TREATISE ONLINE
Number 193

Part R Revised, Volume 1, Structure and Taphonomy of Decapod Cuticle in the Fossil Record

Rodney M. Feldmann, David A. Waugh,
Roy E. Plotnick, and Carrie E. Schweitzer

2026

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
https://journals.ku.edu/treatiseonline

PART R, REVISED, VOLUME 1, TREATISE ONLINE 193:

STRUCTURE AND TAPHONOMY OF DECAPOD CUTICLE IN THE FOSSIL RECORD

Rodney M. Feldmann[1], David A. Waugh[2], Roy E. Plotnick[3]
and Carrie E. Schweitzer[4]

[[1]Department of Earth Sciences, Kent State University, deceased; [2]Department of Anatomy and Neurobiology, Northeast Ohio Medical University, dwaugh@neomed.edu; [3]Department of Earth and Environmental Sciences, University of Illinois Chicago, plotnick@uic.edu; [4]Department of Earth Sciences, Kent State University, cschweit@kent.edu]

The preservation of fossil decapod crustaceans depends in large part on the composition and structure of the cuticle, the noncellular tissue comprising the exoskeleton that is molted during growth. The cuticle comprises not only the external integument of the body and appendages but the linings of the esophagus, foregut, and hindgut (Watling, 2013); the gills and gill chambers (Olesen, 2013); a variety of cuticular outgrowths, such as setae and ornamentation (Garm & Watling, 2013; Waugh, 2013); and internal folds and processes (apodemes) for muscle attachment (McLaughlin, 1980). The physical and chemical properties of the cuticle vary with location, function, and stage within the molt cycle. These variations have a direct impact on the taphonomy of decapods.

COMPOSITION AND STRUCTURE

The decapod cuticle, especially that of brachyurans, is the most intensively studied among the crustaceans. As in other arthropods (Neville, 1975), the decapod cuticle is a noncellular, multilayered, hierarchically organized, variously thick layer secreted by an underlying epithelial layer of cells, the hypodermis (Roer & Dillaman, 1984; Dillaman & others, 2013), which together comprise the integument (Dalingwater & Mutvei, 1990). The structure of cuticle in extant decapods has been detailed as a layered structure comprised of, from exterior to interior, the epicuticle, exocuticle, endocuticle, and membranous layer (Roer & Dillaman, 1984; Dillaman & others, 2013) (Fig. 1). The epicuticle forms the outermost layer and is an extremely thin layer with a waxy surface, a weakly calcified layered region, and an amorphous lower zone at the interface with the exocuticle. The exocuticle is a layered structure formed by a chitinous network serving as a template for precipitation of calcium salts, primarily calcium carbonate. The endocuticle is the lowermost calcified layer within the cuticle. It is distinguished from the exocuticle by possessing thicker

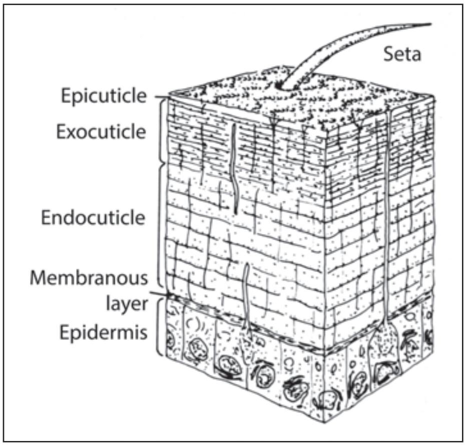


Fig.1. Generalized intermolt decapod cuticle. Adapted from Hadley (1986) and Feldmann & Tshudy (1987).

Treatise Online is a publication of The University of Kansas, Paleontological Institute,

Cite: Feldmann, R. M., D. A. Waugh, R. E. Plotnick, & C. E. Schweitzer. 2026. Part R, Revised, Volume 1, Structure and taphonomy of decapod cuticle in the fossil record. Treatise Online 193:1–18, 21 fig. [https://doi.org/10.17161/to.vi.25000].

layers. The lowermost cuticular layer, the membranous layer, is not mineralized. In fossil forms, only the endocuticle and exocuticle are commonly preserved.

The fundamental units of the cuticle are minute fibers (fibrils) comprised of organic chitin, a polymer composed of poly-*N*-acetylglucosamine, a polysaccharide related to cellulose. These fibrils are wrapped in protein to form nanofibrils that in turn are clustered into long fibers, which can aggregate into sheets where the long axes of the fibers are parallel (Raabe & others 2005; Dillaman & others, 2013). The layers within the exocuticle and endocuticle are made by the stacks of these chitin-protein sheets in much the same arrangement as that of plywood, each of which is rotated relative to the adjacent layers (Dillaman & others, 2013), with a slight rotation between each sheet ("twisted plywood" or Bouligand pattern) (Bouligand, 1972). The spacing between consecutive sheets oriented at 180° to each other produces the observed layering (lamellae) in the cuticle. Internal arches within cut lamellae reflect the rotation of the stacks. The layering varies in thickness and is typically composed of thick layers in the endocuticle and thinner layers in the exocuticle in lobsters, mud shrimp, and crabs, but thinner layers in endocuticle and thicker layers in the exocuticle in shrimp (Fig. 2). This pattern of layering may be well preserved in fossil forms and has been described in detail by Feldmann & Gaździcki (1998).

Although earlier studies identified the biomineralogic component of the decapod cuticle as calcite (Dudich, 1931), more recent work has identified amorphous calcium carbonate as a major constituent (Dillaman & others, 2013; Mergelsberg & others, 2019). Crystalline calcite can vary between low and high magnesium calcite, depending on taxon and body region (Fay & Smith, 2021; Plotnick & McCarroll, 2023). In addition to calcium and magnesium, there can also be appreciable amounts of phosphorus (Vrazo & others, 2018), which has also been documented in branchiopods (Hegna, Czaja, & Rogers, 2020) and stomatopods (Plotnick & McCarroll, 2023).

