, Yunnanolimulus luopingensis Zhang et al. 2009, and Crenatolimulus paluxyensis Feldmann et al. 2011.

Additional species have been recognized but are not included in the present revision of horseshoe crab taxonomy. The oldest example of a xiphosurid with a fused thoracetron from the Early Ordovician of Morocco is currently undescribed (Van Roy, 2008; Briggs et al., 2012), and is therefore noted but not included herein. Paleolimulus juresanensis Chernyshev, 1933, is considered incertae sedis by Babcock and Merriam (2000), who regard the species as being incorrectly assigned at the generic level. Lastly, Paleolimulus fuchsbergensis Hauschke and Wilde, 1987, was revisited by Anderson and Selden (1997) who observed that the species lacked ridges on its thoracetron, and therefore it is incorrectly assigned to Paleolimulus. It has not been placed in another genus and is therefore incertae sedis. In their summary of Chelicerata, Dunlop et al. (2010) did note the species Veltheimia bicorns Beyschlag and Frič, 1899, and the subspecies
Euproops rotunda major (Woodward, 1907a), as nomina nuda. Descriptions of these were never published legitimately.

Belinuropsis wigudensis Matthew, 1910, is considered a nomen dubium by Miller (1995), who understood the type specimen to be too poorly preserved for adequate description and therefore taxonomic placement. Similarly, Limulus nathorsti Jackson, 1906, was regarded by Störmer (1952) as better-suited for the genus Mesolimbus, but the type specimen is too incomplete to warrant inclusion in a taxon, and is therefore considered a nomen dubium.

Additionally, Eller (1940) suggested the species ‘Belinurus’ carterae (Eller, 1940) (see Pickett, 1993 for ‘B.’ carteri spelling explanation) was likely synonymous with Protolimbus eriensis Williams 1885. Protolimbus eriensis was originally identified as a body fossil, but Anderson (1996) determined the specimen to be a trace fossil belonging to the limulid ichnofossil Selenichnites (Babcock, 1995). ‘B.’ carterae is herein considered to be a misidentified species.

Lastly, the description of the species Limulus darwini Kin and Błażejowski, extended the genus range to the Late Jurassic. Based on several characters diagnostic of the genus Crenatolimbus, the placement of the species has been reevaluated herein and is determined to belong within that genus. Limulus darwini is herein considered to be synonymous with the new species Crenatolimbus darwini (Kin and Błażejowski, 2014).
HORSESHOE CRAB TAXONOMY WITH GENERIC ANNOTATIONS

Stratigraphic Abbreviations:

M. = Middle    Neo. = Neogene        Tri. = Triassic     Dev. = Devonian

Arthropoda Latreille, 1829

Hard exoskeleton and jointed legs.

Cheliceriformes Schram, 1978

Chelicera as first pair of appendages.

Chelicerata Heymons, 1901

Somite I exhibits chelate grasping postoral appendages.

Xiphosura Latreille, 1802

Somite VII with partially reduced tergite and chilaria appendages. Anterior opisthosaoma broad. Ophthalmic ridges form arch with median ridge by merging anteriorly; cardiac lobe extends onto anterior half of carapace.

Xiphosurida Latreille, 1802

Trilobate dorsal shield, large prosoma, abdomen segmented, styliform telson.

Opisthosomal tergites VIII – XIV fused into thoracetrion.

Lunataspina n. subord. (U. Ord.)

Xiphosurids with thoracetrion fused into three segments.

Lunataspidae n. fam. (U. Ord.)
Exhibits characters of suborder.

*Lunataspis* Rudkin et al., 2008 (U. Ord.)

Large, lunate prosomal shield with weak ophthalmic ridges and low cardiac lobe. Three segments visible on fused opisthosomal thoracetron.

*L. aurora* Rudkin et al., 2008 (U. Ord.)

Bellinurina Zittel and Eastman, 1913 (M. Dev.-Perm.)

Small primitive forms with ophthalmic ridges meeting in front of cardiac lobe.

Bellinuroidea Zittel and Eastman, 1913 (U. Dev.-U. Carb.)

