

AN OVERVIEW OF PREDATION EVIDENCE FOUND ON FOSSIL DECAPOD CRUSTACEANS WITH NEW EXAMPLES OF DRILL HOLES ATTRIBUTED TO GASTROPODS AND OCTOPODS

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ABSTRACT

Predators of extant decapod crustaceans are fairly well known, but unlike many other invertebrate clades, not much is known regarding predation evidence found on fossil decapods. Herein, we provide an overview of such predation and expand upon this through an extensive study of fossil decapod specimens from multiple museum collections. Thus far most examples of predation come from drill holes and stomach contents; bite marks, incisions or irregular holes, and possible regurgitated material are also known. The currently recognized predators of decapods in the fossil record are fish, plesiosaurs, ammonites, octopods, and gastropods. We also provide new evidence of unambiguous drill-hole predation in decapods, based on 33,593 nonmoldic Cenozoic (middle Eocene–Holocene) decapod remains originating from Europe, Asia, and North America, indicating that drilling predation in decapods is more common than currently recognized. Drill holes attributed to octopods (*Ichnotaxon *Oichnus ovalis**) and gastropods (*O. simplex* and *O. paraboloides*) were found in carapaces and appendages from the Pliocene of the Netherlands, the Pleistocene and Pliocene of the United States (Florida), and the Pleistocene and early Miocene of Japan. Six drill holes attributed to octopods were found in epifaunal and semiburrowing crabs; three drill holes attributed to gastropods were discovered in semiburrowing and epifaunal crabs, and in a burrowing mud shrimp; and the producer of two other drill holes in epifaunal crabs is unknown. Other possible drill holes occur in decapods from the Holocene and early Miocene of Japan and the late Eocene of the United States. Drill-hole predation intensities in decapod faunas by stratigraphic formation are low ($\leq 2.7\%$), at least in part due to multiple biases such as preservation and molting.

INTRODUCTION

Predation plays a crucial role in current ecosystems worldwide in that it expands food webs, redistributes resources, and promotes evolution (e.g., Bengtson, 2002). Stanley (2008) argued that predation can be more important as a process for marine benthic organisms than competition. On macroevolutionary timescales, Huntley and Kowalewski (2007) found that Phanerozoic genus-level marine animal diversity correlates well with predation trace frequency in marine invertebrates, and Vermeij (2002) argued that both predator power and prey defense should increase over time. Thus, predation is an important process in modern and past ecosystems.

Among the most common and easily recognized traces of predation in the fossil record are drill holes, repair scars, stomach contents, and bite marks (e.g., Kowalewski and Kelley, 2002; Kelley et al., 2003; Boucrot and Poinar, 2010). Summaries of predation evidence found on a variety of marine fossil invertebrate clades are known: foraminifera (Culver and Lipps, 2003), trilobites (Babcock, 2003), crinoids (Baumiller and Gahn, 2003), brachiopods (Leighton, 2003), cephalopods (Mapes and Chaffin, 2003; Klompaker et al., 2009), echinoids

(Kowalewski and Nebelsick, 2003), bryozoans (McKinney et al., 2003), scaphopods (Yochelson et al., 1983; Klompaker, 2011a), annelids (Klompaker, 2012a; Martinell et al., 2012), ophiuroids (Aronson, 1987), ostracods (Reyment and Elewa, 2003), and bivalves and gastropods (Kelley and Hansen, 2003; Alexander and Dietl, 2003; Harper and Kelley, 2012).

Herein, we provide an overview of predation evidence on decapod crustaceans, a diverse group of invertebrates with ~15,000 extant (De Grave et al., 2009) and ~3,300 fossil species (Schweitzer et al., 2010). Additionally, we show new examples of drilling predation based on >30,000 nonmoldic Cenozoic decapod specimens indicating that predation evidence on fossil decapods is more common than currently recognized.

PREDATION ON EXTANT DECAPODS

Extant Predators of Decapods

Predators of extant marine decapods are fairly well known and include a wide variety of bony and cartilaginous fish (e.g., Warner, 1977; Heck and Wilson, 1987; Phillips, 2006), decapods (e.g., Heck and Wilson, 1987) including conspecific decapods (=cannibalism) (e.g., Kurihara and Okamoto, 1987; Hines and Ruiz, 1995), birds such as the herring gull, curlew, and eider (Cadée, 1994, 1995, 2007), octopods (e.g., Boyle and Knobloch, 1981; Runham et al., 1997), gastropods (Huelsenken, 2011), cuttlefish (e.g., Halm et al., 2000; Alves et al., 2006), the shelled cephalopod *Nautilus* (Ward and Wicksten, 1980), and mammals including man (Warner, 1977).

Extant Gastropods and Octopods as Predators of Decapods

Gastropod Drill Holes.—Several primary sources mention gastropod predation on decapods, but some do not specifically state whether drilling was used (Galtsoff et al., 1937; Cameron, 1966; Rehder, 1973). Grey (2001) mentioned that the naticid gastropod *Euspira heros* was observed in the field on two separate occasions to feed on dead crabs, which is somewhat surprising as naticids are known as active hunters of live prey (e.g., Kabat, 1990; Kelley and Hansen, 2003). Hunt (1925) reported that the buccinid gastropod *Buccinum undatum*, whether by scavenging or predation, had swallowed, whole, a young specimen of the hermit crab *Eupagurus*. Drilling predation on decapods by gastropods is rarely documented compared to drill-hole predation inflicted on mollusks. Only two reports are known to us. Cake and Smith (1983) mentioned that the muricid *Stramonita haemastoma floridana* drilled the exoskeleton of trapped blue crabs (*Callinectes sapidus*). Secondly, Huelsenken (2011) documented that the Australian moonshell (*Conuber sordidus*) drilled the soldier crab *Mictyris longicarpus* (Latreille, 1806) (see also <http://www.mapress.com/mr/content/v31/data/v.mp4>) (Figs. 1A–B). This crab is relatively small compared to the gastropod. The crab *Mictyris platycheles* and a hermit crab were also preyed upon (Huelsenken, 2011); the former was drilled, whereas no

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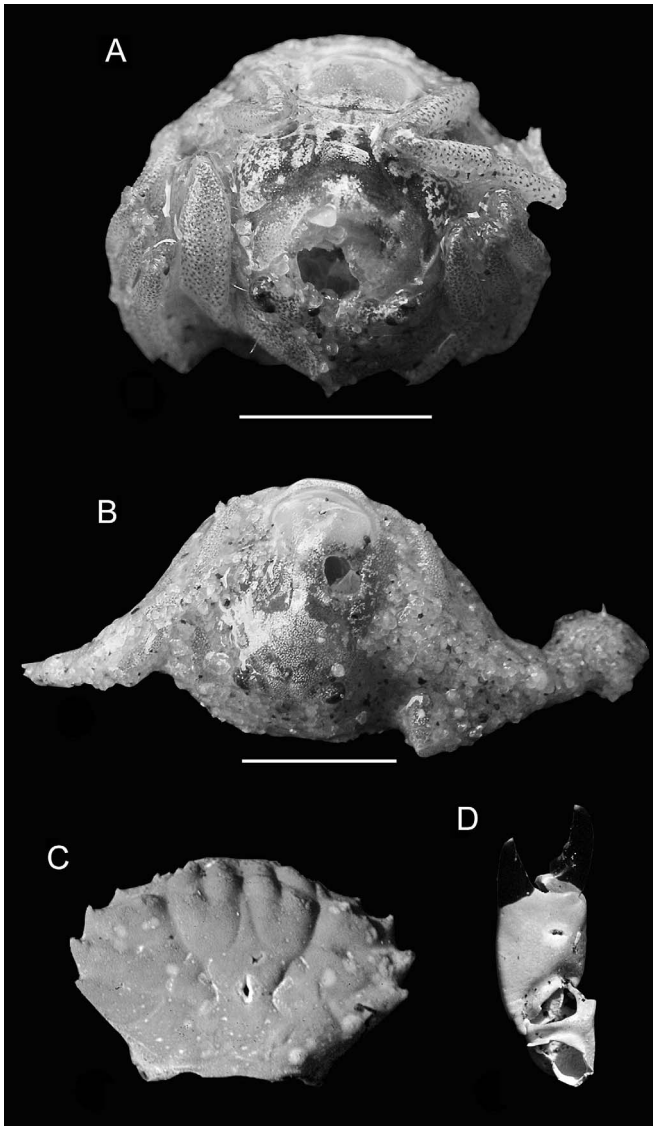


FIGURE 1—Drill holes inflicted on extant decapods. A) Drill hole just above the eyes by the naticid *Conuber sordidus* in the frontal part of the dorsal carapace of the crab *Mictyris longicarpus*. B) Drill hole by *C. sordidus* in the dorsal carapace of *M. longicarpus*; scale bars = 5.0 mm wide (Huelsen, 2011), used with permission from Magnolia Press and Thomas Huelsen). C) Oval octopod drill hole in the crab carapace of *Lophozozymus incisus* by *Octopus vulgaris*. D) Oval octopod drill hole on the propodus of the crab *Lophozozymus incisus* by *Octopus vulgaris* (images courtesy of Peter Wirtz; no indication of scale bars).

evidence for drilling was found on the hermit crab (T. Huelsen, personal communication, October 2012). Drilling by naticid and muricid gastropods on mollusks is performed through a combination of mechanical rasping by the radula and by chemical weakening of the shell by the accessory boring organ (Kelley and Hansen, 2003). The size of the drill hole is positively correlated with gastropod size for both naticids (Kitchell et al., 1981) and muricids (Carriker and Gruber, 1999).

Octopod Drill Holes.—More data are available on extant cephalopods that drill decapods. Members of the Octopodidae do drill decapods, whereas cuttlefish and other cephalopods are not reported to drill (e.g., Halm et al., 2000; Nixon and Young, 2003). More specifically, drilling in dorsal carapaces and chelae (propodi) is reported for *Octopus tehuelchus*, *O. vulgaris*, and *O. dofleini* (e.g., Guerra and Nixon, 1987; Iribarne et al., 1993; Mather and Nixon, 1995; Dodge and Scheel, 1999; Wirtz, 2005; Anderson et al., 2008).

Surprisingly, Iribarne et al. (1993) found that *Octopus tehuelchus* drilled the gastropod shell *Tegula patagonica* inhabited by the hermit crab *Pagurus* sp. In the most comprehensive study on octopods drilling decapods, Boyle and Knobloch (1981) found that *Eledrone cirrhosa* drilled a wide variety of crabs, mostly in the center of the dorsal carapace or slightly posterior to it. They also reported that the hermit crab *Pagurus bernhardus* was drilled on the dorsal carapace, and further mentioned (their table 1) that the lobsters *Homarus vulgaris* (= *Homarus gammarus*) and *Nephrops norvegicus* were drilled, although the location of the drill hole was not provided. Drilling is not restricted to adult octopods: Boyle and Knobloch (1981) also found that juveniles of *Eledrone moschata* drilled crab carapaces and chelipeds.