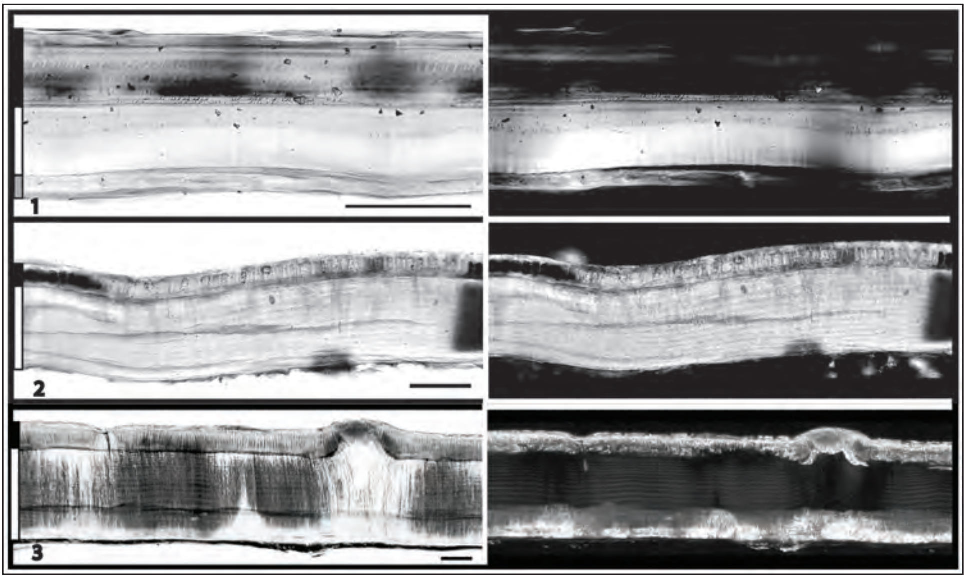


Fig. 2. Thin sections of decapod cuticle from the branchial region; *1*, *Penaeus* sp. (Dendrobranchiata); *2*, *Grimothea quadrispina* (Benedict, 1902) (Anomura); *3*, *Callinectes sapidus* Rathbun, 1896 (Eubrachyura). Bars at far left indicate exocuticle (black), endocuticle (white), and membranous layer (grey). Left column in plain polarized light and right column is cross-polarized light. Adapted from Amato & others (2008, figs.1A, B; 2E).

The degree of mineralization varies in different regions of the cuticle so that the arthrodial membranes and chitinous internal structures tend to be uncalcified. Likewise, the degree of calcification of cuticular layers may vary within different taxa. In shrimp, the cuticle may be completely uncalcified and is generally less well calcified than cuticle of crabs or lobsters (Amato & others, 2008). Uncalcified cuticles, being primarily organic, should decay readily. In the case of arthrodial membranes, decay leads to disarticulation of the sclerites (Briggs & Kear, 1994).

As is characteristic of arthropods in general, the carapace is periodically shed in order to facilitate growth. The process in decapods involves continuous change in the cuticle from fully formed and calcified to the period of molting when calcium salts have been removed, the carapace is reduced in thickness, and the carapace is shed concomitant with formation of the new cuticle. The sequence of events involves reduction of the epicuticle and endocuticle in premolt phases and eventual loss of the cuticle (Roer & Dillaman, 1984; Dillaman & others, 2013). Formation of the new cuticle proceeds from development of the epicuticle and exocuticle at the end of the intermolt stage (apolysis) as the old cuticle is eventually lost. Subsequent development of the endocuticle and hardening of the carapace occurs by addition of calcium salts in the exocuticle and endocuticle. The preservation potential of the cuticle should thus vary during the molt cycle.

Waugh (2013) noted that several styles of nodes, pits, and other structures are expressed on the surface of the cuticle of fossils and are defined by internal structures arising in the endocuticle or exocuticle that may or may not penetrate from one layer to another (Fig. 3). Decapod cuticle surfaces have been characterized based upon size of structure, depth of depression, and presence of perforations (Table 1; Fig. 4, 5). Thus, different expressions of the surface of the endocuticle and exocuticle may be preserved in fossil cuticle (Fig. 4, 5). The different styles of exposure of the fossils may reveal different cuticular surfaces which, in turn, may exhibit different morphologies. The three surfaces most frequently defining exposed fossil decapods are the mold of the interior of the cuticle representing the inner form of the lower surface of the endocuticle, the upper surface of the endocuticle, and the upper surface of the exocuticle. These different surfaces may reveal very different fine detail of pits, nodes, bumps, and ridges (Fig. 6). Thus, it is essential that the identification of the cuticular surface upon which the morphology is described is clearly noted. Because surface ornamentation often is considered to be of systematic significance, differences in morphology may be interpreted as defining different species even though they are simply differences in structure manifested on different cuticle layers. The surface of the endocuticle is frequently considered to be the surface of the specimen because the interface between

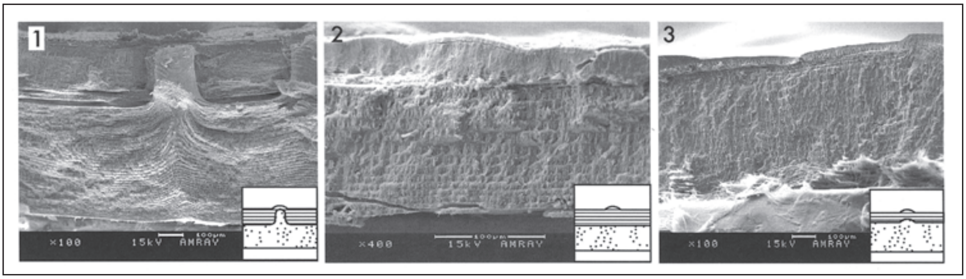


Fig. 3. Scanning electron micrographs of extant decapod cuticle, with interpretive drawing at lower right; *1*, node in endocuticle (center) extending into exo- and epicuticle; *2*, epicuticle and endocuticle only; *3*, all three cuticular layers. Dotted layer in drawing = endocuticle, horizontally lined layer = exocuticle, plain layer = epicuticle. Adapted from Waugh & Feldmann (2003, fig. 1).

