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Scorpion taphonomy: criteria for distinguishing fossil scorpion molts and carcasses

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Abstract. The ability to distinguish fossil arthropod carcasses from their molts is necessary for a more complete understanding of the arthropod fossil record and for more accurately assessing the role of fossil arthropods in paleoecosystems. Taphonomic characteristics, e.g., recurrent patterns of disarticulation of exoskeletal elements, are the primary data that have been used to differentiate fossil exuvia and fossil carcasses among arthropods. This study documents recurrent taphonomic patterns in modern scorpion carcasses and molts and extends these patterns to the fossil record to define criteria by which fossil scorpion molts might be distinguished from fossil scorpion carcasses. The three most useful and statistically significant characters in making the scorpion carcass/molt distinction are: position of the chelicerae (drawn in or extended); position of walking legs (folded or splayed); and body line (straight or curved). Two other characteristics, the position of pedipalps and presence or absence of telescoped segments, approach statistical significance and are also potentially useful. Disarticulation data are not as useful for distinguishing fossil scorpion molts and carcasses, because there are no statistically significant differences in length of time to total disarticulation or in the sequence of disarticulation between scorpion molts and carcasses. Among extant arthropods, scorpions possess the body plan most similar to that of the extinct eurypterids. Therefore, the taphonomic criteria developed for distinguishing fossil scorpion molts and carcasses may have implications for understanding molting among eurypterids.

Keywords: Arthropod, ecdysis, eurypterid

Scorpions are terrestrial chelicerates that have a fossil record extending back more than 400 million years to the Silurian Period. Fossil scorpions, although relatively rare, can be well preserved (Menon 2006). However, the relative importance of fossil scorpions in ancient ecosystems is difficult to assess because of the arthropod trait of growth through ecdysis. An individual scorpion may accumulate a number of molts over its lifetime; these molts may not be distinguished easily from carcasses, especially after becoming fossils, thereby complicating interpretation of the scorpion fossil record. This is also the case with fossil horseshoe crabs (Chelicerata: Xiphosura), whose fossil carcasses and molts are often indistinguishable (Babcock et al. 2000). Therefore, for many fossil arthropod taxa, simple or apparent abundance may not be a reliable reflection of actual abundance. Without accurate abundance estimates, it is difficult to determine the importance of these arthropods in paleoecosystems.

There are a number of differences between modern scorpion molts and carcasses, such as the presence of internal organs in carcasses and the lack of most of these structures in exuvia, but differences based on internal anatomy are not readily apparent in fossils; indeed, internal structures usually cannot be discerned in fossil scorpions (but see: Wills 1925, 1946, 1960; Kjellesvig-Waering 1986). External features of the exoskeleton, such as the presence or absence of appendages, opened sutures, and dislocations (separations) between segments, are more readily accessible characters for making the potential distinction between carcasses and exuvia among fossil arthropods. These kinds of taphonomic observations of the scorpion exoskeleton are the focus of this investigation. The purpose of this paper is twofold: 1) to document whether different taphonomic patterns exist between modern scorpion carcasses and molts; and 2) to use these patterns, if present, to develop criteria for distinguishing fossil scorpion molts from carcasses.

PREVIOUS WORK ON SCORPION MOLTING AND TAPHONOMY

Scorpion molting is well understood (Polis 1990; Brownell & Polis 2001; Gaban & Farley 2002). The steps scorpions follow during molting do not appear to vary significantly among taxa (Rosin & Shulov 1962; De Armas 1986): the anterior suture opens and the animal moves forward to exit the old exoskeleton, in a manner similar to that of a horseshoe crab (Shuster 1982). A scorpion exuvium may include the booklung lamellae, preoral tube, and other internal features and there may be little distortion of delicate hairs, bristles, and setae (Gaban & Farley 2002). The exuvium is commonly intact except for a wedge-shaped gap beneath the carapace (Gaban & Farley 2002). These observations on modern scorpion exuvia suggest that, as in the case of horseshoe crabs, a well-preserved fossil scorpion exuvium may be difficult to distinguish from a well-preserved fossil scorpion carcass. In this study, we identify more readily observed external features of the scorpion exoskeleton as the basis for distinguishing scorpion molts and carcasses.

METHODS

Six species of living scorpions belonging to six genera were used in the taphonomy experiments (Table 1). These taxa were chosen because they were available in sufficient quantity for replicate experiments. The scorpion molts used in this study were donated by arachnid hobbyists; live scorpions were purchased through a commercial supplier (www.swiftinverts.com) or were donated by arachnid hobbyists. Scorpion carcasses were obtained through either the natural death of the animal or mortality through freezing. We collected two categories of taphonomic data on scorpion molts and carcasses: 1) the initial post-mortem (for carcasses) or post-

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Table 1.—Taphonomic characteristics of scorpion molts and carcasses. Significant p-values are in bold. [1]This cell does not total 13 because six exuvia lack appendages. [2]Chi-square with Yates correction, all one degree of freedom.