Drilling by *Octopus* is performed by a structure within the buccal mass, the salivary papilla, which is covered by small teeth (Nixon, 1979). Drilling of the shell occurs by mechanical rasping by the salivary papilla aided by some chemical dissolution through secretions from the salivary glands (Nixon et al., 1980). The radular teeth may be used to remove the organic component of the shell, while the saliva removes the calcium carbonate (Runham et al., 1997). These glands also provide the fluids that relax the muscles of the prey injected after the completion of the drill hole (e.g., Nixon and Maconnachie, 1988). Unlike gastropods that drill, Nixon and Maconnachie (1988) found that the properties of mollusk shells determine the size, shape, and form of the octopod drill hole, and not the size of the predator or the mouth parts of *Octopus vulgaris*. Figures 1C–D provide examples of drill holes in extant decapods made by *Octopus vulgaris*. Octopods also use other means of preying upon decapods. For example, Dodge and Scheel (1999) documented irregular bite marks inflicted by the *Octopus* beak (see their fig. 1C) on propodi of the crab *Telmessus cheiragonus*, and on the crab *Cancer productus*. Cuttlefish bite a particular spot on the fifth pair of pereopods of crabs (Halm et al., 2000).

PREDATION EVIDENCE FOUND ON FOSSIL DECAPODS

Overview

In contrast to predation on extant decapods, not much evidence of predation is known on fossil decapods (Fig. 2, Table 1). Two categories are most frequently encountered: decapods containing drill holes and decapods found as stomach contents, primarily of fish. In terms of number of specimens involved, stomach contents top the list, as some fish are found to contain up to hundreds of decapods (Maisey, 1994). Minor reported categories of predation on decapods include bite marks, incisions or irregular holes, and possible regurgitated material. The recognized predators of decapods in the fossil record are fish, plesiosaurs, ammonoids, octopods, and gastropods. This is less than today's range of predators (see above).

Decapods as Stomach Remains

Decapod remains as stomach contents of fish are known from as early as the late Permian (Malzahn, 1968; Bachmayer and Malzahn, 1983), representing one of the few known Paleozoic decapod records in addition to "*Eryma*" *hoerstgenensis* from contemporaneous strata in Germany, the late Permian lobster *Protoclytiopsis antiqua*, the Late Devonian (Famennian) to early Carboniferous (Tournaisian) lobster *Palaeopalaemon newberryi*, and the Late Devonian (Famennian) shrimp *Aciculopoda mapei* (Whitfield, 1880; Birshtein, 1958; Bachmayer and Malzahn, 1983; Feldmann and Schweitzer, 2010). Favorable preservation conditions appear necessary as most animals with decapod remains preserved in the stomach region are from Lägerstätten (e.g., the Santana Formation in Brazil, the Posidonia Shale in southwestern Germany, and the sublithographic limestones in Lebanon). From that perspective, decapods may also be expected from the stomach contents

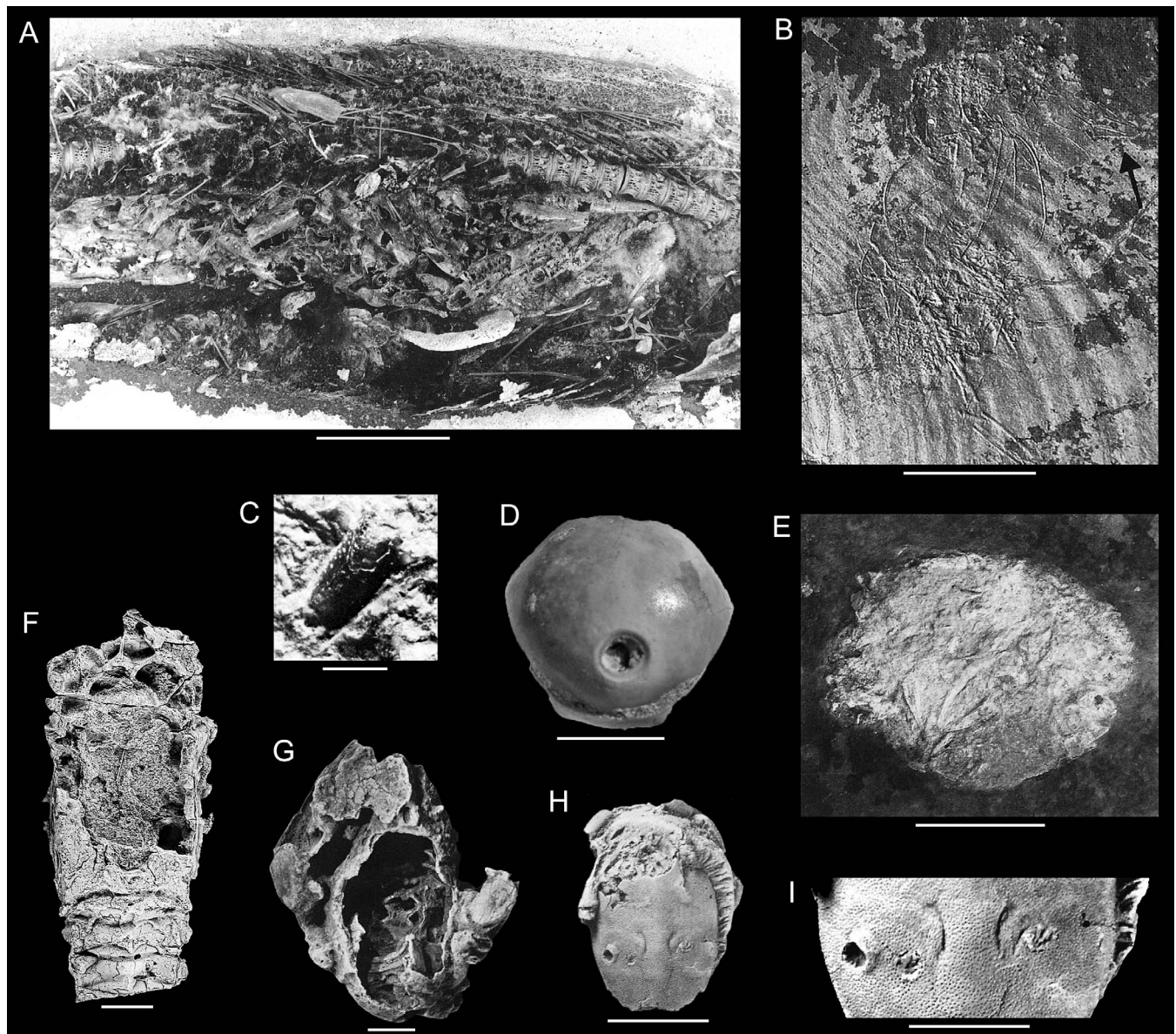


FIGURE 2—Evidence of predation on fossil decapods from known literature. A) Stomach content of the Albian teleost fish *Rhacolepis buccalis* (AMNH DVP 19380) from Brazil containing multiple specimens of the shrimp *Palaemonetes deliciosa*; courtesy The American Museum of Natural History (from Maisey and De Carvalho, 1995). B) Food balls containing pereiopods including chelae within the body chamber of the Toarcian ammonite *Harpoceras falciferum* from Germany; courtesy of The Palaeontological Association (from Jäger and Fraaye, 1997). C) Pereiopod fragment of a late Permian decapod (?lobster) found in the stomach of the fish *Janessa bituminosa* in Germany (provided by Andreas Kroh; figured in Bachmayer and Mahlzahl, 1983). D) An example of a drill hole attributed to a gastropod in a Pliocene crab carapace of *Ristoria pliocaenica* (GPDG 0175a) (from Pasini and Garassino, 2012). E) Possible regurgitated material or fecal pellet containing decapod remnants (IGM-6534) from the Albian of Mexico (from Feldmann et al., 1998). F) An irregular hole in the carapace of the Turonian lobster *Linuparus dzhairantuiensis* (USNM 530052) from Uzbekistan (from Feldmann et al., 2007). G) An irregular hole in a Pleistocene-Holocene cambarid crayfish (USNM 451375) from Oklahoma, United States (from Feldmann and May, 1991). H) Maastrichtian frog crab *Bournelyreidus oaeensis* (USNM 173581) showing bite marks caused by a fish (from Bishop, 1978). I) Close-up of the same specimen (from Bishop, 1972). Scale bars: View C = 1.0 mm; D, I = 5.0 mm; rest = 10.0 mm.

of fish in other decapod-bearing Lagerstätten such as the lower Eocene Green River Formation in the United States, the Upper Jurassic (Kimmeridgian–Tithonian) Solnhofen Limestone in Germany, the Lower Cretaceous (Albian) Tlayúa Formation in Mexico, and the Middle Jurassic (Callovian) La Voulte-sur-Rhône in France.

Drill Holes in Decapods

Unambiguous drill holes in decapods were previously recognized only from the Pliocene of Europe (Klompaker, 2011b; Pasini and Garassino, 2012). With the addition of new examples presented here, drill holes in fossil decapods have been found in Asia, Europe, and North America. Because drilling predation in general became abundant

since the Late Cretaceous (e.g., Kowalewski et al., 1998), coincident with the rise of murcid and naticid gastropods (Kelley and Hansen, 2003; Harper, 2006, fig. 3), unambiguous drill holes produced by gastropods may also be expected in pre-Pliocene decapod faunas.

Examples of Ambiguous Predation of Decapods

Some reported examples are not considered to be convincing evidence of predation and therefore are not listed in Table 1. They include the association of the bowfin fish *Amia fragosa* and *Amia uintaensis* with cambarid crayfish from the lower Eocene Fossil Butte Member of the Green River Formation of Wyoming (see Feldmann et al., 1981; Grande, 1984). Collins and Wierzbowski (1985) suggested a predatory origin of an

TABLE 1—Predation evidence found on decapods based on previous literature and results herein.