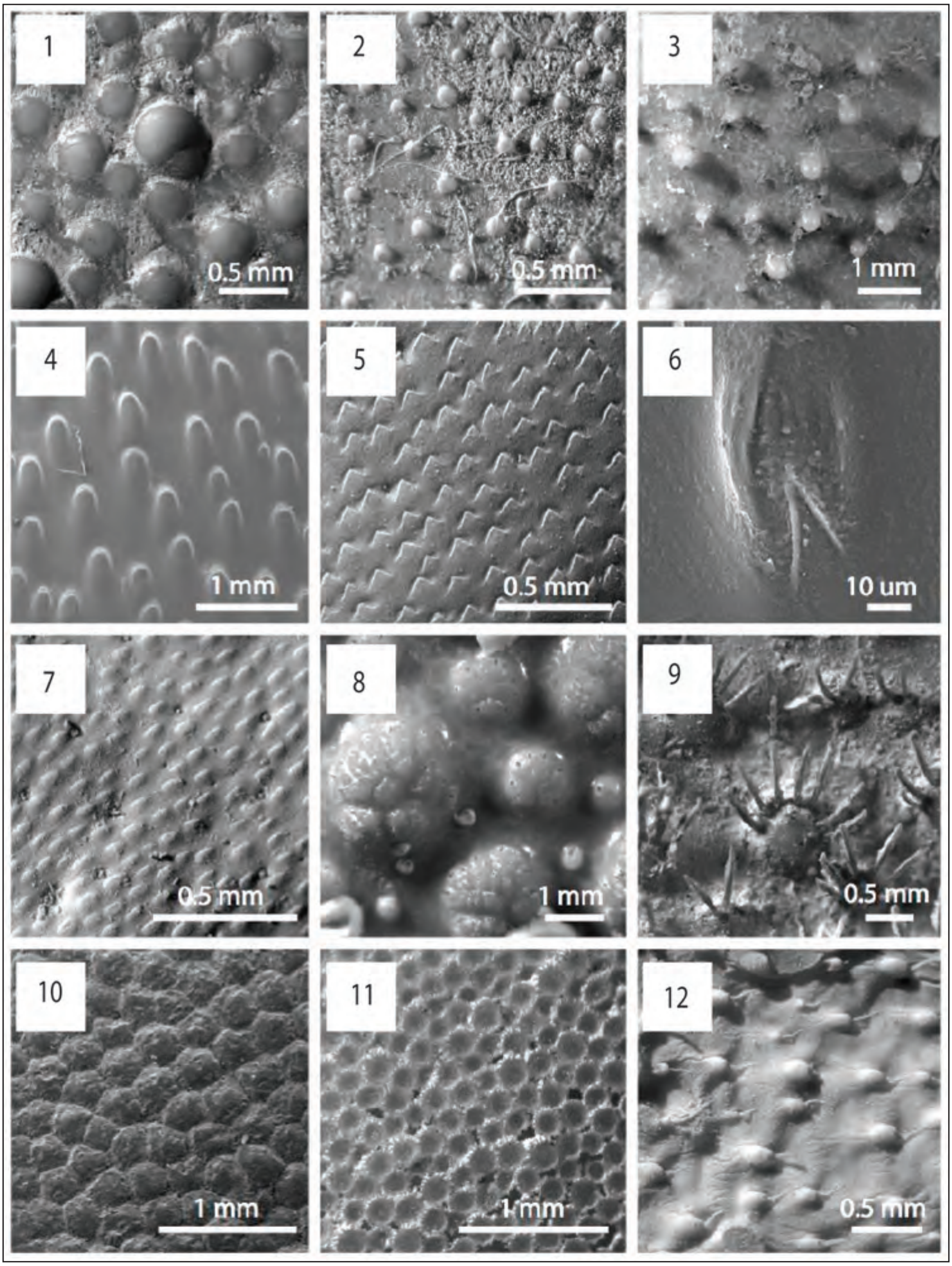


FIG. 4. SEM photomicrographs of surface cuticular features; see text for definitions of structures, all taxa extant unless otherwise indicated; *1*, low nodes, *Cancer borealis* STIMPSON, 1859 (Eubrachyura); *2*, low isolated nodes, *Dorippoides facchino* (HERBST, 1785) (Eubrachyura); *3*, high nodes, *Arcania elongata* YOKOYA, 1933 (Eubrachyura); *4*, inclined nodes, *Umalia misakiensis* (SAKAI, 1937) (Raninoida); *5*, inclined node in a depression, *Notosceles ecuadorensis* (RATHBUN, 1935) (Raninoida); *6*, inclined node in pit, *Raninoides louisianensis* RATHBUN, 1933 (Raninoida); *7*, arcs, *Xantho hydrophilus* (HERBST, 1790) (Eubrachyura); *8*, warts, *Paralomis granulosa* (HOMBRON & JACQUINOT, 1846) (Anomura); *9*, turrets, *Panulirus argus* (LATREILLE, 1804) (Achelata); *10*, fungiform hexagonal, *Eucorystes carteri* (M'COY, 1854) (Raninoida, Cretaceous); *11*, fungiform rounded, *Symethis variolosa* (FABRICIUS, 1787) (Raninoida); *12*, setal nodes, *Astacus astacus* (LINNAEUS, 1758) (Astacida). Adapted from WAUGH (2013, p. 117, fig. 2).