Character	Description	Molt ($n = 13$)	Carcass ($n = 13$)	Chi-square[2]	P
Chelicerae	Extended	12	0	18.73	**1.5×10^{-5}**
	Retracted	1	13		
Pedipalps	Extended	11	6	2.71	0.10
	Retracted	2	7		
Body line	Curved	8	0	8.85	**0.003**
	Straight	5	13		
Walking legs	Splayed	7[1]	3	7.91	**0.005**
	Folded	0	10		
Telescoping of segments	Present	4	0	2.66	0.10
	Absent	9	13		

molt (for exuvia) exoskeletal posture and 2) the order and timing of disarticulation of the exoskeleton (i.e., the disarticulation sequence) through subsequent tumbling experiments.

Death/molt posture.—Intact scorpion carcasses and exuvia were photographed, and the following exoskeletal characteristics were recorded for each specimen: 1) curvature of the mesosoma and metasoma; 2) presence or absence of telescoped mesosomal and metasomal segments; 3) position/orientation of the chelicerae; 4) position/orientation of the walking legs; and 5) position/orientation of the pedipalps. A total of 13 carcasses and 13 molts were used in this study. Twenty-four fossil scorpions from the collections of the Yale Peabody Museum (YPM) were photographed and described following the same five criteria.

Tumbling.—After documenting the initial condition of the exoskeleton, scorpions were treated in one of three ways: 1) tumbling (wet)–13 carcasses and 11 exuvia were tumbled to the point of complete disarticulation in fresh water inoculated by the addition of water from an aquarium; 2) tumbling (dry)--one carcass and two exuvia were tumbled dry until disarticulated; 3) one carcass and one exuvium were left to decay in inoculated freshwater with no agitation as controls. Wet tumbling was done in one of two small (5-cm radius) plastic rock-tumblers available from hobby stores. One tumbler barrel had a smooth interior; the other tumbler had molded invaginations of the barrel wall that acted as interior bails. Dry tumbling of larger specimens was done in a larger (20-cm radius) tumbler with two internal bails. The tumblers were checked daily and the extent of disarticulation of the specimens recorded. Carcasses were kept frozen until used in the tumbling experiments to minimize potential differences in disarticulation between specimens due to differences in the degree of decay (Allison 1986).

Table 2.—Laboratory treatment of scorpion carcasses and molts.

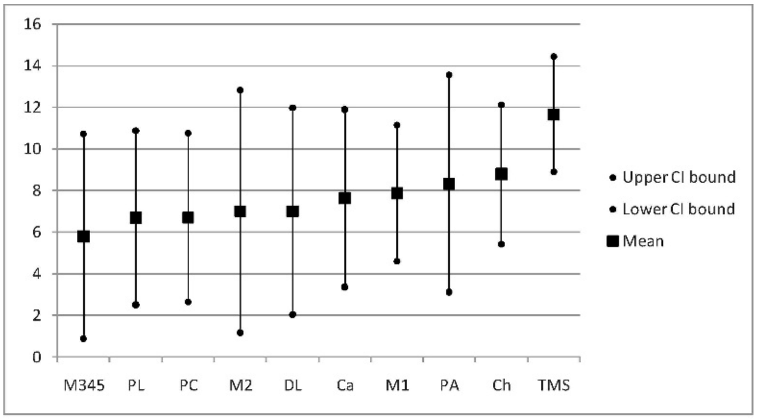
Species	Molt/Carcass	Wet/Dry	Tumbler	Time (days)
Pandinus imperator (C.L. Koch 1841)	molt	dry	bail-lg	2
Leiurus quinquestriatus (Ehrenberg 1928)	molt	dry	smooth	16
P. imperator	molt	wet	smooth	14
P. imperator	molt	wet	smooth	7
Parabuthus transvaalicus	molt	wet	smooth	15
P. transvaalicus	molt	wet	smooth	11
P. imperator	molt	wet	smooth	18
P. imperator	molt	wet	smooth	12
P. imperator	molt	wet	bail	18
P. imperator (juv)	molt	wet	smooth	10
P. imperator	molt	wet	smooth	11
P. imperator	molt	wet	bail	6
P. imperator (juv)	molt	wet	smooth	7
P. imperator (juv)	carcass	dry	bail-lg	4
P. imperator (juv)	carcass	wet	smooth	22
Anuroctonus phaiodactylus (Wood 1863)	carcass	wet	smooth	8
Smeringurus mesaensis (Stanhke 1957)	carcass	wet	smooth	19
S.mesaensis	carcass	wet	bail	18
S.mesaensis	carcass	wet	smooth	11
S.mesaensis	carcass	wet	bail	10
S.mesaensis (juv)	carcass	wet	bail	6
S.mesaensis	carcass	wet	smooth	13
S.mesaensis	carcass	wet	bail	10
S.mesaensis	carcass	wet	smooth	11
S.mesaensis (juv)	carcass	wet	bail	3
S.mesaensis (juv)	carcass	wet	smooth	13
Vaejovis spinigerus (Wood 1863)	carcass	wet	smooth	12