Decapod taxon	Predator	Decapod part affected	Type of predation	Age	Location	Stratigraphic unit	Reference
decapod (?lobster)	fish <i>Janessa bituminosa</i>	peritopod, cephalothorax and abdomen	stomach content	Late Permian	Germany, North Rhine-Westphalia, Rosseuray 2 mine	Lower Rhenish Kupferschiefer	Malzahn (1968); Bachmayer and Malzahn (1983)
multiple remains of ? <i>Coloia</i> sp.	ammonite <i>Harpoceras falcatiferum</i>	peritopods, telsons, and abdomina	stomach content	Early Jurassic (early Toarcian)	Germany, Dotternhausen	Posidonia Shale Formation, <i>Dactyloceras commune</i> Subzone	Jäger and Fraaye (1997)
hundreds of caridean shrimp (?palaemonids) (at least two types)	fish <i>Tharrhias araripis</i> , <i>Rhacolepis buccalis</i> , and undetermined <i>Dastilbe</i> -like gonorynchiform	—	stomach content	Early Cretaceous (middle to late Albian)	NE Brazil, Ceará, Araripe Basin	Santana Formation, Romueldo Member	Maisey (1994)
several taxa of indetermined decapods, shrimplike decapods	fish <i>Rhacolepis</i> sp. and <i>Notelops</i> sp.	eye, abdomen, and ?telson	stomach content	Early Cretaceous (middle to late Albian)	NE Brazil, Ceará, Araripe Basin	Santana Formation, Romueldo Member	Wilby and Martill (1992)
<i>Palaemonattea deliciosa</i> ; brachyuran larvae	fish <i>Rhacolepis buccalis</i> (two specimens were also reported in Maisey, 1994); <i>Tharrhias araripis</i> (same as in Maisey, 1994)	carapaces, abdomina, and appendages	stomach content	Early Cretaceous (middle to late Albian)	NE Brazil, Ceará, Araripe Basin	Santana Formation, Romueldo Member	Maisey and De Carvalho (1995)
<i>Paraneocarcinus</i> cf. <i>P. milbournei</i>	catfish <i>Scyllorhinus</i> sp.	carapace, abdomen, chelipeds	stomach content	Late Cretaceous, Cenomanian	Lebanon, Hadjoulia	sublithographic limestones of Hadjoulia	Pasini and Garassino (2011)
Decapoda indet.	elasmosaur plesiosaur	carapace	stomach content	Early Cretaceous (late Albian)	Australia, Great Artesian Superbasin	Allaru Formation	McHenry et al. (2005)
<i>Bournehyreidus oabeensis</i>	fish	carapace	bite marks	Late Cretaceous (early Maastrichtian)	USA (South Dakota), Ft. Pierre locality	Pierre Shale Formation, zone of <i>Bacallites grandis</i>	Bishop (1972, 1978)
<i>Callianassa</i> sp. and <i>Dakoticancer</i> sp.	—	accumulations of claws of <i>Callianassa</i> and skeletal elements	possible regurgitated material	Late Cretaceous	USA (South Dakota)	Pierre Shale Formation	Bishop (1975)
Decapoda indet.	—	cheliped and possibly walking legs	possible regurgitated material or fecal pellet	Early Cretaceous (Albian)	S. Mexico, Puebla, Tepexi de Rodríguez	Tlayúa Formation, Middle Member	Feldmann et al. (1998)
3 specimens of cambriid crayfish	possibly birds, small mammals, or man	cephalothorax and abdomen	incisions	Holocene–Pleistocene	USA (Oklahoma), near Temple and Randlett	—	Feldmann and May (1991)
1 specimen of <i>Limnarus dzhentaitiensis</i>	—	cephalothorax	irregular hole	Late Cretaceous (middle–late Turonian)	Uzbekistan, Kyzylkum Desert, Dzhetysay	Bisseky Formation	Feldmann et al. (2007)
? <i>Cancer</i> sp.	gastropod	right dactylus	drill hole	Pliocene (early Zanclean to early Piacenzian)	The Netherlands, Langenboom pit	Oosterhout Formation	herein; Klompmaaker (2011b)
<i>Platylambus</i> sp.	octopod	left merus	drill hole	Late Pliocene (Piacenzian)	USA (Florida), Langston Quarry 1, unit 7	Intracoastal Formation	herein
<i>Callinectes major</i>	?naidic gastropod	left merus	drill hole	?Middle Pleistocene	USA (Florida), 101 Ranch Pit, bed 5	Bermont Formation	herein
<i>Cancer</i> (s.l.) <i>tomonoi</i>	gastropod or octopod	dactylus	drill hole	Early Miocene	Japan, Higashihora (Loc. 1-2 of Karasawa, 1990), Yamaoka-cho, Ena City, Gifu Prefecture	Mizunami Group, Toyama Formation, Higashihora Member	herein

TABLE 1—Continued.

Decapod taxon	Predator	Decapod part affected	Type of predation	Age	Location	Stratigraphic unit	Reference
<i>Urnalana haematosicta</i>	gastropod	carapace	drill hole	Middle Pleistocene	Japan, Takamatsu (Karasawa and Tanaka, 1994, fig. 1), Akabane-cho, Tahara City, Aichi Prefecture	Toyohashi Formation, Atsumi Group	herein
Dromiidae	gastropod or octopod	fixed finger of propodus	drill hole	Middle Pleistocene	Japan, Takamatsu (Karasawa and Tanaka, 1994, fig. 1), Akabane-cho, Tahara City, Aichi Prefecture	Toyohashi Formation, Atsumi Group	herein
<i>Philyra syndactyla</i>	octopod	propodus	drill hole	Middle Pleistocene	Japan, Takamatsu (Karasawa and Tanaka, 1994, fig. 1), Akabane-cho, Tahara City, Aichi Prefecture	Toyohashi Formation, Atsumi Group	herein
<i>Urnalana haematosicta</i>	octopod	propodus	drill hole	Middle Pleistocene	Japan, Takamatsu (Karasawa and Tanaka, 1994, fig. 1), Akabane-cho, Tahara City, Aichi Prefecture	Toyohashi Formation, Atsumi Group	herein
<i>Hiphyra platycheir</i>	octopod	merus	drill hole	Middle Pleistocene	Japan, Takamatsu (Karasawa and Tanaka, 1994, fig. 1), Akabane-cho, Tahara City, Aichi Prefecture	Toyohashi Formation, Atsumi Group	herein
<i>Hiphyra platycheir</i>	octopod	carapace	drill hole	Middle Pleistocene	Japan, Ogushi, Amakusa City, Kumamoto Prefecture	Ogushi Formation	herein
<i>Paradorippe</i> cf. <i>P. granulata</i>	octopod	propodus	drill hole	Middle Pleistocene	Japan, Ogushi, Amakusa City, Kumamoto Prefecture	Ogushi Formation	herein
<i>Ristoria pliocaenica</i>	?octopods, gastropods	carapaces	drill holes	Early Pliocene (Zanclean)	Italy, Tuscany, Pisa, "La Serra" quarry near San Miniato	Unit 4	Pasini and Garassino (2012)
<i>Seulocia rhomboidalis</i>	gastropod	carapace	drill hole	Pliocene (now Early Pleistocene)	Western Taiwan (locality unknown)	Tongxiao Formation	Hu and Tao (1996, pl. 21.13)
<i>Ocalina floridana</i>	?	right propodus	?drill hole	Late Eocene	USA (Florida), Dell Limerock Mine	Ocala Limestone (Upper)	herein
<i>Lyphira heterograna</i>	?	carapace	?drill hole	Holocene	Japan, Nagoya Harbour, Aichi Prefecture	Nanyo Formation	herein
<i>Philyra nishimotoi</i>	?	carapace	?drill hole	Early Miocene	Japan, Inkyoyama (loc. 22 of Karasawa (1989), Toki City, Gifu Prefecture	Mizunami Group, Akeyo Formation, Kujiri Facies	herein; Karasawa (1989, pl. 3.6a)
<i>Philyra nishimotoi</i>	?	carapace	?drill hole	Early Miocene	Japan, Inkyoyama (loc. 22 of Karasawa (1989)), Toki City, Gifu Prefecture	Mizunami Group, Akeyo Formation, Kujiri Facies	herein

TABLE 2.—Summary of the drill holes found in fossil decapod collections by formation (ichnotaxa *Oichinus* spp.); see Supplementary Data¹ for full details by taxon.

Country	Age	Formation	Number of appendages drilled (at least one part of appendage preserved)	Number of appendages total (at least one part of appendage preserved)	Percentage drilled appendages (at least one part of appendage preserved)	Number of carapaces drilled (at least carapace preserved)	Number of carapaces total (at least carapace preserved)	Percentage drilled carapaces (at least carapace preserved)	Total number	Percentage per formation
The Netherlands	Pliocene (Zanclean–Piacenzian)	Oosterhout Formation	1	11	9.09	0	32	0.00	43	2.33
Japan	Middle Pleistocene (MIS9)	Toyohashi Formation, Asumi Group	4	5379	0.07	1	131	0.76	5510	0.09
Japan	Early Miocene (N6)	Toyama Formation, Mizunami Group	1	37	2.70	0	0	0.00	37	2.70
Japan	Early Miocene (N6)	Akeyo Formation, Mizunami Group	0	53	0.00	0	23	0.00	76	0.00
Japan	Holocene (about 6,000 B.P.)	Nanyo Formation	0	736	0.00	0	377	0.00	1114	0.00
Japan	Middle Pleistocene (MIS7)	Ogushi Formation	1	122	0.82	1	30	3.33	152	1.32
USA (Florida)	Late Eocene	Ocala Limestone	0	227	0.00	0	134	0.00	361	0.00
USA (Florida)	Early Miocene	Parachucla Formation	0	443	0.00	0	0	0.00	443	0.00
USA (Florida)	Early Miocene	Chipola Formation	0	818	0.00	0	9	0.00	827	0.00
USA (Florida)	Early Miocene	Torreya Formation	0	70	0.00	0	0	0.00	70	0.00
USA (Florida)	Middle Miocene	Coosawhatchie Formation	0	754	0.00	0	0	0.00	754	0.00
USA (Florida)	Middle Miocene	Shoal River Formation	0	26	0.00	0	0	0.00	26	0.00
USA (Florida)	Late Pliocene	Tamiami Formation	0	529	0.00	0	4	0.00	533	0.00
USA (Florida)	Early Pliocene	Intracoastal Formation	1	11	9.09	0	921	0.00	932	0.11
USA (Florida)	Pliocene	Jackson Bluff Formation	0	70	0.00	0	12	0.00	82	0.00
USA (Florida)	Early Pleistocene	Caloosahatchee Formation	0	2228	0.00	0	34	0.00	2262	0.00
USA (Florida)	Early Pleistocene	Nashua Formation	0	36	0.00	0	0	0.00	36	0.00
USA (Florida)	Middle Pleistocene	Bermont Formation	1	16383	0.01	0	38	0.00	16421	0.01
USA (Florida)	Late Pleistocene	Fort Thompson Formation	0	87	0.00	0	27	0.00	114	0.00
Jamaica	Middle Eocene	Guys Hill Formation	0	47	0.00	0	0	0.00	47	0.00
Jamaica	Early Pliocene	Bowden Formation	0	171	0.00	0	3	0.00	174	0.00
Cuba	Late Pleistocene	Jaimanitas Formation	0	138	0.00	0	1	0.00	139	0.00
Panama	Late Pleistocene–Holocene	indeterminate	0	3439	0.00	0	2	0.00	3441	0.00
		Total	9	31815	0.03	2	1778	0.11	33593	0.03