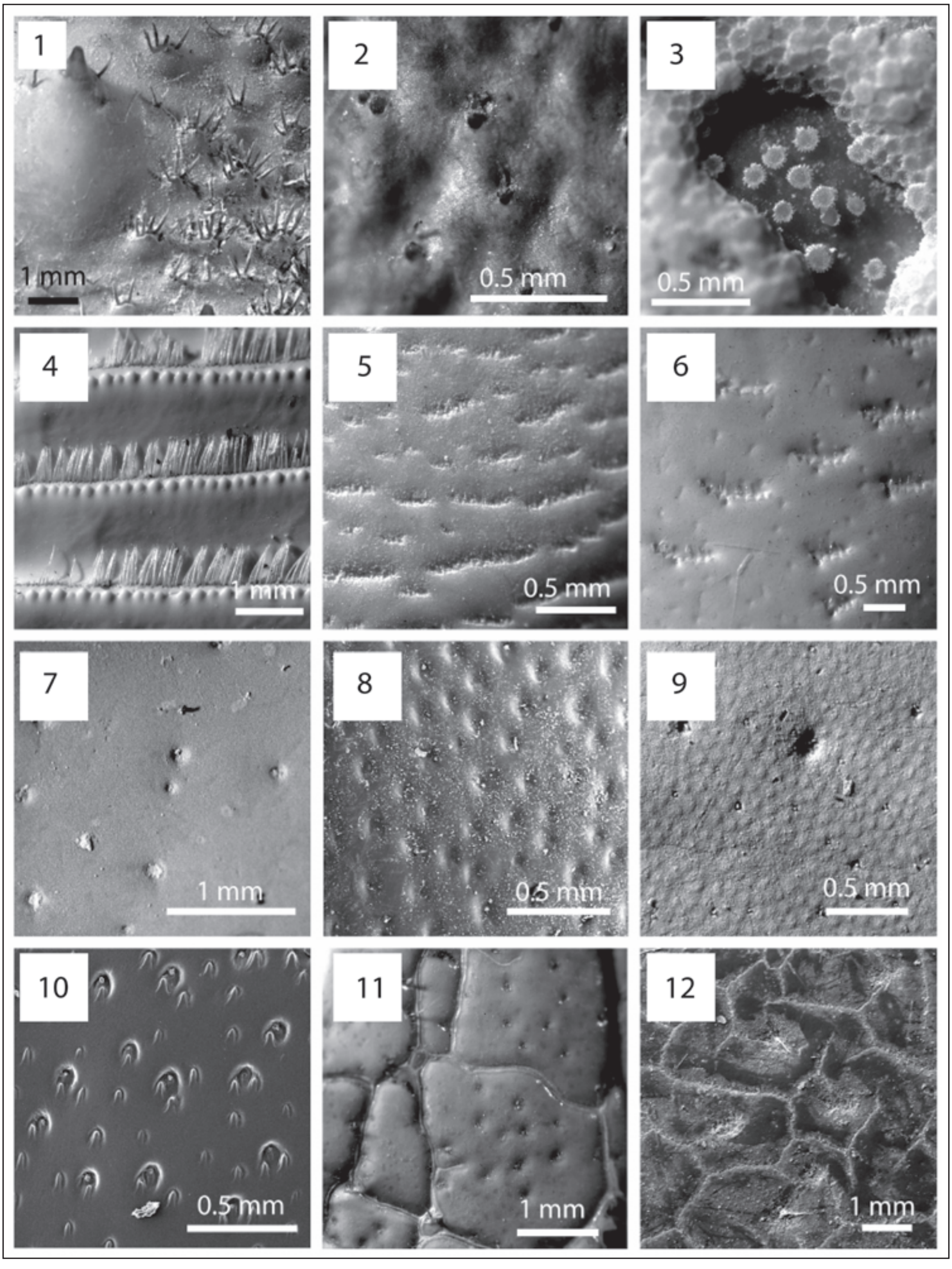


Fig. 5. Surface cuticular features; see text for definitions of structures; all taxa extant unless otherwise indicated; *1*, amber-tipped feature on node just to the right of white box, *Panulirus argus* (Latreille, 1804) (Achelata); *2*, amber-tipped features, *Aegla platensis* Schmitt, 1942 (Anomura); *3*, dissected surface, *Symethis variolosa* (Fabricius, 1787) (Raninoida); *4*, continuous ridges, *Grimothea johni* (Porter, 1903) (Anomura); *5*, broken ridges, *Petrolisthes eriomerus* Stimpson, 1871 (Anomura); *6*, isolated ridges, *Lepidopa deamae* Benedict, 1903 (Anomura); *7*, perforations, *Antrimpos undenarius* Schweigert, 2001 (Dendrobranchiata, Jurassic); *8*, pits, *Lyreidus tridentatus* De Haan, 1841 (Raninoida); *9*, multistage pits, *Atergatis floridus* (Linnaeus, 1767) (Eubrachyura); *10*, pits with nodes and perforations, *Raninoides bouvieri* Capart, 1951 (Raninoida); *11*, islands, *Coenobita brevimanus* Dana, 1852 (Anomura); *12*, polygons/cracks, *Hemigrapsus nudus* (Dana, 1851) (Eubrachyura). Adapted from Waugh (2013, p. 121, fig. 3).

Table 1. Surface features of decapod cuticle.*

Cuticle Feature	Description
Low nodes	Low, broad elevations that are wider than high; may be circular or ovate (Fig. 4.1)
Low, isolated nodes	Similar to low nodes but more broadly spaced and smaller in diameter (Fig. 4.2)
High nodes	Elevations that are higher than wide; may be asymmetrical; lack hair or perforation (Fig. 4.3)
Inclined nodes	Node erupted at low angle to cuticle so its base is not fully defined around its circumference; usually directed anteriorly; may be nearly parallel to cuticular surface or directed upward (Fig. 4.4–4.6); may be adjacent to a depression (Fig. 4.5) or within a circular pit (Fig. 4.6)
Arcs	Small arcuate projections of the cuticular surface, usually asymmetrical in cross-section (Fig. 4.7)
Warts	Elevations on the cuticular surface with a verrucose surface, with setal hairs or perforations around the base (Fig. 4.8)
Turrets	Arcuate elevations with an array of anteriorly directed perforations or setal hairs along the anterior surface; larger and more equant than arcs (Fig. 4.9)
Fungiform hexagonal	Nodes in which the base is narrower than the top, resembling a mushroom; each node in contact with neighboring nodes (Fig. 4.10)
Fungiform circular	Nodes in which the base is narrower than the top, resembling a mushroom; adjacent node tops not touching one another (Fig. 4.11)
Setal nodes	Nodes with a hair or perforation at its tip; node usually inclined anteriorly (Fig. 4.12)
Amber-tipped features	Small, amber-colored regions of variable shape, ranging from barely elevated to termination of larger nodes (Fig. 5.1, 5.2)
Dissected surface	Surface with depressed regions of large size and irregular shape (Fig. 5.3)
Ridges	Ridges of cuticle that may be continuous across the surface, broken into discrete segments that remain laterally adjacent, or found in isolated clusters (Figs. 5.4–5.6)
Perforations	Small holes penetrating the upper surface of the cuticle; almost always associated with a setal hair except in fossils where not preserved (Fig. 5.7)
Pits	Ovate or circular depressions of the surface, without a perforation (Fig. 5.8)
Multistage pits	Pits as above in the case where the pits exist in multiple discrete size classes; it is hypothesized that these result from conservation and enlargement of existing pits during subsequent molting; all contain a central perforation (Fig. 5.9)
Pits with nodes	Pits with a node emanating from the posterior margin (Fig. 5.10)
Pits with nodes and perforations	Like pits with nodes but with a perforation within the pit (Fig. 5.10)
Islands	Regions of cuticle delimited by reticulate network of linear depressions; differentiated from polygons/cracks in larger size and more irregular pattern (Fig 5.11)
Polygons/Cracks	Cuticular surface with narrow grooves or cracks forming a reticulate pattern (Fig. 5.12)