Table 3.—Comparison of molt/carcass and tumbler effects on disarticulation. *P*-values from the *t*-tests on the mean time to separation of exoskeletal tergites; significant *P*-values are in bold. S = smooth tumbler, B = tumbler with bails, PC = pedipalp claws, PA = pedipalp appendages, DL = distal leg segments, PL = proximal leg segments, M345 = third, fourth and fifth metasomal segments as one unit, M2 = second metasomal segment, M1 = first metasomal segment, Ch = chelicerae, Ca = carapace, and TMS = total mesosomal separation (= total exoskeletal disarticulation). The lack of significant *P*-values in the first row indicates that there are no differences in the timing of disarticulation between molts and carcasses. In the second row, the majority of the *P*-values are significant, reflecting differences in the timing of disarticulation between specimens in the smooth tumbler and specimens in the tumbler with the bail.

	PC	PA	DL	PL	M345	M2	M1	Ch	Ca	TMS
molt vs carcass	0.6817	0.7332	0.9333	0.9858	0.65	0.932	0.605	0.4175	0.363	0.891
S- vs. B-tumbler	**0.0001**	**0.0001**	**0.0083**	**0.0085**	**0.005**	**0.0025**	0.939	**0.0053**	0.089	0.255

Statistics.—Standard chi-square tests of independence with Yates correction (Preacher 2001) were used to compare the frequency of each of the five exoskeletal characteristics of death/molt postures listed above. To adjust for multiple tests, we modified the standard alpha level of 0.05 as per the conservative Bonferroni correction by dividing by 5 (the number of characteristics tested), so that *P*-values less than 0.01 were considered statistically significant (Preacher 2001). The chi-square calculations were carried out on an online calculator (Preacher 2001).

We used *t*-tests to compare the mean time-to-separation of various exoskeletal elements: pedipalp claws, pedipalp appendages (tibia and brachium), distal leg segments, proximal leg segments, last three metasomal segments, second metasomal segment, first metasomal segment, chelicerae, carapace, and total mesosomal separation. Two variables were considered: specimen type (molt or carcass) and tumbler type (smooth interior/bails). *P*-values less than 0.05 were considered significant. The sequence of disarticulation suggested by the mean time-to-separation of each



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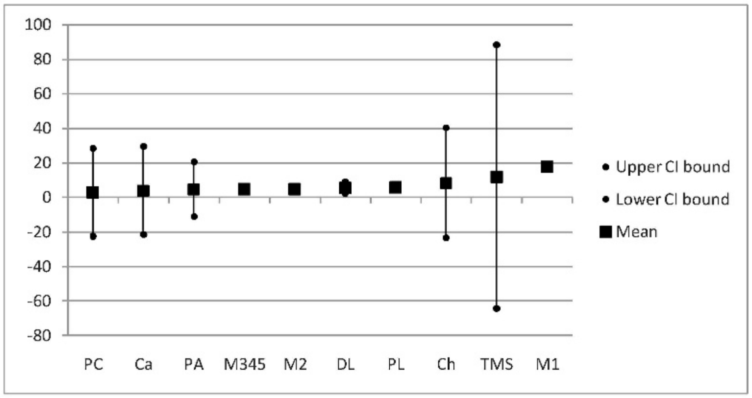