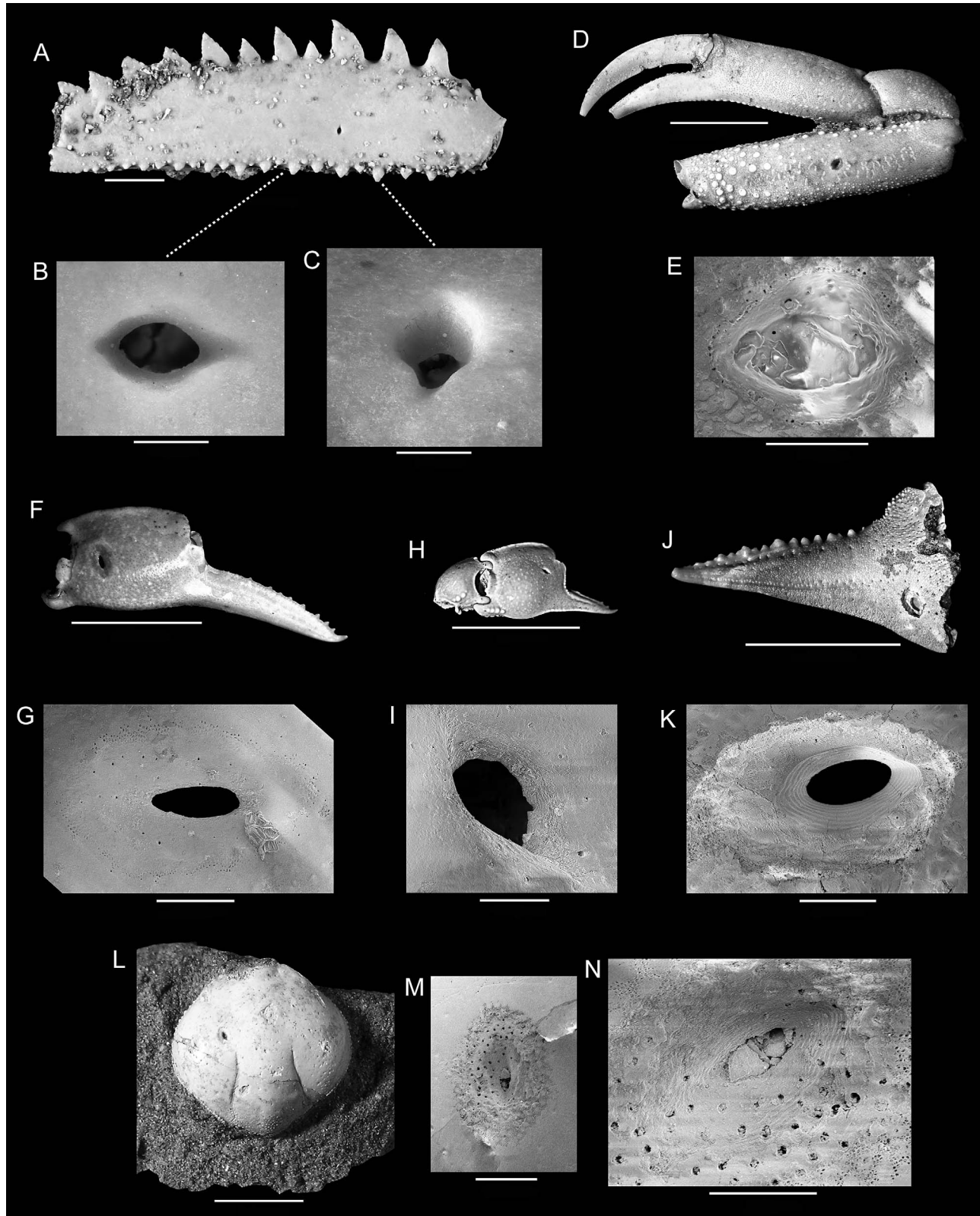


FIGURE 3—Drill holes attributed to octopods in fossil decapods (ichnotaxon *Oichmus ovalis*). A–C) A merus of the crab *Platylambrus* sp., Pliocene, Florida, United States, containing an octopod drill hole (UF 222610) with close-ups of the drill hole showing the morphology in plan view (B) and an angled view showing the gutter on one of the long ends (C). D–E) Drilled merus and close-up of the drill hole in the Pleistocene crab *Hiplyra platycheir* (MFM142517) from Japan. F–G) Drilled propodus and close-up of the drill hole in the Pleistocene crab *Philyra syndactyla* (MFM142515) from Japan. H–I) Drilled propodus and close-up of the drill hole in the Pleistocene crab *Urnalana haematosticta* (MFM142516) from Japan. J–K) Drilled propodus and close-up of the drill hole in the Pleistocene crab *Paradorippe* cf. *P. granulata* (MFM142518) from Japan. L–N) Drilled carapace and close-ups of the drill hole in the Pleistocene crab *Hiplyra platycheir* (MFM142518) from Japan. Scale bars: Views A, D, H, J, L = 5.0 mm; F = 2.5 mm; B, C, M = 0.5 mm; E, G, K, N = 0.25 mm; I = 0.1 mm.

TABLE 3—Measurements (in mm) of oval drill holes attributed to octopods (ichnotaxon *Oichnus ovalis*) in fossil decapods.

Taxon	Affected part	Country	Formation	Age	Oval drill holes attributed to octopods			
					Outer diameter width	Outer diameter length	Inner diameter width	Inner diameter length
<i>Platylambrus</i> sp. (Parthenopidae)	ventral side left merus	USA (Florida)	Intracoastal Fm.	Late Pliocene (Piacenzian)	0.50	1.00	0.35	0.55
<i>Philyra syndactyla</i> (Leucosiidae)	inner side left propodus	Japan	Toyohashi Fm.	Middle Pleistocene (MIS9)	0.48	0.83	0.10	0.28
<i>Urnalana haematosticta</i> (Leucosiidae)	outer side right propodus	Japan	Toyohashi Fm.	Middle Pleistocene (MIS9)	0.15	0.36	0.11	0.14
<i>Hiplyra platycheir</i> (Leucosiidae)	outer side right merus	Japan	Toyohashi Fm.	Middle Pleistocene (MIS9)	0.37	0.49	0.15	0.25
<i>Hiplyra platycheir</i> (Leucosiidae)	dorsal carapace	Japan	Ogushi Fm.	Middle Pleistocene (MIS7)	?0.7	?1.1	0.1	0.2
<i>Paradorippe</i> cf. <i>P. granulata</i> (Dorippidae)	inner side right propodus	Japan	Ogushi Fm.	Middle Pleistocene (MIS7)	0.27	0.49	0.13	0.28

infilled hole in the mesobranchial region of a Late Jurassic (Oxfordian) internal mold of the crab *Goniidromites serratus* from Poland. It is likely that this hole was also present in the cuticle, but it is not stated whether this is a corpse or a molt; in the latter case it cannot be considered predation. Pasini and Garassino (2012) did show convincing examples of gastropod drill holes in Pliocene crab carapaces of *Ristoria pliocaenica*, but the claimed octopod drill holes in conspecific carapaces may be considered ambiguous because close-up images of the ≤ 0.4 -mm-sized drill holes, typically provided in the literature for octopod drill holes in extant invertebrates, were not provided.

Predation of Crustaceans

Some authors have suggested predation on crustaceans, but did not specify which group of crustaceans, perhaps at least in part related to poor preservation. Some of these crustaceans could be decapods. One example is crustaceans in coprolites of Carboniferous (Mississippian) fish from Montana (Lund, 1990), although Schram and Horner (1978) did not report any decapods from that formation. Although no conclusive evidence was provided, Nybelin (1958) suggested that the fish *Thrissops formosus* may have fed on pelagic crustaceans in southern Germany during the Late Jurassic. Decapods are well known from these lithographic limestones (e.g., Garassino and Schweigert, 2006; Schweigert, 2011). Another example from the Jurassic are Sinemurian fragments of crustacean carapaces in the alimentary tract of the thylacocephalan crustacean *Ostenocaris cypriformis* from Italy (Pinna et al., 1985). Examples from the Cretaceous are also known. In addition to a decapod carapace, McHenry et al. (2005) mentioned that stomach contents of an Early Cretaceous (Albian) plesiosaur contained crustacean fragments while Sanz et al. (1996) reported Early Cretaceous (Barremian) birds yielded crustacean remains, also in the stomach region.

MATERIALS AND METHODS

To study drill-hole predation evidence on fossil decapods, 33,593 decapod remains originating from 23 formations and stored in museum collections in the United States (Florida), Japan, and the Netherlands were studied. The decapods originate from the Netherlands, Japan, United States, Jamaica, Cuba, and Panama; and range in age from the middle Eocene to the Holocene (Table 2; see also Supplementary Data¹). Only nonmoldic decapods were included in the table because drill holes in moldic material are not readily observable. Moldic material was examined but did not yield drill holes.

Institutional abbreviations: UF = University of Florida, Florida Museum of Natural History (Invertebrate Paleontology), Gainesville, United States; MAB k = Oertijdmuseum De Groene Poort, Boxtel, The Netherlands; MFM = Mizunami Fossil Museum, Mizunami, Japan; AMNH = American Museum of Natural History, New York, United States; IGM = Museo de Paleontología of the Instituto de Geología, Universidad Nacional Autónoma de México, Mexico City, Mexico; USNM = United States National Museum of Natural History, Washington, D.C., United States; GPDG = Paleontological Collections of the Gruppo Paleontologico “C. De Giuli,” Biblioteca Comunale Vallesiana, Castelfiorentino, Florence, Italy.

NEW EXAMPLES OF PREDATION: DRILL HOLES IN CENOZOIC DECAPODS

Drill-hole predation percentages in decapods vary per formation from 0%–2.7%; the overall drill-hole predation percentage is as low as 0.03% (Table 2; see also Supplementary Data¹). Nine drill holes were found in appendage material (0.03%), whereas two drill holes were encountered in carapaces (0.11%). Drill holes are mainly found in epifaunal to semiburrowing decapods (primarily crabs) and less so in burrowing decapods such as callianassoid shrimp.