*** Adapted from WAUGH (2013).**

TAPHONOMY

Cuticle preserved in the fossil record thus can be subjected to both chemical and physical alteration. Because different parts of the cuticle can be variously calcified, entire parts of the external anatomy can be lost either by separation of regions as membranous connective tissue weakens or as loss of entire regions of the exoskeleton that are less calcified. These observations have been tested by experimental taphonomic studies (Schäfer, 1972; Plotnick, 1986; Plotnick, Baumiller, & Wetmore, 1988; Briggs & Kear, 1994; Mutel & others, 2008). Mutel & others (2008) reported the effects of placement of *Callinectes sapidus* Rathbun, 1896, in an array of depth, water chemistry, and submersion time in sites in the Gulf of Mexico and the Bahamas (Parsons & others, 1997; Parsons-Hubbard & others, 1999). Although rates and amount of fragmentation varied at different sites, the degree of calcification as an indicator of preservational potential of regions was clearly evident (Fig. 18). Movable fingertips, mandibles, and anterolateral spines were preferentially present after 8 years of submersion. The V-notch in the finger indicates the presence of less well-calcified cuticle in that part of the finger (Fig. 18).

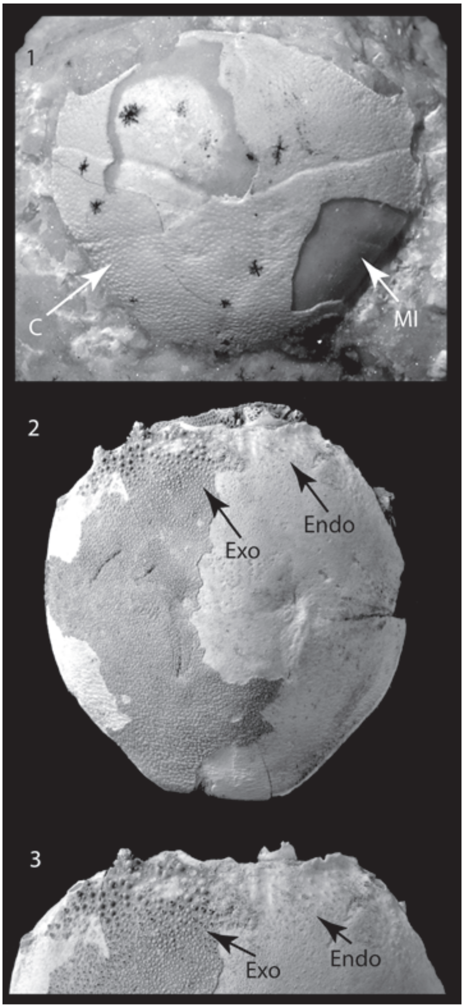


Fig. 6. Differential appearance depending on presence of cuticle; *1*, *Cycloprosopon stenofrons* Schweitzer & Feldmann, 2010, NHMW 2007z0149/0049, C = cuticle, MI = mold of the interior of the cuticle; *2–3*, *Antonioranina fusseli* (Blow & Manning, 1996), CM 18558, dorsal carapace (*2*) and close-up of frontal region (*3*). Exo = exocuticular surface, Endo = endocuticular surface.

Chemical components within the cuticle of fossil decapods have received little attention (Vrazo & others, 2018; Plotnick & McCarroll, 2023) (Fig. 19). Plotnick & McCarroll (2023) found that apatite apparently wholly replaced calcite in some fossil crabs, whereas Vrazo & others (2018) found evidence of both minerals in crabs from the Upper Cretaceous Coon Creek Lagerstätte.

Although some decapod exoskeletons are preserved in their entirety, others become separated into regional units. As a general rule, regions can be ranked in descending order of preservational potential from chelipeds, cephalothorax, pleon and telson, pereiopods, and cephalic appendages. Because of this differential probability of preservational potential, coupled with separation of skeletal elements, taxonomic identity may be based on different regions, which makes precise relationships among and between taxa difficult or impossible. As a result, many species are based on isolated cephalothoraxes or chelipeds.

As a result of differential calcification of the exoskeleton, it is far more likely to find decapods preserved only as chelipeds than as entire bodies (Mutel & others,

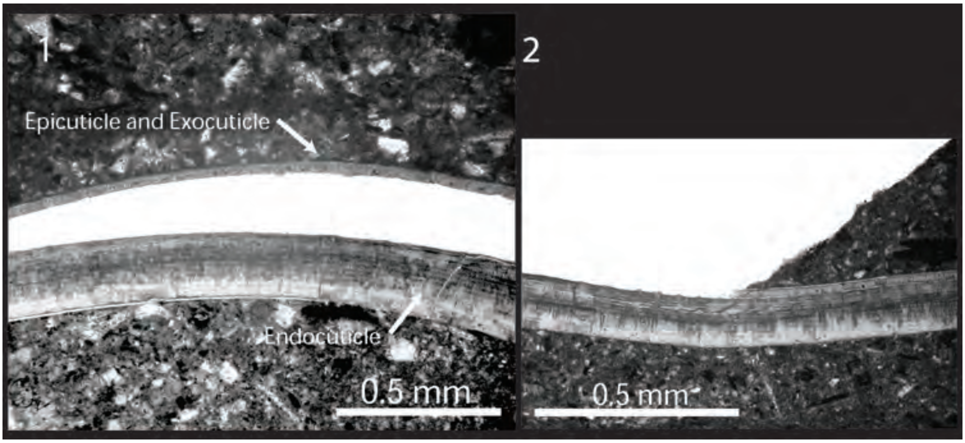


FIG. 7. *1*, Part (bottom) and counterpart (top) of cuticle of *Orbitoplax tuckerae* SCHWEITZER, 2000, showing separation of exocuticle and endocuticle upon splitting crab-bearing concretion open; *2*, same specimen, showing loss of epi- and exocuticle in which counterpart has been removed. Adapted from WAUGH & others (2004, fig. 4).

FIG. 8. *Chasmocarcinus seymourensis* FELDMANN & ZINSMEISTER, 1984, USNM 365455, preserved in concretion. Scale bar = 1 cm.

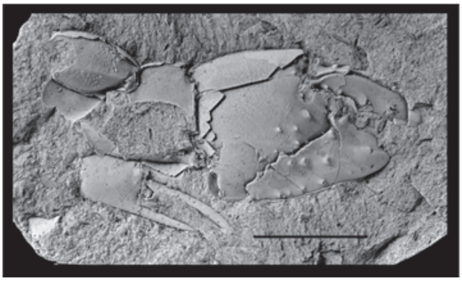


FIG. 9. Distal elements of major cheliped and chela of minor cheliped, *Callianopsis clallamensis* (WITHERS, 1924), USNM 490217. Scale bar = 1 cm.