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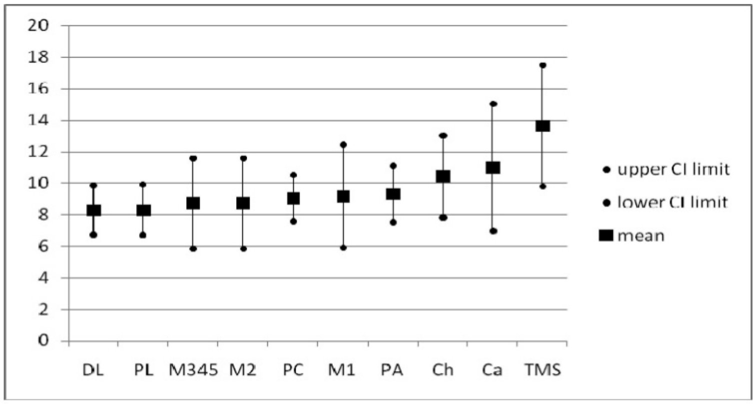
Figures 1, 2.—Plots of mean time to separation data showing order and timing of disarticulation for scorpion molts under different tumbling conditions. The y-axis is days. The vertical bars represent 95% confidence intervals. A small sample size results in a large standard deviation, which explains 'negative days' in Figure 2. The bars are ordered according to increasing mean time to separation (the center of each bar); the arms of the bars show the entire expected range of time to separation: 1. molts tumbled in smooth canister $n = 9$; 2. molts tumbled with agitation (bail), $n = 2$; PC = pedipalp claws, PA = pedipalp appendages, DL = distal leg segments, PL = proximal leg segments, M345 = third, fourth and fifth metasomal segments as a single unit, M2 = second metasomal segment, M1 = first metasomal segment, Ch = chelicerae, Ca = carapace, and TMS = total mesosomal separation (= total exoskeletal disarticulation).



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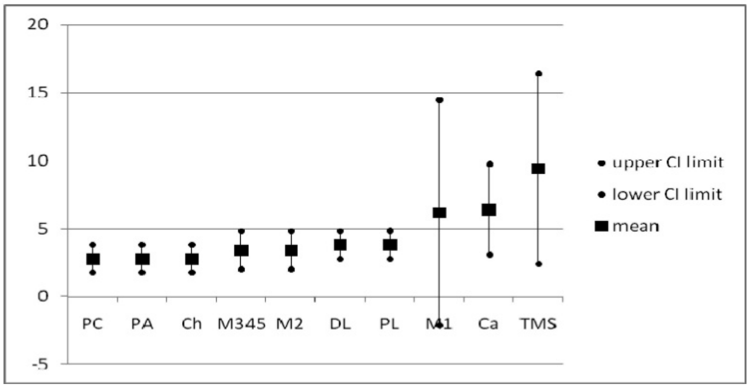

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Figures 3, 4.—Plots of mean time to separation data showing order and timing of disarticulation for scorpion carcasses under different tumbling conditions. The y-axis is days. The vertical bars represent 95% confidence intervals. The bars are ordered according to increasing mean time to separation (the center of each bar), the arms of the bars show the entire expected range of time to separation: 3. carcasses tumbled in smooth canister, $n = 8$; 4. carcasses tumbled with agitation, $n = 5$. PC = pedipalp claws, PA = pedipalp appendages, DL = distal leg segments, PL = proximal leg segments, M345 = third, fourth and fifth metasomal segments as a single unit, M2 = second metasomal segment, M1 = first metasomal segment, Ch = chelicerae, Ca = carapace, and TMS = total mesosomal separation (= total exoskeletal disarticulation).

exoskeletal element was also tested using 95% confidence intervals.

The *t*-tests and 95% confidence intervals were generated using SAS software, version 9.2 of the SAS System for Windows (SAS Institute Inc., Cary, NC, USA).

RESULTS

Taphonomic patterns, I. Death/molt posture.—The scorpion carcasses examined for this study exhibited the following characters: 1) retracted chelicerae (100% of the specimens); 2) straight body line (in dorsal view) with the metasoma extended straight back (100%); 3) pedipalps pulled in toward the prosoma (54%); and 4) walking legs folded against the body (77%) (Table 1 and Figures 7–18). In contrast, molts were characterized by the following features: 1) extended chelicerae (92%); 2) curved body line and curved metasoma (62%); 3) pedipalps pulled well back from the prosoma in an extended position (85%); and 4) splayed walking legs (100%) (Table 1 and Figures 7–18). Four of 13 molts (31%) exhibited telescoped mesosomal segments and overlap of the ventral surface on the dorsomedial surface (Figures 11, 15). These observations held across the six different scorpion genera examined for this study, suggesting taxonomic independence of these body-posture criteria. The low *P*-values obtained in the chi-squared test (Table 1) indicate that our sample size is sufficiently large to reflect a significant difference ($P < 0.05$) between scorpion death and molt postures.

Taphonomic pattens, II. Disarticulation.—Previous actuotaphonomic studies on tumbling segmented, exoskeleton-bearing invertebrates suggested that freezing the animals does not affect the exoskeletal disarticulation sequence (Kidwell & Baumiller 1990 on echinoids). We detected no differences in disarticulation between scorpions that had been frozen versus scorpions that had died naturally. Time-to-total disarticulation of the specimens is given in Table 2.

Wet vs. Dry: Both exuvia and carcasses released complete, intact tergites under wet tumbling conditions. These elements were not broken by subsequent tumbling (tumbling was terminated with the dissociation of the last exoskeletal elements). Carcasses tumbled dry behaved as carcasses tumbled wet. However, molts tumbled dry were quickly (2–3 days) reduced to ragged-edged, broken exoskeletal pieces rather than separated, unbroken tergites.