Drill Holes Attributed to Octopods

Morphology of Drill Holes.—Drill holes attributed to octopods were found in specimens from the Pleistocene of Japan and the Pliocene of the United States (Fig. 3), with the outer drill-hole diameters usually being <1 mm (Table 3), which is comparable to, and somewhat smaller than, those found in extant decapods (see Boyle and Knobloch, 1981; Nixon and Boyle, 1982; Guerra and Nixon, 1987; Mather and Nixon, 1995), and smaller than those observed in mollusks (e.g., Arnold and Arnold, 1969; Nixon and Maconnachie, 1988). The form and size of these drill holes conform with drill holes produced by octopods and reported from extant invertebrates including decapods, even though variation exists in the shape and form of these drill holes (e.g., Arnold and Arnold, 1969; Boyle and Knobloch, 1981; Nixon and Maconnachie, 1988). Bromley (1993) erected the ichnotaxon *Oichnus ovalis* for these oval drill holes attributed to octopods. Subcircular, often irregular drill holes in cross section are also produced by extant octopods, however (e.g., Arnold and Arnold, 1969, figs. 2C, H; Nixon and Maconnachie, 1988, pl. 3A), resembling *Oichnus simplex* (Bromley, 1981). A part of the drill holes attributed to octopods shows a relatively gentle tapering down toward the center of the hole, (or gutter *sensu* Harper, 2002, p. 292) typically on the long sides, whereas others show less pronounced notches or concavities here (Fig. 3). The outer margin

¹ palaios.ku.edu

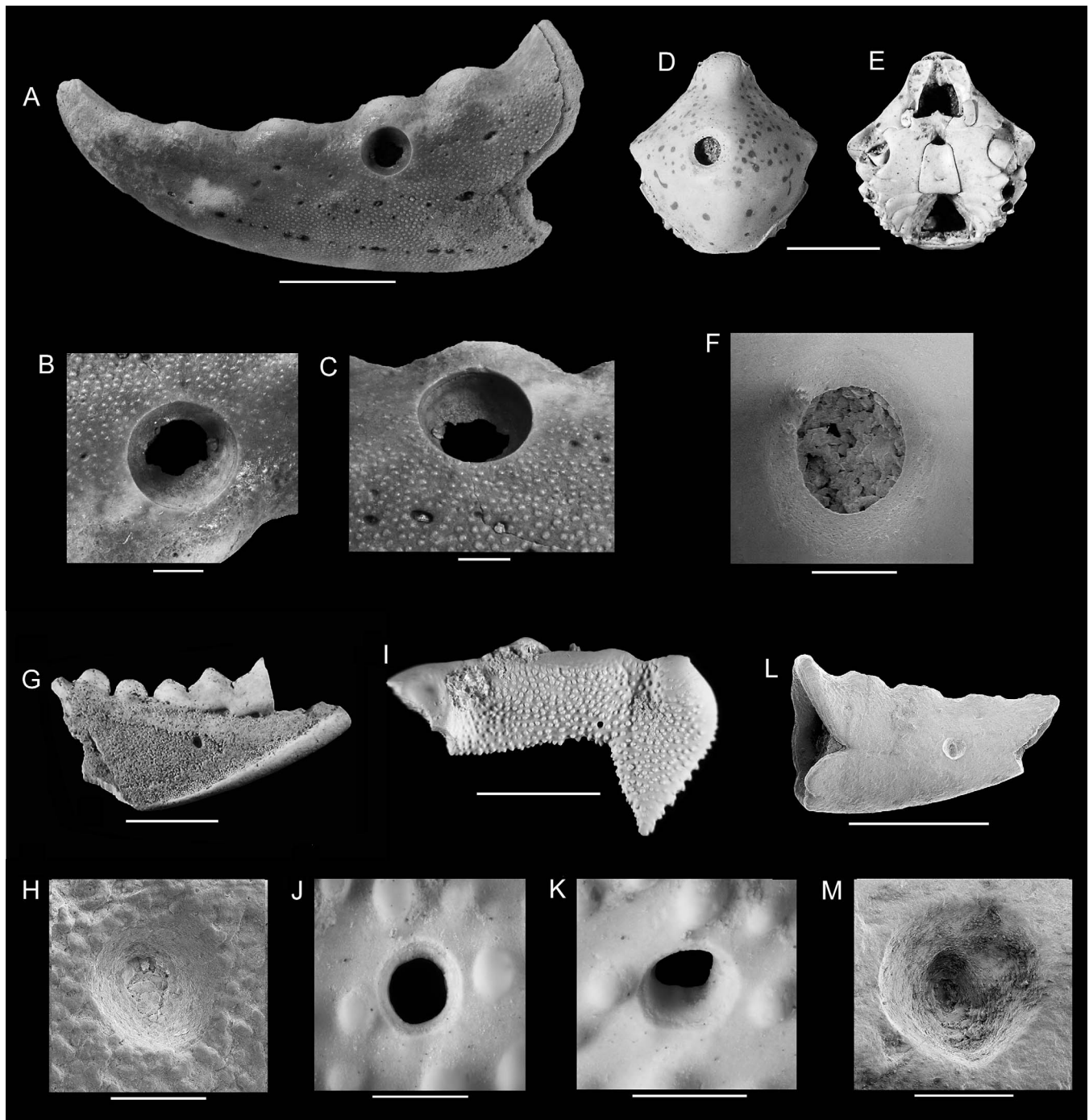


FIGURE 4—New drill holes in fossil decapods, in part attributed to gastropods (ichnotaxa *Oichnus paraboloides* and *O. simplex*). A–C) Dactylus of the crab ?*Cancer* sp. from the Pliocene of the Netherlands containing a naticid drill hole (MAB k3276). D–F) Dorsal (view D) and ventral (view E) carapace as well as a close-up (view F) of the crab *Urnalana haematosticta* from the Pleistocene of Japan showing a drill hole attributed to a gastropod (MFM142511). G–H) Fixed finger of the propodus of a dromiid crab from the Pleistocene of Japan exhibiting a drill hole (MFM142514). I–K) Outer side of a left merus of the mud shrimp *Callinectes major* from the Pleistocene of the United States (Florida) (UF 108508) showing a probable gastropod drill hole. L–M) Dactylus of the crab *Cancer* (s.l.) *tomowoi* from the early Miocene of Japan showing a drill hole (MFM9172). Scale bars: Views A, D–E, G, I, L = 5.0 mm; B–C, F = 1.0 mm; H, J–K, M = 0.5 mm.

of the drill holes in remains of the crabs *Paradorippe* cf. *P. granulata* and *Hiplyra platycheir* (Ogushi Formation) appears to have degraded since the drill hole was made, possibly explaining the relatively high outer to inner drill-hole ratio compared to the octopod drill holes for the latter. The additional degradation was not taken into account in the measurements for the former, which implies the outer diameter of the drill hole was wider initially.

Holes in Crabs.—Drill holes attributed to octopods (*Oichnus ovalis*) have been found only in crabs thus far, not in lobsters, shrimps, or

anomurans (Table 3). This may mean that octopods preferred crabs over other decapods, that crabs were more abundant than other decapods, and/or that drill holes were better preserved on the crab cuticle. All decapods with drill holes attributed to octopods were either living on the bottom (epifaunal) or were semiburrowers. Leucosiids and parthenopids are semiburrowers (Gore and Scotto, 1979; Davie, 2002), whereas dorippids, or carrier crabs (Davie, 2002), are not known to burrow. Burrowing crabs would most likely escape predation, because octopods typically hunt for prey on the bottom and in the water column.

TABLE 4—Measurements (in mm) of subcircular drill holes in fossil decapods (ichnotaxa *Oichnus paraboloides* and *O. simplex*).

Taxon	Affected part	Country	Formation	Age	(Sub)circlear drill hole	
					Outer diameter	Inner diameter
? <i>Cancer</i> sp. (Cancridae)	outer side right dactylus	The Netherlands	Oosterhout Fm.	Pliocene (early Zanclean to early Piacenzian)	2.2	1.3
<i>Callichirus major</i> (Callianassidae)	outer lateral side left merus	USA (Florida)	Bermont Fm.	Middle Pleistocene	0.44–0.49	0.31–0.34
<i>Urnalana haematosticta</i> (Leucosiidae)	dorsal carapace	Japan	Toyohashi Fm.	Middle Pleistocene (MIS9)	2.3	1.4
Dromiidae	outer side right fixed finger of propodus	Japan	Toyohashi Fm.	Middle Pleistocene (MIS9)	0.66–0.69	~0.28
<i>Cancer</i> (s.l.) <i>tomowoi</i> (Cancridae)	inner side right dactylus	Japan	Toyama Fm.	Early Miocene (N6)	0.80–0.85	0.49–0.54

Position of Drill Holes.—The few drill holes in the propodi are on both the inner (2) and outer (1) sides of the propodus, whereas Wirtz (2005) noted that drill holes attributed to octopods were always located on the inner side of the propodus. The position of these drill holes on carapaces is mostly recorded from the dorsal side of the carapace for modern crabs (Boyle and Knobloch, 1981; Guerra and Nixon, 1987), which is in agreement with the single specimen reported here. Although

the elbow crab *Platylambrus* sp. was drilled in the left merus (Figs. 3A–C), drill holes attributed to octopods in meri are unknown from extant decapods. The drill hole is located on the smooth side of the merus, which is oriented ventrally in extant specimens of *Platylambrus*. To drill that part, the octopod had to flip over the specimen. The dorsal side of *Platylambrus* spp. generally contains tubercles or spines, which may have made it difficult for the octopod to drill, suggesting that drilling on