2008). Carapaces are frequently preserved either as molted remains separated from the remainder of the exoskeleton or as well-calcified structures dissociated from a corpse after being subjected to mechanical attrition. Distinguishing between decayed corpses and molted remains is difficult in many cases. Burial of a dead organism as a corpse is interpreted when the animal is preserved more or less in its entirety, with all regions articulated in life position. Molts are often characterized by preservation of skeletal remains associated with one another in the so-called Salter's position (FIG. 20) or dissociated from one another. Because a single individual molts several times through its lifetime, it is probable, in the absence of other evidence, that most fossils represent molts. Molted remains may also be recognized by examination of the cuticle structure. Because exsolution of the cuticle during the molt cycle results in differential loss of the endocuticle, molted remains may be anticipated to have thinner and more flexible cuticle.

Predation on decapod remains may result in loss of some body parts differentially. Extant lobsters, for example, are subject to a host of predators that are not present in their nonmarine counterparts. Cephalopods have been demonstrated to prey on lobsters by differentially attacking the telson and pleon regions, possibly to avoid the chelipeds and to gain access to the fleshier parts of the animal (TSHUDY, FELDMANN, & WARD, 1989). This approach may result in dissociation of the pleon from the cephalothorax. This attack has been demonstrated experimentally (FIG. 21).

Figures 10 –21 appear after the end of the References section.

ABBREVIATIONS

BSPG:	Bayerische Staatsammlung für Paläontologie und Geologie München (Munich), Germany
CM:	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA
KSU D:	Decapod Comparative Collection, Department of Earth Sciences, Kent State University, Kent, Ohio, USA
NHMW:	Naturhistorisches Museum Wien (Natural History Museum of Vienna), Austria
USNM:	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

ACKNOWLEDGEMENTS

This chapter benefitted from careful reviews by Abby Smith, University of Otago, Dunedin, New Zealand; Thomas Hegna, SUNY Fredonia, New York, USA; and Günter Schweigert, Staatliches Museum für Naturkunde Stuttgart, Germany. Conversations and collaborations with Sten Jakobsen, Natural History Museum of Denmark, greatly informed this work.

REFERENCES

Amato, Crystal, R. M. Feldmann, D. A. Waugh, & C. E. Schweitzer. 2008. Density and calcification of cuticle in decapod crustaceans: a key to lifestyle? Journal of Crustacean Biology 28(4):587–595. [DOI:10.1651/08-2985.1].

Benedict, J. E. 1902. Description of a new genus and forty six new species of crustaceans of the family Galatheidae with a list of the known marine species. Proceedings of the United States National Museum 26(1311):243–334.

Benedict, J. E. 1903. Revision of the Crustacea of the genus *Lepidopa*. Proceedings of the United States National Museum 26(1337):889–895.

Bishop, G.A. 1986. Taphonomy of the North American decapods. Journal of Crustacean Biology 6(3):326–355. [DOI:10.1163/193724086X00190].

Blow, W. C. & R. B. Manning, 1996. Preliminary descriptions of 25 new decapod crustaceans from the Middle Eocene of the Carolinas, U.S.A. Tulane Studies in Geology and Paleontology 29(1):1–26, pl. 1–5.

Bouligand, Y. 1972. Twisted fibrous arrangements in biological materials and cholesteric mesophases. Tissue and Cell 4(2):192–217.

Briggs, D. E. G., & A. J. Kear. 1994. Decay and mineralization of shrimps. PALAIOS 9:431–456.

Capart, André. 1951. Crustaces Decapodes Brachyures. Expédition océanographique belge dans les eaux côtières africaines de l’ Atlantique sud (1948-1949) 3(1):13–205.

Dalingwater, J. E. & Harry Mutvei. 1990. Arthropod exoskeletons. *In* J. G. Carter, ed., Skeletal Biomineralization: Patterns, Process and Evolutionary Trends. American Geophysical Union. Washington, DC. p. 83–96.

Dana, J. D. 1851. Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Faederate Duce, lexit et descripsit. Crustacea Grapsoidea, (Cyclometopa, Edwardsii). Proceedings of the Academy of Natural Science of Philadelphia 5(10):247–254.

Dana, J. D. 1852. Crustacea, Part I. United States Exploring Expedition. During the Years 1838, 1839, 1840, 1841, 1842. Under the Command of Charles Wilkes, U.S.N. 13:i–viii, 1–685.

De Haan, William. 1833–1850. Crustacea. *In* P. F. von Siebold, ed., Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suspecto, Annis 1823-1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit. Lugduni-Batavorum. Amsterdam. p. i–xxxi, ix–xvi, 1–243, pl. A–J, L–Q, 1–55.

Dell, R. K. 1969. A new Pliocene fossil crab of the genus (*Trichopeltarion*) from New Zealand. Records of the Canterbury Museum 8(4):367–371.

Dillaman, R. M., Robert Roer, Thomas Shafer, & Shannon Modla. 2013. The crustacean integument: Structure and function. *In* Les Watling & Martin Thiele, eds., The Natural History of the Crustacea: Functional Morphology and Diversity. Oxford University Press. New York. p. 140–166.

Dudich, Endre. 1931. Systematische und biologische untersuchungen über die kalkeinlagerungen des crustaceenpanzers in polarisiertem lichte. Zoologica 80:1–154.

Fabricius, J. C. 1787. Mantissa Insectorum Sistens Eorum Species Nuper Detectas Adjectis Characteribus Genericis Differentiis Specificis, Emendationibus, Observationibus. Tome I. Hafniae: Christ. Gottl. Proft. xvi + 348 p.

Fay, A.M. & A. M. Smith. 2021. In a pinch: skeletal carbonate mineralogy of crabs (Arthropoda: Crustacea: Decapoda). Palaeogeography, Palaeoclimatology, Palaeoecology 565:110219. [DOI:10.1016/j.palaeo.2021.110219].

Feldmann, R. M., Silvio Casadío, Luis Chirino-Galvéz & Maria Aguirre Urreta, 1995. Fossil decapod crustaceans from the Jagüel and Roca Formations (Maastrichtian-) of the Neuquén Basin, Argentina. Paleontological Society Memoir 43(S43):1–22. [DOI:10.1017/S0022336000061060].