Forms with full fusion of the opisthosoma into a thoracetron.

Bellinuridae Zittel and Eastman, 1913 (U. Dev.-U. Carb.)

Exhibits characters of superfamily.

*Bellinurus* Pictet, 1846 (U. Dev.-U. Carb.)

Small to medium size, prosoma with genal spines and cardiac lobe of variable width.

*B. arcuatus* Baily, 1863 (U. Carb.)

*B. reginae* Baily, 1863 (U. Carb.)

*B. baldwini* Woodward, 1907b (U. Carb.)

*B. kiltorkensis* Baily, 1869 (Carb.)

*B. trilobitoides* (Buckland, 1837) (Carb.)

*B. iswariensis* (Chernyshev, 1928) (Carb.)

*B. metschetensis* (Chernyshev, 1928) (Carb.)

*B. stepanovi* (Chernyshev, 1928) (Carb.)

*B. carwayensis* Dix and Pringle, 1929 (Carb.)
B. concinnum Dix and Pringle, 1929 (Carb.)
B. pustulosus Dix and Pringle, 1929 (Carb.)
B. truemanii Dix and Pringle, 1929 (Carb.)
B. morgana Dix and Pringle, 1930 (Carb.)
B. grandaevus Jones and Woodward, 1899 (Carb.)
B. lunatus (Martin, 1809) (Carb.)
B. lacoel Packard, 1885 (Carb.)
B. bellulus Pictet, 1846 (Carb.)
B. koenigianus Woodward, 1872a (Carb.)
B. longicaudatus Woodward, 1907b (Carb.)
B. trechmanni Woodward, 1918 (Carb.)
‘Belinurus’ alleghenyensis Eller, 1938a (U. Dev.)

Euproopoidea Eller, 1938b (Carb.-Perm.)

Cardiophthalmic ridges converging backward from eyes; abdomen broad and rounded, composed of six or seven ankylosed segments, with or without lateral spines.

Euproopidae Eller, 1938b (Carb.-Perm.)

Small forms with wedge-shaped cardiac lobe bordered by distinct axial furrows, abdominal shield with annulated axis bearing a high boss on last segment.

Euproops Meek, 1867 (Carb.-Perm.)
Prosoma with flat genal spines and carinate ophthalmic spines; cardiophthalric region with or without intercardiophthalric area; abdomen with raised pleural ridges that cross flattened rim and are prolonged as marginal spines; annulated axis with knob on first and third segments and elevated boss or short spine on hindmost segment; telson long.

*E. orientalis* Kobayashi, 1933 (Perm.?)

*E. sp.* Brauckmann (1982) (Carb.)

*E. mariae* Crônier and Courville, 2005 (Carb.)

*E. cambrensis* Dix and Pringle, 1929 (Carb.)

*E. meeki* Dix and Pringle, 1929 (Carb.)

*E. nitida* Dix and Pringle, 1929 (Carb.)

*E. danae* (Meek and Worthen, 1865) (Carb.)

*E. longispina* Packard, 1885 (Carb.)

*E. anthrax* (Prestwich, 1840) (Carb.)

*E. rotundatus* Prestwich, 1840 (Carb.)

*E. bifidus* Siegfried, 1972 (Carb.)

*Liomesaspis* Raymond, 1944 (Carb.-Perm.)

Cardiac lobe on prosoma bulbous. Opisthosoma exhibits raised pleural ridges and lacks fixed marginal spines.

Adult lacks genal spines.

*L. leonardensis* (Tasch, 1961) (Perm.)

*L. laevis* Raymond, 1944 (Carb.)
L. (?) *birtwelli* (Woodward, 1872a) (Carb.)

*Anacontium* Raymond, 1944 (Perm.)

Genal spines vestigial, no ophthalmic spines, cardiophthalmic region tripartite.

*A. carpenteri* Raymond, 1944 (Perm.)

*A. brevis* Raymond, 1944 (Perm.)

*Prolinulus* Friè, 1899 (Carb.)

Prosoma and abdomen broad, well-rounded, both without marginal spines.