Disarticulation Sequence: A disarticulation sequence comprises two components: order and timing. Order refers to the sequence in which a given exoskeletal element separates in relation to the other exoskeletal elements. For example, “legs, pedipalps, chelicerae” is a different disarticulation order than

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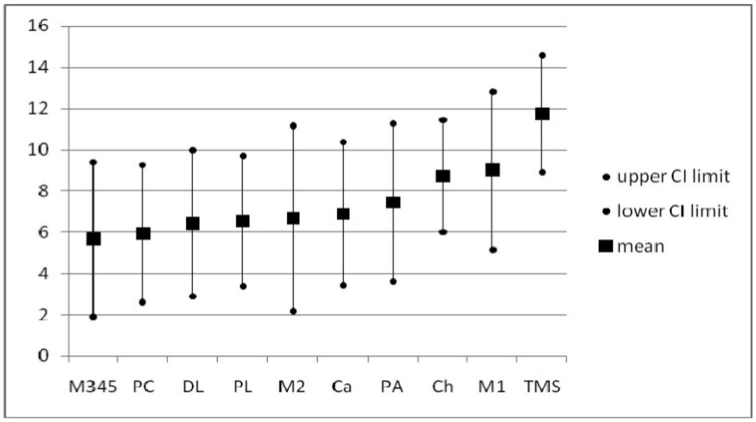

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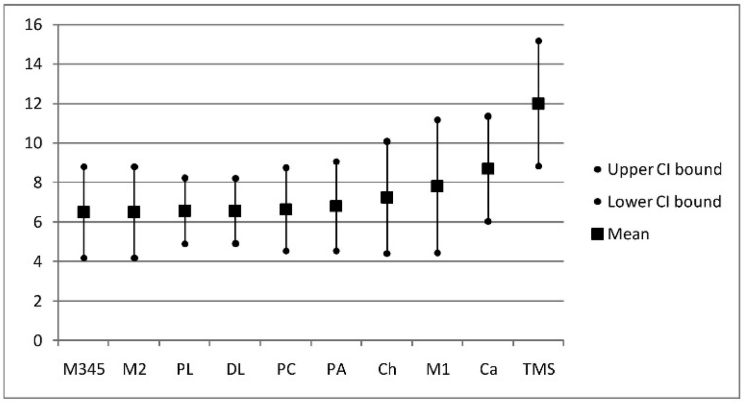


Figures 5, 6.—Plots of mean time to separation data showing order and timing of disarticulation for all scorpion molts and carcasses. The y-axis is days. The vertical bars represent 95% confidence intervals. The bars are ordered according to the mean time-to-separation (the center of each bar); the arms of the bars show the entire expected range of time to separation: 5. all molts, *n* = 11; 6. all carcasses, *n* = 13. PC = pedipalp claws, PA = pedipalp appendages, DL = distal leg segments, PL = proximal leg segments, M345 = third, fourth and fifth metasomal segments as a single unit, M2 = second metasomal segment, M1= first metasomal segment, Ch = chelicerae, Ca = carapace, and TMS = total mesosomal separation (= total exoskeletal disarticulation).

"pedipalps, legs, chelicerae." Timing refers to the elapsed time before an exoskeletal element separates. Only differences in order are noticeable in fossils, but a difference in order necessarily requires a difference in timing.

Molts and carcasses showed no significant differences in mean time to separation in any of the exoskeletal elements (Table 3, Row 1), indicating that there is no significant difference in the sequence or order of disarticulation for scorpion molts as compared to scorpion carcasses. Plots of 95% confidence intervals of the mean time to separation for each exoskeletal element (Figures 1–6) show a general pattern shared by molts and carcasses. The appendages (PC, PA, DL, PL, Ch in Figures 1–6) and metasoma (M345, M2, M1 in Figures 1–6) tend to separate from the rest of the body before the mesosoma disarticulates (TMS in Figures 1–6). For example, in Figure 6, the pedipalps separate on day 6, and the mesosoma disarticulates on day 12.

Using the rock-tumbler with the internal bails shortened disarticulation time for both molts (compare Figures 1 and 2) and carcasses (compare Figures 3 and 4). This tumbler effect is also reflected in the statistically significant values in Table 3, Row 2. However, the tumbler effect does not result in a statistically significant difference in disarticulation timing between molts and carcasses, as shown by the overlapping confidence intervals (compare Figure 1 with Figure 3 and Figure 2 with Figure 4).

A somewhat unexpected result was the comparison of times to total disarticulation. Molts proved to be as durable as carcasses when tumbled in water, as evidenced by the fact that the mean time to total disarticulation (see Table 3, Row 1, Column TMS, and Figures 5, 6) is not significantly different between molts and carcasses.