Feldmann, R. M., Adina Franţescu, O. D. Franţescu, A. A. Klompmaker, Greg Logan, Jr., C. M. Robins, C. E. Schweitzer, & D. A. Waugh. 2012. Formation of lobster-bearing concretions in the Late Cretaceous Bearpaw Shale, Montana, United States, in a complex geochemical environment. PALAIOS 27(12):842–856. [DOI:10.2110/palo.2012.p12-035r].

Feldmann, R. M., & Andrzej Gaździcki. 1998. Cuticular ultrastructure of fossil and living homolodromiid crabs (Decapoda: Brachyura). Acta Palaeontologica Polonica 43(1):1–19.

Feldmann, R. M., & C. B. McPherson. 1980. Fossil decapod crustaceans of Canada. Geological Survey of Canada, Paper 79-16. Minister of Supply and Services Canada. Quebec. 20 p.

Feldmann, R. M., & Dale Tshudy. 1987. Ultrastructure in cuticle from *Hoploparia stokesi* (Decapoda: Nephropidae) from the Lopez de Bertodano Formation (Late Cretaceous-Paleocene) of Seymour Island, Antarctica. Journal of Paleontology 61(S28):1194–1203. [DOI:10.1017/S0022336000062077].

Feldmann, R. M., & W. J. Zinsmeister. 1984. New fossil crabs (Decapoda: Brachyura) from the La Meseta Formation (Eocene) of Antarctica: Paleogeographic and biogeographic implications. Journal of Paleontology 58(4):1046–1061.

Garm, Anders, & Les Watling. 2013. The crustacean integument: setae, setules, and other ornamentation. *In* Les Watling & Martin Thiel, eds., Functional Morphology & Diversity. Oxford University Press. Oxford, UK. p. 167–198.

Hadley, N. F. 1986. The arthropod cuticle. Scientific American 225(1):104–112. [DOI:10.1038/scientificamerican0786-104].

Hegna, T. A., A. D. Czaja, & D. C. Rogers. 2020. Raman spectroscopic analysis of the composition of the clam-shrimp carapace (Branchiopoda: Laevicaudata, Spinicaudata, Cyclestherida): A dual calcium phosphate-calcium carbonate composition. Journal of Crustacean Biology 40(6):756–760. [DOI:10.1093/jcbiol/ruaa078].

Herbst, J. F. W. 1782–1790. Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten. Erster Band. Krabben. Joh. Casper Fuessly, Zürich/Gottlieb August Lange. Berlin und Stralsund. iv + 274 p., 21 pl.

Hombron, J. B., & Honoré Jacquinot. 1842–1854. Crustacés. Atlas d'Histoire Naturelle. Zoologie. Voyage au Pôle Sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélée pendant les années 1837-1838-1839-1840. Crustacés, pl. 1–9.

Latreille, P. A. 1804. Des langoustes du Muséum national d'Histoire naturelle. Annales du Muséum national Histoire naturelle 3:388–395.

Linnaeus, Carolus von. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata, 10th ed., vol. 1. Laurentius Salvius. Holmiae. Stockholm. 824 p.

Linnaeus, Carolus von. 1767. Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 12. 1., Regnum Animale. 1 & 2. Laurentii Salvii. Holmiae. Stockholm. p. 1–532 (1766). p. 533–1327 (1767).

Luque, J., Lida Xing, D. E. G. Briggs, E. G. Clark, Alex Duque, Junbo Hui, Huijuan Mai, & R. C. McKellar. 2021. Crab in amber reveals an early colonization of nonmarine environments during the Cretaceous. Science Advances 7(43):eabj5689. [DOI:10.1126/sciadv.abj5689].

McLaughlin, P. A. 1980. Comparative morphology of Recent Crustacea. W.H. Freeman & Company. San Francisco, CA. 177 p.

M'Coy, Frederick. 1854. XI.—On some new Cretaceous Crustacea. The Annals and Magazine of Natural History; Zoology, Botany, and Geology 14:116–122, pl. 4. [DOI:10.1080/037454809494314].

Mergelsberg, S. T., R. N. Ulrich, S. H. Xiao, & P. M. Dove. 2019. Composition systematics in the exoskeleton of the American lobster, *Homarus americanus* and implications for Malacostraca. Frontiers in Earth Science 7:69. [DOI:10.3389/feart.2019.00069].

Milne-Edwards, Alphonse. 1868. Description de quelques Crustacés nouveaux provenant des Voyages de M. Alfred Grandidier a Zanzibar et a Madagascar. Nouvelles Archives du Muséum d'Histoire naturelle de Paris 4:69–92; pl. XIX–XXI.

Milne Edwards, Henri. 1834–1840. Histoire Naturelle des Crustacés, Comprenant l´Anatomie, la Physiologie et la Classification de ces Animaux. Encyclopédique Roret, Paris vol I(1834):i–xxxv + 1–468; vol. II(1837):1–532; vol. III(1840):1–638, pl. 1–42. Roret. Paris. p. 1–532. 1–32. pl. 1–42.

Münster, G. G., zu. 1839. Abbildung und Beschreibung der fossilen langschwänzigen Krebse in den Kalkschiefern von Bayern. Beiträge zur Petrefactenkunde, 2.

Mutel, M. H. E., D. A. Waugh, R. M. Feldmann, & K. M. Parsons-Hubbard. 2008. Experimental taphonomy of *Callinectes sapidus* and cuticular controls on preservation. PALAIOS 23:615–623. [DOI:10.2110/palo.2008.p08-024r].

Neville, A. C. 1975. Biology of the Arthropod Cuticle. Springer Verlag. New York.

Olesen, Jørgen. 2013. The crustacean carapace: morphology, function, development, and phylogenetic history. *In* Les Watling & Martin Thiel, eds., Functional Morphology & Diversity. Oxford University Press. Oxford, UK. p. 103–139.

Parsons, K. M., E. N. Powell, C. E. Brett, S. E. Walker, & W.R. Callender. 1997. Shelf and Slope Experimental Taphonomy Initiative (SSETI): Bahamas and Gulf of Mexico. Proceedings of the 8th International Coral Reef Symposium 2:1807–1812.

Parsons-Hubbard, K. M., W. R. Callender, E. N. Powell, C. E. Brett, S. E. Walker, & A. L. Raymond. 1999. Rates of burial and disturbance of experimentally-deployed mollusks: implications for preservation potential. PALAIOS 14(4):337–351. [DOI:10.2307/3515461].