*P. woodwardi* Friè, 1899 (Carb.)

*Alanops* Racheboeuf et al., 2002 (Carb.)

Prosoma subhemispherical and subtriangular, with cardiac lobe not well defined and bounded posterolaterally by short, shallow furrows. Opisthosoma vaulted; axis posteriorly elevated with four axial rings and apodemes. Both prosoma and opisthosoma lack spines and ridges.

*A. magnificus* Racheboeuf et al., 2002 (Carb.)

Bellinuroopina n. subord. (U.Dev.)

Exhibits fixed opisthosomal lateral spines.

Bellinuroopoidea n. superfam. (U. Dev.)

Medium size, prosoma with distinct wedge-shaped cardiac lobe; rounded abdomen with eight movable segments, the last one double, fixed pleural
spines present. Fused opisthosoma indicated by modified opercular tergite (VIII, which is unfused) and transverse ridge nodes.

Bellinuroopsidae n. fam. (U. Dev.)

Exhibits characters of superfamily.

Bellinuroopsis Chernyshev, 1933 (U. Dev.)

Exhibits characters of superfamily.

B. rossicus (Chernyshev, 1933) (U. Dev.)

Rollfeoidea n. superfam. (Carb.)

Exhibits pleural ribs with the axial ring of somite VIII present on thoracetron. No longitudinal pleural ridges. Opisthosomal spines are fixed. Prosomal ophthalmic ridges are parallel posteriorly but curve anteriorly, meeting in front of the eyes. Opercular tergite (VIII) is unfused. Lacks fixed and movable spines on tergite IX.

Rolfeiidae Selden and Siveter, 1987 (Carb.)

Exhibits characters of superfamily.

Rolfeia Waterson, 1985 (Carb.)

Exhibits characters of superfamily.

R. fouldenensis Waterson, 1985 (Carb.)

R. longispinus Schram, 1979 (Carb.)

Limulina Richter and Richter, 1929 (Carb.-Quat.)

Large prosoma with ophthalmic ridges, cardiac lobe, lateral eyes, and ocelli.

Opisthosoma may exhibit up to nine segments, all or posterior segments fused, with movable spines. Telson longer than opisthosoma.

Paleolimuloidea Raymond, 1944 (Carb.-Jur.)
Pyramidal cheek node on carapace.

Paleolimulidae Raymond, 1944 (Carb.-Jur.)

Prosoma with ophthalmic ridges that meet in front of cardiac lobe. Annulations on axial portion of opisthosoma readily visible, with axial ridge keeled. Opisthosoma with articulated segment in advance of the telson.

Limulitella Størmer, 1952 (Tri.-Jur.)

Genal angle inner margin forms angle with anterolateral margin of subtriangular opisthosoma.

L. (?) liasokeuperinus (Braun, 1860) (Jur.)

L. vicensis (Bleicher, 1897) (Tri.)

L. henkeli Fritsch, 1906 (Tri.)

L. sp. Hauschke et al. (2004) (Tri.)

L. volgensis Ponomarenko, 1985 (Tri.)

L. bronii (Schimper, 1853) (Tri.)

Paleolimus Dunbar, 1923 (Carb.-Tri.)

Interophthalmic region lobed, with pyramidal cheek node. Transverse ridge nodes and longitudinal ridges exhibited. Opercular tergite VIII fused to thoracetron.

P. peetae (Pickett, 1984) (Tri.)

P. jakovlevi Glushenko, 1961 (Perm.)

P. signatus (Beecher, 1904) (Carb.-Perm.)

Valloisella Racheboeuf, 1992 (Carb.)
Opercular tergite VIII fused to thoracetrion. Axial ridge is continuous and carinate. Lacks opisthosomal ridge nodes. Prosoma elongate with long genal spines. Six pairs of movable spines on opisthosoma.

*V. lievinensis* Racheboeuf, 1992 (Carb.)

*Panduralimus* Allen and Feldmann, 2005 (Perm.)

Small forms with violin-shaped cardiac lobe; smoothly curving, parabolic ophthalmic ridge; broad somite XIII with pronounced posterolaterally-directed marginal spines; well-developed, distally-directed terminal spines on somite XIII.