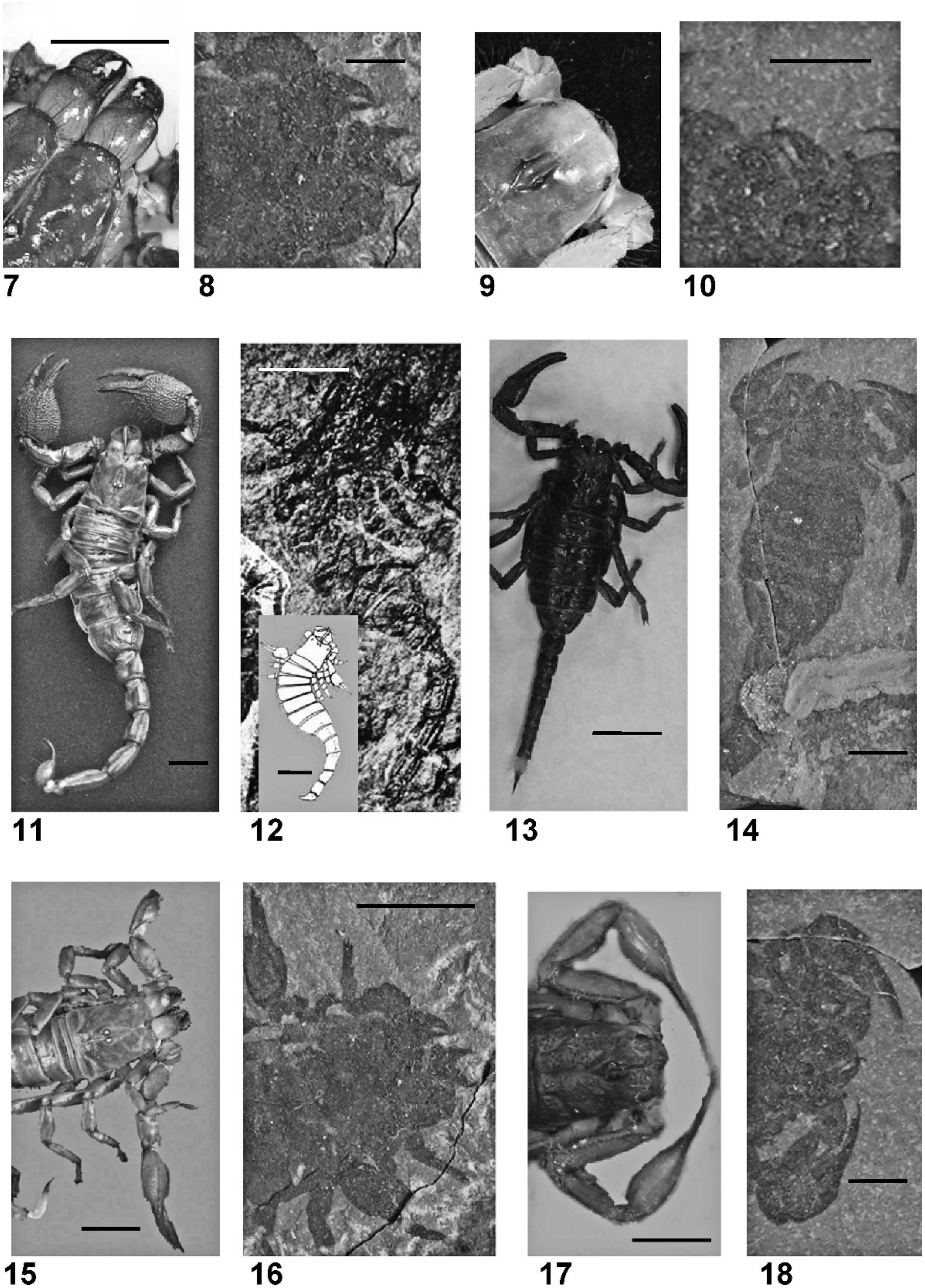
To summarize the statistical analysis of the tumbling data, molts and carcasses generally release appendages and metasomal segments early, the mesosoma is the most resilient exoskeletal unit for both exuvia and carcasses, and molts take as long as carcasses to reach total disarticulation.

DISCUSSION AND APPLICATION TO FOSSIL SCORPIONS

Scorpion molting and exuvia taphonomy.—Observations on ecdysis in modern scorpions support the criteria defined here of appendage position and body posture as diagnostic for distinguishing carcasses and exuvia. De Armas (1986) concluded that the position of the legs on a suitable substrate is critical for scorpions to successfully complete the process of ecdysis,

Table 4.—YPM specimens and identification as molt or carcass based on the criteria defined herein; "+"indicates presence, "-" denotes missing features or that determination could not be made, "?" denotes identification could not be determined due to poor preservation. E = extended, R = retracted, C = curved, St = straight, Sp = splayed, F = folded, P = present, A = absent. In the age column, MP = Middle Pennsylvanian, LS = Late Silurian.