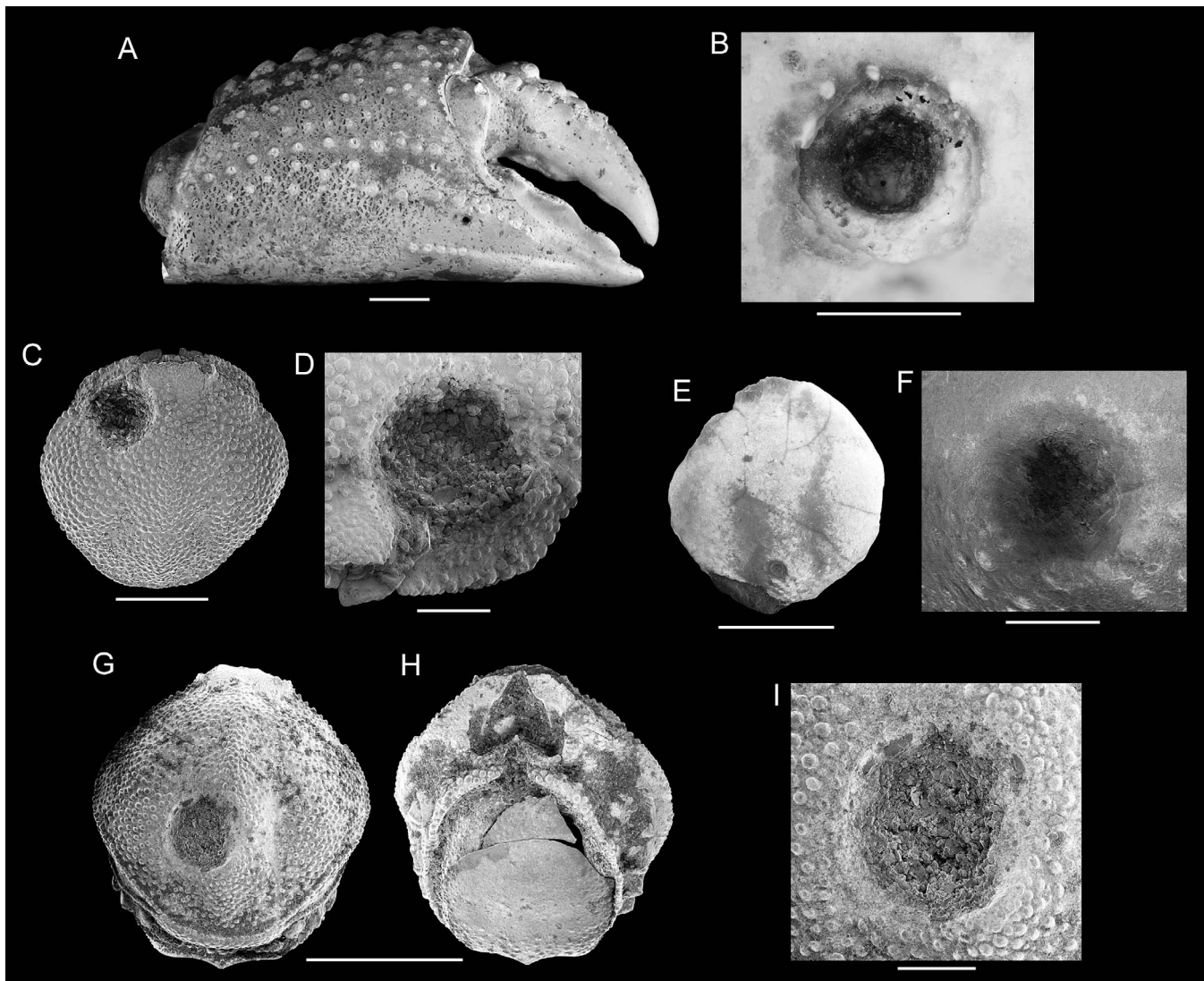


FIGURE 5—Possible drill holes in fossil decapods (ichnotaxon *Oichnus* sp.). A–B) The propodus (with hole) and dactylus of the crab *Ocalina floridana* from the late Eocene of the United States (Florida) (UF 17712) and a close-up of the hole. C–D) The dorsal carapace of the crab *Philyra nishimotoi* from the early Miocene of Japan (MFM9171) and a close-up of the hole. E–F) The dorsal carapace and a close-up of the hole in the crab *Lyphira heterograna* from the Holocene of Japan (MFM142510). G–I) Dorsal view (G) with a hole and ventral side (view H) of the carapace of the paratype of the crab *Philyra nishimotoi* (MFM9009) from the early Miocene of Japan. Close-up of the hole (view I). Scale bars: View A = 10.0 mm; C, E, G/H = 5.0 mm; B, D = 1.0 mm; F, I = 0.5 mm.

the smooth ventral side of the merus was intentional. After the cephalotoxin was injected through the hole, the crab was likely paralyzed within minutes. Parts of the crab would then have disintegrated and the muscle attachment dissolved, allowing the meat to be removed from the carapace and appendages with little damage to the exoskeleton (see Altman and Nixon, 1970; Nixon, 1984). Even though both ends of the merus of *Platylambrus* sp. are quite narrow, the octopod may have been able to remove the meat without damaging the merus. A comparable scenario may apply for the drilled merus of *Hipplyra platycheir*.

Drill Holes Attributed to Octopods in Other Fossil Invertebrates.—The drill holes in Pleistocene and Pliocene decapods add to the scarce fossil evidence of drill holes attributed octopods. These holes were previously documented in fossil scallops from the Plio-Pleistocene Bermont (*Euvola ziczac*, *Euvola raveneli*, *Pecten* sp.), Caloosahatchee (*Argopecten irradians*, *Chlamys anteampliocostatus*, *Argopecten comparilis*), Jackson Bluff (*Euvola ochlockonensis*, *Argopecten comparilis*, *Pecten* sp.), and Tamiami (Pinecrest beds) (*Pecten tamiamiensis*, *Pecten* sp.) formations (Harper, 2002) from the United States (Florida). Furthermore, Bromley (1993) showed two scallop valves with drill holes attributed to octopods from the late Pliocene of Greece, and Robba and Ostinelli (1975) recognized similar holes in bivalves and gastropods from the early Pliocene of Italy. Recently, Todd and Harper (2011) considered the early Eocene (Ypresian) bivalve *Venericor clarendonensis* to contain subcircular octopod drill holes, and claimed these are the oldest known drill holes produced by octopods. With the addition of drill holes from the Pliocene and Pleistocene of Florida and Japan, the types of prey inferred to be drilled by octopods included decapods as well as mollusks from the Pliocene onward. It is conceivable to find octopod drill holes in pre-Pliocene decapods, because drill holes attributed to octopods occur in Eocene mollusks, and octopods similar to those living today were present since the Late Cretaceous (Strugnell et al., 2006; Fuchs et al., 2009; Todd and Harper, 2011).

Drill Holes Attributed to Gastropods and Other Drill Holes

Drill holes attributed to gastropods are found in a variety of skeletal parts of fossil decapods (Fig. 4, Table 4) and are known from the Pliocene and Pleistocene of several countries (Japan, The Netherlands, and the United States).

Hole in Dactylus.—The drill hole in the dactylus of the crab? *Cancer* sp. from the Pliocene of the Netherlands (Figs. 4A–C) is parabolic in cross section (ichnotaxon *Oichnus paraboloides*) consistent with the morphology of a naticid drill hole, but lacks a clear beveled edge. The mainly infaunal naticid gastropods are the predominant drill-hole producing gastropods at the Langenboom locality (Klomp maker, 2009), and are the most likely candidate to have drilled the dactylus, although modern *Cancer* spp. are not reported to burrow (e.g., Nations, 1975). The placement of the drill hole is remarkable because it is located in a thick part of the decapod cuticle near the teeth of the dactylus and near an area where little meat would be located. Whether this drill hole, oriented on the outside of the dactylus of the *Cancer* specimen in its living position, was produced during the life of the crab, when it could still defend itself, or after the animal died, cannot be determined. The latter may be more likely, given the position of the drill hole. Mistaken predation (i.e., predation on organisms that are not part of the predator's normal diet) on invertebrates has been discussed previously (e.g., Walker and Behrens Yamada, 1993; Kowalewski et al., 2005; Leighton et al., 2013).

Hole in Merus.—The drill hole in the merus of the middle Pleistocene mud shrimp *Callichirus major* from the Bermont Formation, United States (Figs. 4I–K), contains a beveled edge below which the drill hole is nearly perfectly cylindrical (resembling *Oichnus simplex*). The drill hole is located on the outer lateral side of the merus in its living position. This still-extant species is a cryptic and solitary burrower and is found on sandy beaches, oftentimes below mean sea level (Frankenberg et al.,

1967; Rodrigues and Shimizu, 1997). This suggests that the producer of the drill hole lived infaunally as well. Infaunal naticids produce countersunk drill holes with beveled edges and a typically parabolic cross section (Kitchell et al., 1981), which is not seen in this specimen. The exact identity of the predator cannot be determined, but may have been a gastropod given the high number of gastropod taxa that are known to drill (e.g., Kowalewski, 2002) and the fact that drilling gastropods are common in the Bermont Formation (Portell and Kittle, 2010). Similarly-sized, subcircular holes may also be caused by boring clionid sponges, known as the ichnotaxon *Entobia* (e.g., Bromley, 1970); but clionid holes do not show a countersunk profile, and multiple, rather than solitary, holes are generally present. Because of the location of the drill hole in the merus positioned on the lateral side of the body, the shrimp may not have been able to defend itself, if it was alive at the time the drill hole was produced. The drill hole was probably made by a small gastropod given its ~0.5 mm size (Table 4).

Hole in Carapace.—The circular drill hole in the dorsal carapace of the leucosiid crab *Urnalana haematosticta* from the middle Pleistocene of Japan (Figs. 4D–F) is somewhat parabolic in cross section and a beveled edge is present (resembling *Oichnus paraboloides*). This species was probably a semiburrower with its rostrum protruding above the sediment-water interface as with most extant leucosiids (Davie, 2002). The shape of the drill hole and the fact that this crab probably lived infaunally suggests a naticid predator, species of which have been found in the same formation (*Glossaulax didyma*, *Euspira sagamiensis*, *Natica vitellus spadicea*, and *Cryptonatica janthostomoides*). The fact that the venter is preserved shows that this can be considered an act of predation instead of a mistaken drill hole in a molt.

Other Predatory Drill Holes.—Two other holes (Figs. 4G–H, L–M) are likely to be predatory drill holes because of the combination of the smooth walls of the hole, the perpendicular orientation relative to the cuticle, and the location with respect to the soft tissue inside. They resemble *Oichnus paraboloides*. The likely predator is difficult to suggest because of the slightly irregular nature of the drill hole. Both extant gastropods and octopods are also known to produce irregular, subcircular drill holes (e.g., Arnold and Arnold, 1969, fig. 2; Nixon, 1979, fig. 1; Nixon and Maconnachie, 1988, pl. 3A; Morton, 2005, fig. 3; Huelsken, 2011, fig. 4B–C).

Possible Drill Holes.—Other holes (*Oichnus* sp.) may be considered to represent drill holes, some of which are shown in Figure 5. The hole in the propodus of the crab *Ocalina floridana* is found in a similar position as the drill holes attributed to octopods in the propodus of extant specimens of *Panopeus herbstii* (see Mather and Nixon, 1995). The uncertainty in these examples stems from the fact that both the specimens and the holes are not well preserved. As noted above, drill holes on decapods are not necessarily perfectly circular or oval even when recently produced. The irregularity is enhanced by degradation of the cuticle after the death of the animal. However nondrilling causes for these holes cannot be excluded.

PRESERVATIONAL BIAS OF DRILL HOLES IN DECAPOD FAUNAS

Most of the unambiguous drill holes were discovered in well-preserved specimens during this study (Figs. 3–4) and in Pasini and Garassino (2012). This suggests that drill holes are easily observable in well preserved compared to less well preserved decapods, in which drill holes may be obliterated to the extent that they cannot be identified as a drill hole with certainty (see Fig. 5). Decapods preserved as internal or external molds, decapods with only a part of the cuticle preserved, and highly abraded cuticles are unlikely to show convincing evidence of drill-hole predation.

Another preservational bias occurs when decapods known to be drilled by gastropods in the modern environment are absent from the fossil record. As mentioned above, Huelsken (2011) reported drilling on

soldier crabs (Mictyridae). Unfortunately, these crabs have no known fossil record (see Schweitzer et al., 2010). Given the low reported occurrence of drill holes in extant decapods, decapods are not likely a large part of the diet of extant gastropod taxa that are known to drill decapods (e.g., *Stramonita haemastoma floridana* and *Conuber sordidus*). This suggestion is supported by Huelsken (2011) for *C. sordidus* and by Butler (1985) for *S. haemastoma floridana*. Neither species are specialized in feeding on decapods, but may opportunistically prey upon them.