*Panduralimus babcocki* Allen and Feldmann, 2005 (Perm.)

Moravuridae Příbyl, 1967 (Carb.)

Prosoma with dorsal posteromarginal facet and ophthalmic ridges that are parallel behind the eyes. Opisthosoma exhibits a free lobe, with transverse and longitudinal pleural ridges on the thoracetrion. Each intersection is marked with a quadriradiate node (three on pleural area). Axis with six segments and four axial ridges, each with a median node.

*Moravurus* Příbyl, 1967 (Carb.)

Exhibits a single thoracetrion with intersecting transverse and longitudinal pleural ridges and nodes.

*M. rehori* Příbyl, 1967 (Carb.)
Xaniopyramis Siveter and Selden, 1987 (Carb.)

Opisthosoma with movable spines. A pyramidal cheek node with anteriorly-running ridge exhibited. Genal spine narrow that is three-fifths as long as the carapace. Free lobe on anterolateral margin. Has at least two anteriorly-positioned curved spines radiating from lateral margin. Thoracetron with fourth axial ridge continues into transverse pleural ridge. Transverse ridge nodes and longitudinal opisthosomal ridges; opercular tergite VIII fused to thoracetron.

X. linseyi Siveter and Selden, 1987 (Carb.)

Limulacea Zittel, 1885 (Tri.-Quat.)

Cardiophthalmic region on prosoma not well defined. Posterior anal angle of opisthosoma parallel. Opisthosoma subtrapezoidal with movable marginal spines.

Heterolimulidae Boada and Villalta, 1966 (Tri.)

Ovoid, trilobitiform carapace. Prosoma has weakly developed genal angles and ophthalmic ridges converge posteriorly. Semicircular opisthosoma is about same width as prosoma.

Heterolimulus Boada and Villalta, 1966 (Tri.)

Exhibits characters of family.

H. gadeai Boada and Villalta, 1966 (Tri.)

Limulidae Zittel, 1885 (Tri.-Quat.)
Prosomal ophthalmic ridges do not meet in front of cardiac lobe, with well-developed genal angles directed posteriorly or posterolaterally. Opisthosoma hexagonal and composed of single fused plate, bearing variably placed movable lateral spines, and distinct axial furrows.

Limulinae Zittel, 1885, (Jur.-Quat.)

Prosoma moderately to strongly vaul ted. Moveable spines decrease in size posteriorly, and opisthosoma exhibits posterior prolongations.

*Limulus* Müller, 1785 (Tri.-Quat.)

Opisthosoma vaulted with straight sides, six fixed spines and broad, deep V-shaped posterior margin. Two blunt nodes on pronounced axial ridge that is carinate and runs full length of opisthosoma. Six pits on either side of axis extend from anterior margin to mid-length where large concave-forward muscle scars separate anterior from posterior part of opisthosoma. Opercular tergite VIII fused to thoracetron.

*L. polyphemus* Müller, 1785 (Quat.)

*L. priscus* Münster, 1839 (Cret.)

*L. coffini* Reeside and Harris, 1952 (Cret.)

*Tarracolimulus* Romero and Boada, 1977 (Tri.)

Arched, semicircular carapace, genal spines relatively short, underdeveloped, although finely spinous, barely
interrupt the oval contour of the whole body. Prosomal rim does not exist or not very noticeable. Ophthalmic ridges and cardiac lobe very pronounced. The opisthosoma features similar to those of Paleolimulidae.

Six pairs of movable spines.

*T. rieki* Romero and Boada, 1977 (Tri.)

*Casterolimulus* Holland et al., 1975 (Cret.)

Weakly vaulted prosoma, ophthalmic ridges that converge anteriorly but do not reach midline; deep axial furrows that converge anteriorly, cardiac lobe with smooth axial crest.

*C. kletti* Holland et al., 1975 (Cret.)

*Crenatolimulus* Feldmann et al., 2011 (Cret.)