		Chelicerae		Pedipalps		Body Line		Walking legs		Telescoping					
Specimen #	Taxon	E	R	E	R	C	St	Sp	F	P	A	ID	Locality	Age	Formation
typical carcass		-	+	-	+	-	+	-	+	-	+	carcass			
typical molt		+	-	+	-	+	-	+	-	+	-	molt			
YPM 126	*Anthracoscorpio? sp.*	-	-	-	-	-	+	-	-	-	+	?	Grundy Co., IL	MP	Carbondale
YPM 206691	*'Archaeophonus eurypteroides'*	+	-	+	-	-	+	+	-	-	-	molt	Herkimer, NY	LS	Willimsville
YPM 00128	*Eoscorpius carbonarius*	+	-	+	-	-	+	+	-	-	-	molt	Grundy Co., IL	MP	Carbondale
YPM 139	*E. carbonarius*	-	-	-	-	-	-	-	-	-	-	?	Grundy Co., IL	MP	Carbondale
YPM 138	*E. danielsi*	-	-	+	-	-	-	+	-	-	-	molt	Grundy Co., IL	MP	Carbondale
YPM 212155	*Mazonia woodiana*	+	-	+	-	-	+	-	-	-	-	molt	Welland, ON	LS	Fiddler's Green
YPM 127	*Palaeobuthus distinctus*	-	-	-	-	-	+	-	-	-	-	?	Grundy Co., IL	MP	Carbondale
YPM 212157	*P. distinctus*	-	-	-	-	+	-	-	-	-	-	molt	Grundy Co., IL	MP	Carbondale
YPM 140	*Palaeopisthacanthus schucherti*	+	-	+	-	-	-	-	-	-	-	molt	Grundy Co., IL	MP	Carbondale
YPM 130	*Proscorpius distinctus*	+	-	+	-	-	+	+	-	-	-	molt	Grundy Co., IL	MP	Carbondale
YPM 133	*P. distinctus*	-	-	+	-	+	-	-	-	-	-	molt	Grundy Co., IL	MP	Carbondale
YPM 208121	*P. osborni*	-	-	+	-	+	-	+	-	+	-	molt	Herkimer, NY	LS	Williamsville
YPM 208125	*P. osborni*	+	-	+	-	-	+	+	-	-	+	molt	Herkimer, NY	LS	Williamsville
YPM 208126	*P. osborni*	-	-	+	-	+	-	+	-	-	-	molt	Herkimer, NY	LS	Williamsville
YPM 208127	*P. osborni*	-	-	-	-	-	+	-	-	+	-	?	Herkimer, NY	LS	Fiddler's Green
YPM 208129	*P. osborni*	-	+	-	+	-	+	-	+	-	+	carcass	Herkimer, NY	LS	Williamsville
YPM 208130	*P. osborni*	+	-	+	-	+	-	+	-	-	-	molt	Herkimer, NY	LS	Williamsville
YPM 208131	*P. osborni*	-	-	+	-	-	+	-	-	-	+	carcass	Herkimer, NY	LS	Williamsville
YPM 209823	*P. osborni*	+	-	+	-	+	-	+	-	-	-	molt	Herkimer, NY	LS	Williamsville
YPM 212926	*P. osborni*	-	-	+	-	-	+	+	-	-	-	molt	Herkimer, NY	LS	Fiddler's Green
YPM 212927	*P. osborni*	-	-	-	-	-	+	-	-	-	-	?	Herkimer, NY	LS	Fiddler's Green
YPM 212928	*P. osborni*	-	-	-	-	-	-	-	-	-	-	?	Herkimer, NY	LS	Fiddler's Green
YPM 206692	*'Stoermeroscorpio delicatus'*	-	-	+	-	+	-	+	-	-	-	molt	Herkimer, NY	LS	Williamsville



Figures 7–18.—Comparison of fossil scorpion molts and carcasses: 7. Modern scorpion molt with extended chelicerae, scale bar is 5 mm; 8. Fossil scorpion molt with extended chelicerae, scale bar is 5 mm; 9. Modern scorpion carcass with retracted chelicerae, scale bar is 5 mm; 10. fossil scorpion carcass with retracted chelicerae, scale bar is 10 mm; 11. Modern scorpion molt with highly curved body line, scale bar is 10 mm; 12. Fossil scorpion molt with highly curved body line, each scale bar is 5 mm, from *Treatise on Invertebrate Paleontology,* ©1956, courtesy of the Geological Society of America and the University of Kansas; 13. Modern scorpion carcass with straight body line, scale bar is 10 mm; 14. Fossil scorpion carcass with straight body line, scale bar is 10 mm; 15. Modern scorpion molt with extended pedipalps, scale bar is 10 mm; 16. Fossil scorpion molt with extended pedipalps, scale bar 10 mm; 17. Modern scorpion carcass with retracted pedipalps, scale bar 10 mm; 18. Fossil scorpion carcass with retracted pedipalps, scale bar is 5 mm.