The third and fourth biases are related to the body parts in which the decapod is drilled and the shape of the drill hole itself. Huelsken (2011, fig. 4) showed drill holes in different regions of the carapace, one being on the frontal part of the carapace (his fig. 4C), which may not be commonly preserved, particularly when compared with the central, more easily preserved, part of the carapace. Grisley et al. (1996) documented that 45% of the specimens of the extant crab *Carcinus maenas* were drilled in the eye by *Eledrone cirrhosa*. This is an area that is not easily preserved and thus is likely underrepresented in the fossil record. Furthermore, because decapods consist of numerous segments, drilling on the border of segments results in a drill hole that is not easily discernible in fossilized remains of decapods, which are often disarticulated. Huelsken (2011) also showed a serrated drill hole, which would not be easily recognizable as a drill hole after the fossilization process. Additionally, in the majority of the cases only parts of a decapod exoskeleton is preserved, which substantially reduces the chance of finding evidence of predation. Shrimp are suggested to have an exoskeleton that is less calcified compared to other decapods and, thus, exhibit a lower preservation potential (e.g., Förster, 1985; Müller et al., 2000), hampering preservation of drill holes, if present.

A fifth bias affecting the preservation of decapods with drill holes is the potential preferential breakage of drilled specimens compared to specimens not drilled. This has been suggested (Roy et al., 1994; Hagstrom, 1996; Zuschin and Stanton, 2001) and contested (Wainwright et al., 1982; Kelley, 2008) for bivalve mollusks, but has yet to be tested for decapods.

Perhaps the most important factor, besides preservation, in substantially lowering the actual observed drill-hole predation intensity on fossil decapods is the abundant presence of molts in the fossil record. Molts should not show evidence of successful predation because decapods must have been alive during the molting process. Other than Mertin (1941), not much is known about the ratio of decapod corpses to molts in the fossil record. Mertin (1941, p. 251) estimated that the ratio of molts to corpses was about 5:1 based on 94 molts and 20 corpses of fossilized lobsters from the Late Cretaceous of Germany. Distinction between corpses and molts may be possible for exceptionally well-preserved decapod faunas.

In summary, although abundant drilled decapod fossils, comparable to mollusks, are not expected (given the low reported occurrence today), the drill-hole percentages given in Table 2 likely significantly underestimate the actual percentage of decapods that were actually drilled.

FINAL REMARKS AND FUTURE DIRECTIONS

Decapods are well-known predators in the fossil record (e.g., Vermeij, 1977a, 1977b; Dietl and Vega, 2008; Schweitzer and Feldmann, 2010), yet not much is known about predation on decapod crustaceans despite evidence of predation since the late Permian (Table 1). The reasons for this are many: (1) decapods possess multicomponent skeletons and, upon disarticulation and abrasion, traces of predation can be obliterated; (2) the low incidence of repair scars found in fossil decapods; (3) the abundance of decapod molts that typically do not show evidence of successful predation (see also above); (4) the low preservation potential for decapod fossils; (5) a focus on systematics in decapod paleontology (see Glaessner, 1969; Schweitzer et al., 2010); (6) the fact that many predators do not leave recognizable traces, especially when the entire exoskeleton is crushed; and (7) a

collecting bias exists toward more common and better preserved other invertebrates such as mollusks and echinoids, resulting in an underrepresentation of decapods in collections.

Many questions concerning predation on decapods remain unanswered. Decapods likely provided an increasingly abundant source of food for predators from the Mesozoic onward, when decapod diversity (and probably also abundance) is suggested to have increased (Glaessner, 1969; Sepkoski, 2000; Klompmaker, 2012b). However, not much is known about predation on Cenozoic decapods except for relatively rare drilled specimens (Table 1). It remains uncertain when drilling in decapods began. The present research, which focused on Eocene–Holocene decapod faunas, only revealed definite drilling predation from the Miocene to the Pleistocene. Whether drill holes attributed to gastropods in carapaces are present in tiny specimens only, as the limited information thus far obtained suggests, and whether certain decapod parts were targeted by drilling octopods in the past (as is shown from modern examples) remains uncertain. Bulk sampling of decapod-rich deposits, preferably those where molts and corpses can be distinguished, should yield more accurate drill-hole predation frequencies. Furthermore, targeting the stomach contents of fish and marine reptiles in Lagerstätten can help identify decapods as prey. In general, more types of predators are likely to be recognized in the future because the number of recognized predators of decapods from the fossil record is limited compared to those from modern environments. In conclusion, much more research can be done on predation evidence in fossil decapods.

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Country	State/Province	Locality	Age	Formation	Number of appendages drilled (at least one part of appendage preserved)	Number of appendages drilled (at least one part of appendage preserved)	Percentage drilled (at least one part of appendage preserved)	Number of carapaces least drilled (at least one part of carapace preserved)	Number of carapaces total (at least one part of carapace preserved)	Percentage drilled carapaces (at least one part of carapace preserved)	Total number	Percentage per formation
The Netherlands	Noord-Brabant	Langenboom	Pliocene (Zanclean-Piacenzian)	Oosterhout Formation	0	1	0.00	0	14	0	14	0.00
					0	0	0.00	0	0	0	5	0.00
					0	3	0.00	0	0	0	3	0.00
					0	1	0.00	0	0	0	0	0.00
					0	1	0.00	0	0	0	1	0.00
					0	1	0.00	0	0	0	1	0.00
					0	0	0.00	0	2	0	2	0.00
					0	1	0.00	0	0	0	1	0.00
					1	3	33.33	0	11	0	3	33.33
					1	11	9.09	0	32	0.00	43	2.33
Japan	Aichi	Takamatsu, Tahara City	Middle Pleistocene (MIS9)	Toyohashi Formation, Atsumi Group	0	121	0	0	0	0	121	0.00
					0	18	0	0	0	0	18	0.00
					0	3048	0	0	0	0	3048	0.00
					0	10	0	3	3	0	13	0.00
					0	5	0	7	7	0	12	0.00
					1	1	100	0	1	0	1	100.00
					0	337	0	0	1	0	338	0.00
					0	86	0	0	0	0	86	0.00
					0	31	0	0	0	0	31	0.00
					0	14	0	1	1	0	15	0.00
					1	1	100.00	0	2	0	2	50.00
					1	120	0.83	33	33	0	153	0.65
					0	51	0	5	5	0	56	0.00
					0	17	0	1	1	0	18	0.00
					0	12	0	9	9	0	21	0.00
					1	25	4	13	13	7.69	38	5.26
					0	457	0	2	2	0	459	0.00
					0	0	0	0	1	0	1	0.00
					0	0	0	1	1	0	1	0.00
					0	14	0	4	4	0	18	0.00
					0	14	0	4	4	0	18	0.00
					0	62	0	1	1	0	63	0.00
					0	0	0	2	2	0	2	0.00
					0	43	0	1	1	0	44	0.00
					0	40	0	1	1	0	41	0.00
					0	0	0	1	1	0	1	0.00
					0	0	0	18	18	0	18	0.00
					0	0	0	1	1	0	1	0.00
					0	852	0	20	20	0	872	0.00
					4	5379	0.07	1	131	0.76	5510	0.09
Japan	Gifu	Kubohara, Ena City	Early Miocene (N6)	Toyama Formation, Mizunami Group	0	2	0	0	0	0	2	0.00
					1	34	2.94	0	0	0	34	2.94
					0	1	0	0	0	0	1	0.00
					1	37	2.70	0	0	0	37	2.70
					0	20	0	0	0	0	20	0.00
					0	4	0	0	0	0	4	0.00
					0	29	0	23	23	0.00	52	0.00
					0	53	0	23	23	0.00	76	0.00
					0	153	0	23	23	0	176	0.00
					0	2	0	1	1	0	2	0.00
					0	0	0	0	0	0	0	0.00
					0	43	0	63	63	0.00	106	0.00
					0	4	0	3	3	0	7	0.00
					0	3	0	3	3	0	6	0.00
					0	56	0	4	4	0	60	0.00
					0	10	0	0	0	0	10	0.00
					0	0	0	1	1	0	1	0.00