Large, highly vaulted; prosoma with prominent, depressed posterior rim; opisthosoma triangular with scalloped lateral margins and crenulate flanks. Beaded rim on margin of posterior prosoma between ophthalmic ridge and genal angle.

*C. paluxyensis* Feldmann et al., 2011 (Cret.)

*C. darwini* (Kin and Błażejowski) (U. Jur.)

*Mesolimulus* Størmer, 1952 (Tri.-Cret.)

Prosoma wider than long, with narrow parallel-sided cardiac lobe with scalloped margins. Opisthosoma wider
than long and has margins with five moveable and six fixed spines.

*M. (?) syriacus* (Woodward, 1879) (Cret.)

*M. walchi* (Demarest, 1822) (Jur.)

*M. sibiricus* Ponomarenko, 1985 (Jur.)


*M. (?) woodwardi* (Watson, 1909) (Jur.)

*M. crespelli* Boada, 1987 (Tri.)

*Psammolimulus* Lange, 1923 (Tri.)

Genal spines blunt but prolonged; opisthosoma trapezoidal with postlateral prolongations.

*P. gottingensis* Lange, 1923 (Tri.)

*Victalimulus* Riek and Gill, 1971 (Cret.)

Prosoma with three protuberances on axial crest of cardiac lobe, axial furrows that converge anteriorly and nearly meet axially; ophthalmic ridges that don’t converge anteriorly; opisthosoma with convex margins, a distinct free lob; marginal spines are long and posteriorly directed.

*V. mcqueeni* Riek and Gill, 1971 (Cret.)

*Yunnanolimulus* Zhang et al., 2009 (Tri.)

Prosoma semicircular, with conical axis between ophthalmic ridges that tapers anteriorly. Opisthosoma unsegmented and wider than interophthalmic region of
prosoma. Opisthosomal axial region one-third the width of the opisthosoma, tapering both anteriorly and posteriorly. Exhibits six pairs of movable spines.

*Y. luopingensis* Zhang et al., 2009 (Tri.)

*Tachypleinae* Pocock, 1902 (Tri.-Quat.)

Prosoma less vaulted than in *Limulinae*; hexagonal abdomen with less prominent posterior prolongations, movable lateral spines not decreasing in length backwards.

*Carcinoscorpius* Pocock, 1902 (Quat.)

Movable spines of abdomen short, second and third longest, others progressively decreasing backwards in male, becoming abruptly shorter in female.

*C. rotundicauda* Pocock, 1902 (Quat.)

*Tachypleus* Leach, 1819 (Neo.-Quat.)

Movable lateral spines of abdomen different between sexes, long and equal in male and young female; posterior three short and apically acute in adult female.

*T. tridentatus* Leach, 1819 (Quat.)

*T. gigas* Müller, 1785 (Quat.)

*T. decheni* (Zinken, 1862) (Neo.)

*Austrolimulidae* Riek, 1955 (Tri.)

Genal angles wide, drawn into slender spines and directed laterally. Opisthosoma has two posterior segments that are

66
clearly defined, but ankylosed; margin is smooth without evidence of movable spines.

*Austrolimulus* Riek, 1955 (Tri.)

Exhibits characters of family.

*A. fletcheri* Riek, 1955 (Tri.)
CONCLUSIONS

The Late Jurassic horseshoe crab population excavated from the Owadów-Brzezinki carbonate quarry near Sławno, Poland has been described by Kin and Błażejowski (2014) as consisting entirely of juvenile molts. Taphonomic analyses were conducted that considered prosomal width and length, the presence of epibions, and the degrees of disarticulation and breakage associated with 67 individuals.