Table 5.—Literature survey with identification of illustrated specimens as molt or carcass based on the criteria defined herein; "+" indicates presence, "-" denotes missing features or poor preservation. E = extended, R = retracted, C = curved, St = straight, Sp = splayed, F = folded, P = present, A = absent.

		Chelicerae		Pedipalps		Body Line		Walking legs		Telescoping		
Author	Figure	E	R	E	R	C	St	Sp	F	P	A	Identification
typical carcass		-	+	-	+	-	+	-	+	-	+	carcass
typical molt		+	-	+	-	+	-	+	-	+	-	molt
Carvalho & Lourenco 2001	Figure 2	-	+	+	-	-	+	-	+	-	-	carcass
Lourenco & Gall 2004		-	-	+	-	-	+	-	+	-	-	molt
Santiago-Blay 1988	Figure 1–2	-	-	+	-	+	-	+	-	-	-	molt
Santiago-Blay et al. 2004	Figure 1	-	+	-	-	-	+	-	-	-	-	carcass

and Gaban & Farley (2002) noted that the walking legs become rigid and fixed in place before ecdysis begins. These observations suggest that ecdysial leg position may be retained after ecdysis, although Gaban & Farley (2002) also observed that *Paruroctonus mesaensis* (Stahnke 1957) pulls its appendages medially during ecdysis. The exuvia of all the scorpion genera examined in our study show the splayed walking leg posture.

The position of the pedipalps differs between the exuvia and carcasses examined for this study. Our observations compliment those of Gaban & Farley (2002), who noted that *Androctonus australis* (Linnaeus 1758) holds its pedipalps in a distinctive position before ecdysis, with the chelae sharply angled toward each other. These authors noted that this pre-molt posture contrasts with the posture of scorpions at rest, in which the pedipalps are retracted. More than half of the carcasses examined in this study retained their pedipalps in a retracted position, suggesting that the relaxed position also served as a post-mortem posture.

Observations on modern scorpions also support body line as a criterion for distinguishing exuvia (curved) from carcasses (straight). Gaban & Farley (2002) cite examples of exuvia of *A. australis*, *P. mesaenis*, and *Parabuthus transvaalicus* Purcell 1899 that are curved dorsally or to one side.

Fossil scorpion taphonomy.—We examined 24 well-preserved, nearly complete fossil scorpions from the Ciurca collection at the Yale Peabody Museum (YPM; Table 4) and applied our taphonomic criteria in an attempt to characterize each specimen as molt or carcass. One or more of the four distinguishing criteria (body line, position of chelicerae, position of walking legs, and position of pedipalps) could be identified in 85–90% of the YPM specimens (Table 4). Approximately 89% of the classifiable YPM specimens fit the criteria for molts (Table 4). The results of the YMP census support the conclusion of other authors that the bulk of the scorpion fossil record comprises exuvia (Kjellesvig-Waering 1986).

Most authors of papers on scorpion systematics do not include taphonomic data in their description of new specimens, nor do they make a determination of whether their illustrated specimens represent molts or carcasses. The taphonomic criteria developed herein can also be used to make the molt/carcass determination for fossil scorpions illustrated in the literature (Table 5).

The results of the tumbling experiments suggested that scorpion molts in water are nearly as durable as scorpion carcasses, as measured by time to total disarticulation (Tables 2, 3). This observation is interesting because it runs counter to the intuitive conclusion that molts must be more fragile than carcasses, and it calls into question the assumption that intact fossil scorpions are more likely the remains of the more "robust" carcass than the presumably "fragile" exuvium (Wills 1959; Jeram 2001; Gaban & Farley 2002).

The scorpion body plan is strikingly similar to that of the extinct eurypterids (Chelicerata: Eurypterida), and on this basis, scorpions can be considered reasonable taphonomic analogues for their extinct chelicerate cousins. Therefore, the criteria for distinguishing fossil scorpion molts and carcasses may also be useful for distinguishing fossil eurypterid molts and carcasses. A recent study of eurypterid molting (Tetlie et al. 2008) concluded that eurypterids indeed molted in much the same manner as modern scorpions, in spite of the obvious ecological differences between the aquatic eurypterids and the terrestrial scorpions.

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