Country	State/Province	Locality	Age	Formation	taxa	Number of appendages drilled (at least one part of appendage preserved)	Number of appendages drilled (at least one part of appendage preserved)	Percentage drilled appendage (preserved)	Number of carapaces drilled (at least one carapace preserved)	Number of carapaces drilled (at least one carapace preserved)	Percentage drilled carapaces (at least one carapace preserved)	Total number	Percentage per formation
					<i>Eucrate crenata</i>	0	62	0	0	0	0	12	0.00
					<i>Arges parallelus</i>	0	16	0	0	0	0	121	0.00
					<i>Macrophthalmus latreillei</i>	0	22	0	0	0	0	145	0.00
					unidentified	0	358	0	0	0	0	358	0.00
					Total	0	736	0	0	0	0	377	0.00
Japan	Kumamoto	Ogushi, Amakusa City	Middle Pleistocene (MIS7)	Ogushi Formation	Alpheidae	0	98	0	0	0	0	0	98
					<i>Paradorippe cf. P. granulata</i>	1	1	100	0	0	0	1	100.00
					<i>Hiplyra platycheir</i>	0	0	0	1	1	100	1	100.00
					<i>Calappa</i> sp.	0	5	0	0	0	0	0	5
					Parthenopidae	0	1	0	0	0	0	0	1
					<i>Charybdis</i> sp.	0	2	0	0	0	0	2	0.00
					<i>Scylla</i> sp.	0	2	0	0	0	0	2	0.00
					Xanthidae	0	1	0	0	0	0	1	0.00
					<i>Eucrate</i> sp.	0	4	0	0	0	0	3	0.00
					<i>Macrophthalmus leptophthalmus</i>	0	0	0	0	0	0	6	0.00
					unidentified	0	8	0	0	0	0	20	0.00
					Total	1	122	0.82	1	30	3.33	152	1.32
USA	Florida		Late Eocene	Ocala Limestone	<i>Callinassa inglisestrus</i>	0	30	0	0	0	0	30	0.00
					<i>Lopharina</i> sp.	0	2	0	0	0	0	16	0.00
					<i>Calappa robertsi</i>	0	10	0	0	0	0	10	0.00
					<i>Calappia brooksi</i>	0	4	0	0	0	0	22	0.00
					<i>Montezumella microporosa</i>	0	0	0	0	0	0	3	0.00
					<i>Acalina floridana</i>	0	48	0	0	0	0	53	0.00
					<i>Palaeocarpiulus brodkorbi</i>	0	0	0	0	0	0	17	0.00
					unidentified	0	133	0	0	0	0	156	0.00
					Total	0	227	0	0	0	0	134	0.00
USA	Florida		Early Miocene	Parachucla Formation	<i>Neocallichirus matsoni</i>	0	404	0	0	0	0	404	0.00
					Portunidae	0	8	0	0	0	0	8	0.00
					unidentified	0	31	0	0	0	0	31	0.00
					Total	0	443	0	0	0	0	443	0.00
USA	Florida		Early Miocene	Chipola Formation	<i>Callinassa</i> sp.	0	156	0	0	0	0	156	0.00
					<i>Petrochirus inequalis</i>	0	1	0	0	0	0	1	0.00
					<i>Calappa flammea</i>	0	43	0	0	0	0	44	0.00
					<i>Callinectes</i> sp.	0	1	0	0	0	0	1	0.00
					<i>Portunus sayi</i>	0	2	0	0	0	0	2	0.00
					<i>Menippe nodifrons</i>	0	3	0	0	0	0	3	0.00
					<i>Parthenope</i> sp.	0	7	0	0	0	0	7	0.00
					<i>Hepatus</i> sp.	0	1	0	0	0	0	1	0.00
					<i>Eurytium limosum</i>	0	1	0	0	0	0	1	0.00
					Portunidae	0	58	0	0	0	0	3	0.00
					unidentified	0	545	0	0	0	0	550	0.00
					Total	0	818	0	0	0	0	827	0.00
USA	Florida		Early Miocene	Torreya Formation	<i>Neocallichirus matsoni</i>	0	57	0	0	0	0	57	0.00
					unidentified	0	13	0	0	0	0	13	0.00
					Total	0	70	0	0	0	0	70	0.00
USA	Florida		Middle Miocene	Coosawhatchie Formation	<i>Callinassa cf. C. floridana</i>	0	750	0	0	0	0	750	0.00
					unidentified	0	4	0	0	0	0	4	0.00
					Total	0	754	0	0	0	0	754	0.00
USA	Florida		Middle Miocene	Shoal River Formation	<i>Calappa</i> spp.	0	20	0	0	0	0	20	0.00
					unidentified	0	6	0	0	0	0	6	0.00
					Total	0	26	0	0	0	0	26	0.00
USA	Florida		Late Pliocene	Tamiami Formation	<i>Petrolisthes myaklensis</i>	0	20	0	0	0	0	21	0.00
					<i>Libinia</i> sp.	0	10	0	0	0	0	10	0.00
					<i>Persephona</i> sp.	0	49	0	0	0	0	49	0.00
					<i>Calappa</i> sp.	0	17	0	0	0	0	17	0.00
					<i>Menippe</i> sp.	0	15	0	0	0	0	16	0.00
					<i>Petrochirus</i> sp.	0	14	0	0	0	0	14	0.00
					Portunidae	0	4	0	0	0	0	5	0.00
					unidentified	0	400	0	0	0	0	401	0.00
					Total	0	529	0	0	0	4	533	0.00
USA	Florida		Early Pliocene	Intraoceanic Formation	<i>Ranilla</i> sp.	0	3	0	0	0	0	921	0.00
					<i>Calappa</i> sp.	0	1	0	0	0	0	1	0.00
					<i>Platylambrus</i> sp.	1	2	0	0	0	0	2	50.00

Country	State/Province	Locality	Age	Formation	taxa	Number of appendages drilled (at least one part of appendage preserved)	Number of appendages drilled (at least one part of appendage preserved)	Percentage drilled appendage (preserved)	Number of carapaces drilled (at least one part of carapace preserved)	Number of carapaces drilled (at least one part of carapace preserved)	Percentage drilled carapace (preserved)	Total number	Percentage per formation
					taxa	0	0	0	0	0	0	0	0.00
					unidentified	0	5	0	0	0	0	5	0.00
					Total	1	11	0	0	0	0	932	0.11
USA	Florida		Pliocene	Jackson Bluff Formation	<i>Petrochirus bouvieri</i>	0	0	0	0	0	0	0	0.00
					<i>Galappa</i> sp.	0	5	0	0	0	0	5	0.00
					<i>Menippe floridana</i>	0	1	0	0	0	0	1	0.00
					unidentified	0	59	0	0	0	0	71	0.00
					Total	0	70	0	0	0	0	82	0.00
USA	Florida		Early Pleistocene	Caloosahatchee Formation	<i>Callichirus major</i>	0	0	0	0	0	0	60	0.00
					<i>Callichirus islagrande</i>	0	2	0	0	0	0	2	0.00
					<i>Neatrypaea</i> sp.	0	16	0	0	0	0	16	0.00
					<i>Sergia trilobatus</i>	0	48	0	0	0	0	48	0.00
					<i>Petrochirus</i> sp.	0	20	0	0	0	0	20	0.00
					<i>Persephona</i> sp.	0	712	0	0	0	0	719	0.00
					<i>Libinia</i> sp.	0	20	0	0	0	0	38	0.00
					<i>Platylambrus charlottensis</i>	0	4	0	0	0	0	4	0.00
					<i>Ovalipes stephensoni</i>	0	60	0	0	0	0	60	0.00
					<i>Portunus</i> spp.	0	92	0	0	0	0	92	0.00
					<i>Menippe</i> sp.	0	28	0	0	0	0	30	0.00
					unidentified	0	1166	0	0	0	0	1173	0.00
					Total	0	2228	0	0	0	0	2262	0.00
USA	Florida		Early Pleistocene	Nashua Formation	<i>Galappa</i> sp.	0	1	0	0	0	0	1	0.00
					<i>Persephona</i> sp.	0	10	0	0	0	0	10	0.00
					unidentified	0	25	0	0	0	0	25	0.00
					Total	0	36	0	0	0	0	36	0.00
USA	Florida		Middle Pleistocene	Bermont Formation	<i>Callichirus islagrande</i>	1	1252	0	0	0	0	5	0.08
					<i>Neocallichirus</i> sp.	0	8	0	0	0	0	8	0.00
					<i>Neatrypaea</i> sp.	0	230	0	0	0	0	230	0.00
					<i>Sergia trilobatus</i>	0	1229	0	0	0	0	1229	0.00
					<i>Gtenacheles</i> sp.	0	4	0	0	0	0	4	0.00
					<i>Upogebia affinis</i>	0	5	0	0	0	0	5	0.00
					<i>Petrochirus diagenes</i>	0	14	0	0	0	0	14	0.00
					<i>Galappa</i> sp.	0	24	0	0	0	0	24	0.00
					<i>Hepatus</i> sp.	0	2	0	0	0	0	2	0.00
					<i>Persephona</i> sp.	0	859	0	0	0	0	869	0.00
					<i>Libinia</i> sp.	0	57	0	0	0	0	21	0.00
					<i>Ovalipes</i> sp.	0	351	0	0	0	0	351	0.00
					<i>Portunus depressifrons</i>	0	7	0	0	0	0	7	0.00
					<i>Portunus gibbesii</i>	0	161	0	0	0	0	161	0.00
					<i>Portunus spinimanus</i>	0	3	0	0	0	0	3	0.00
					<i>Pilumnus</i> sp.	0	3	0	0	0	0	3	0.00
					<i>Pinixa</i> sp.	0	10	0	0	0	0	10	0.00
					<i>Uca</i> sp.	0	8	0	0	0	0	8	0.00
					unidentified	0	12151	0	0	0	0	12158	0.00
					Total	1	16383	0	0	0	0	16421	0.01
USA	Florida		Late Pleistocene	Fort Thompson Formation	<i>Menippe mercenaria</i>	0	27	0	0	0	0	53	0.00
					<i>Persephona</i> sp.	0	4	0	0	0	0	1	0.00
					<i>Callinassa</i> sp.	0	2	0	0	0	0	2	0.00
					unidentified	0	54	0	0	0	0	54	0.00
					Total	0	87	0	0	0	0	114	0.00
Jamaica			Middle Eocene	Guys Hill Formation	Callinassidae	0	9	0	0	0	0	9	0.00
					unidentified	0	38	0	0	0	0	38	0.00
					Total	0	47	0	0	0	0	47	0.00
					<i>Callinectes sapidus</i>	0	5	0	0	0	0	5	0.00
					<i>Piltho</i> sp.	0	5	0	0	0	0	5	0.00
					<i>Calappa springeri</i>	0	15	0	0	0	0	15	0.00
					<i>Panopeus herbstii</i>	0	5	0	0	0	0	5	0.00
					<i>Eurypanopeus</i> sp.	0	2	0	0	0	0	2	0.00
					<i>Persephona punctulata</i>	0	9	0	0	0	0	10	0.00
					<i>Eurytium limosum</i>	0	2	0	0	0	0	3	0.00
					<i>Micropanope</i> spp.	0	5	0	0	0	0	5	0.00
					<i>Pilumnus</i> spp.	0	12	0	0	0	0	12	0.00
					<i>Ovalipes</i> spp.	0	2	0	0	0	0	2	0.00

Country	State/Province	Locality	Age	Formation	taxa	Number of appendages drilled (at least one part of appendage preserved)	Number of appendages drilled (at least one part of appendage preserved)	Percentage drilled appendage preserved	Number of drilled carapaces (at least one part of carapace preserved)	Number of drilled carapaces (at least one part of carapace preserved)	Percentage drilled carapace preserved	Number of drilled carapaces total (at least one part of carapace preserved)	Percentage drilled carapace preserved	Total number	Percentage per formation
					<i>Neopanope</i> sp.	0	2	0	0	0	0	0	0	2	0.00
					<i>Portunus</i> sp.	0	3	0	0	0	0	0	0	3	0.00
					<i>Hepatus</i> sp.	0	2	0	0	0	0	0	0	2	0.00
					<i>Cancer</i> sp.	0	2	0	0	0	0	0	0	2	0.00
					unidentified	0	100	0	0	0	0	1	0	101	0.00
					Total	0	171	0	0	0	0	3	0	174	0.00
Cuba			Late Pleistocene	Jaimanitas Formation	<i>Galappa</i> sp.	0	44	0	0	0	0	1	0	45	0.00
					<i>Petrochirus</i> sp.	0	7	0	0	0	0	0	0	7	0.00
					Callianassidae	0	21	0	0	0	0	0	0	21	0.00
					Panopeidae	0	11	0	0	0	0	0	0	11	0.00
					unidentified	0	55	0	0	0	0	0	0	55	0.00
					Total	0	138	0	0	0	0	1	0	139	0.00
Panama		Armador and Farfan Beaches	Late Pleistocene-Holocene	Indeterminate	Callianassidae	0	3439	0	0	0	0	0	0	3439	0.00
					<i>Hepatus</i> sp.	0	0	0	0	0	0	1	0	1	0.00
					Portunidae	0	0	0	0	0	0	1	0	1	0.00
					Total	0	3439	0	0	0	0	2	0	3441	0.00
Grand Total						9	31815	0.03	2	1778	0.11	33593	0.03		