Overall, prosomal lengths and widths of the Polish specimens are comparable to sizes observed in older juvenile specimens of the modern Limulus polyphemus (Kin and Błażejowski, 2014). However, comparing sizes between Mesozoic and extant forms may not be useful, as Mesozoic adult forms may have been smaller than modern adult horseshoe crabs. Epibions like polychaete serpulid worms can also be indicative of limulid age, as juveniles molt too frequently to act as suitable substrates, and adults no longer molt once matured, allowing epibions to attach to matured carapaces. Serpulid worms were found to infest variable prosomal lengths and widths from the Polish carbonates that included the smallest specimens, as well as medium-sized and large-sized individuals. A Mann-Whitney $U$ statistical analysis indicated serpulids preferred individuals with wider prosomas to those that are more equidimensional. However, overall, serpulids were found on nearly all limulid sizes, so it is most likely that even the smallest specimens are matured adults. Additionally, ventral appendages, particularly the presence or absence of the modified clasper claws, are useful for determining adult male horseshoe crabs. Unfortunately the ventral prosoma is rare in the fossils, and those that exist are not well preserved within specimens examined for this study. Preservation bias may also be a factor. Individuals of the modern adult Limulus polyphemus prefer to inhabit sediment in waters up to 40 meters deep, unlike juveniles, that prefer the near-shore shoal and intertidal areas. The carbonates at Owadów-Brzezinki represent a near-shore depositional environment, leading to the possibility that the
specimens observed are primarily juveniles. However, unless juveniles molted less frequently than modern species do, the presence of epibionts on small individuals suggests these limulids are, in fact, mature adults.

Also in question is whether the Polish assemblage consists of molts, corpses, or a combination of both. After only 7 days of decay, corpses and molts can look very similar (Babcock et al., 2000), except that molts are often dented on the ventral anterior prosoma which occurs after the limulid has shed its carapace. Most of the fossils are partially or completely disarticulated, and many are broken, possibly a result of the mega-storm event that led to the deposition of the quarry carbonates (Kin et al., 2013). Previous studies (Babcock and Chang, 1997; Babcock et al., 2000) were conducted to note the time it takes for limulid carcasses to disarticulate over time while being vigorously tumbled, and found that it can take up to 40 days for a corpse prosoma to separate from the opisthosoma. A similar experiment was conducted on horseshoe crab molts, and after 132 days of being tumbled, the molt remained nearly entirely articulated. These experiments reinforce the hypothesis that corpses disarticulate much more quickly than do molts, and this is likely because corpses are actually decaying, unlike molted exuviae. They also show that both corpses and molts take an exceptionally long time to decay excluding bioturbators and scavengers. Corpses and molts act similarly in other ways as well: both become very pliable in water, and brittle when allowed to dry. The broken nature of more than half of the specimens analyzed suggest that these may have become desiccated and brittle, perhaps after being washed to shore. Breakage may have occurred as a result of the mega-storm that deposited the Owadów-Brzezinki carbonates, or because of strong wave movement, before being rapidly buried. These observations show that horseshoe crab corpses and molts are similarly affected when rigorously tumbled, reintroduced to water, and desiccated, and may therefore be difficult to distinguish from one another in the fossil record, including within the
Late Jurassic carbonates at Owadów-Brzezinki. Further testing on the effects of compression on limulid carcasses and molts should be conducted in the future, and may help determine whether prosomal wrinkling or crushing are corpse- or molt-specific behaviors.

Finally, *Crenatolimulus darwini* (Kin and Błażejowski, 2014) is reevaluated and described from the Late Jurassic sediments of central Poland. The species bears characters diagnostic of the genus *Crenatolimulus*, including depressed occipital bands on the posterior prosoma with beaded anterior rims, and a small, triangular opisthosoma with scalloped and crenulated lateral margins. *Crenatolimulus darwini* also exhibits well-defined opisthosomal pleural ridges and beading along the axial ridge that extends from the anterior to posterior abdomen. The species has been included within a taxonomic analysis of the Order Xiphosura, in which subordinal and familial placement of several species has been reevaluated based on previous phylogenetic studies (Anderson and Selden, 1997; Lamsdell, 2013). This compilation is meant to inspire additional phylogenetic work that can lead to better understanding of horseshoe crab phylogenetic relationships.
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APPENDIX

The following tables consist of raw morphometric data used in graphical and statistical analyses.

Table 4. - Table of varying degrees of disarticulation, breakage, as well as the presence of serpulid epibionts or *Corbulomima* bivalves. P = prosoma, O = opisthosaoma, T = telson.

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