Plotnick. R. E. 1986. Taphonomy of a modern shrimp: implications for the arthropod fossil record. PALAIOS 1(3):286–293. [DOI:10.2307/3514691].

Plotnick, R. E., & Steve McCarroll. 2023. Variation and taphonomic implications of composition in modern and fossil malacostracan cuticles (Decapoda: Malacostraca). Journal of Crustacean Biology 43(3):ruad047. [DOI:10.1093/jcbiol/ruad047].

Plotnick, R. E., Tomasz Baumiller, & K. L. Wetmore. 1988. Fossilization potential of the mud crab, *Panopeus* (Brachyura: Xanthidae) and temporal variability in crustacean taphonomy. Palaeogeography, Palaeoclimatology, Palaeoecology 63(1–3):27–43. [DOI:10.1016/0031-0182(88)90089-2].

Porter, C. E. 1903. Carcinología Chilena. Descrptíon de un nuevo galatéido. Revista Chilena de Historia Natural 7:274–277.

Raabe, Dierk, C. Sachs, & Patricia Romano. 2005. The crustacean exoskeleton as an example of a structurally and mechanically graded biological nanocomposite material. Acta Materialia, 53: 4281-4292. doi.org/10.1016/j.actamat.2005.05.027

Rathbun, M. J. 1896. The genus *Callinectes*. Proceedings of the United States National Museum, 18(1070):349–375, pl. XIII–XXVIII.

Rathbun, M. J. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America. United States National Museum Bulletin 138:i–viii, 1–155.

Rathbun, M. J. 1933. Preliminary descriptions of nine new species of Oxystomatous and allied crabs. Proceedings of the Biological Society of Washington 46:183–186.

Rathbun, M. J. 1935. Preliminary desciptions of seven new species of oxystomatous and allied crabs. Proceedings of the Biological Society of Washington 48:1–4.

Roer, Robert, & Richard Dillaman. 1984. The structure and calcification of the crustacean cuticle. American Zoologist 24(4):893–909. [DOI:10.1093/icb/24.4.893].

Sakai, Tune. 1937. Studies on the Crabs of Japan. II. Oxystomata. Science Reports of the Tokyo Bunrika Daigaku, Section B 3(Suppl. 2):67–192, pl. 10–19.

Schäfer, Wilhelm. 1972. Ecology and palaeoecology of marine environments. University of Chicago Press. Chicago. 568 p.

Schlotheim, E. F. 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt erläutert. Becker. Gotha (Thuringia). 437 p + atlas.

Schmitt, W. L. 1942. The species of *Aegla*, endemic South American fresh-water crustaceans. Proceedings of the United States National Museum 97(3132):431–524.

Schweigert, Günter. 2001. Eine neue Art der Gattung *Antrimpos* Münster (Crustacea, Decapoda, Penaeidae) aus dem Nusplinger Plattenkalk (Oberjura, Ober-Kimmeridgium, SW-Deutschland). Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie) 307:1–17.

Schweitzer, C. E. 2000. Tertiary Xanthoidea (Decapoda: Brachyura) from the Pacific Northwest of North America. Journal of Crustacean Biology 20(4):715–742. [DOI:10.1163/20021975-99990095].

Schweitzer, C. E., and R. M. Feldmann. 2000. First notice of the Chirostylidae (Decapoda) in the fossil record and new Tertiary Galatheidae (Decapoda) from the Americas. Bulletin of the Mizunami Fossil Museum 27:147–165.

Schweitzer, C. E., & R. M. Feldmann. 2010. Revision of *Cycloprosopon* and additions to *Eodromites* (Brachyura: Homolodromioidea: Goniodromitidae). Annalen des Naturhistorischen Museums in Wien, Serie A 112:169–194.

Sowerby, G. B., II. 1849. Monograph of the genus *Nautilus*. *In* G. B. Sowerby II, ed., Thesaurus Conchyliorum, or Monographs of Genera of Shells, vol. 2(9):463–465, pl. 97–98.

Stimpson, William. 1859. Notes on North American Crustacea, no. 1. Annals of the Lyceum of Natural History of New York 7(11):49–93, 1 pl.

Stimpson, William. 1871. Notes on North American Crustacea in the museum of the Smithsonian Institution. No. III. Annals of the Lyceum of Natural History of New York 10:92–163.

Tshudy, D. M., R. M. Feldmann, & P. D. Ward. 1989. Cephalopods: biasing agents in the preservation of lobsters. Journal of Paleontology 63(5):621–626. [DOI:10.1017/S002233600004124X].

Vrazo, M. B., A. F. Diefendorf, B. E. Crowley, & A. D. Czaja. 2018. Late Cretaceous marine arthropods relied on terrestrial organic matter as a food source: Geochemical evidence from the Coon Creek Lagerstätte in the Mississippi Embayment. Geobiology 16(2):160–178. [DOI:10.1111/gbi.12270].

Watling, Les. 2013. Feeding and digestive system. *In* Les Watling & Martin Thiel, eds., Functional Morphology & Diversity. Oxford University Press. Oxford, UK. p. 237–260.

Waugh, D. A. 2013. Utility of Fossil Cuticle Morphology Applied to the Taphonomy and Taxonomy of Decapod Crustaceans. Unpublished Ph.D. dissertation, Kent State University.

Waugh, D. A., & R. M. Feldmann. 2003. Cuticle microstructure as a new tool in systematic paleontology. Contributions to Zoology 72(2):191–193. [DOI:10.1163/18759866-0720203025].

Waugh, D. A., R. M. Feldmann, R. S. Crawford, S. L. Jakobsen, & K. B. Thomas. 2004. Epibiont preservational and observational bias in fossil marine decapods. Journal of Paleontology 78(5):961–972. [DOI:10.1666/0022-3360(2004)078<0961:EPAOBI>2.0.CO;2].

Whitfield, R. P. 1907. Notice of an American species of the genus *Hoploparia* McCoy from the Cretaceous of Montana. Bulletin of the American Museum of Natural History 23:459–462.

Withers, T. H. 1924. Some decapod crustaceans (*Callianassa* and *Ranina*) from the Oligocene of Washington State, U.S.A. Annals and Magazine of Natural History 14(9):121–127, pl. 4.

Yokoya, Yu. 1933. On the distribution of decapod crustaceans inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. Sôyô-Maru, during the year 1923–1930. Journal of the College of Agriculture. Tokyo Imperial University 12(1):1–226.

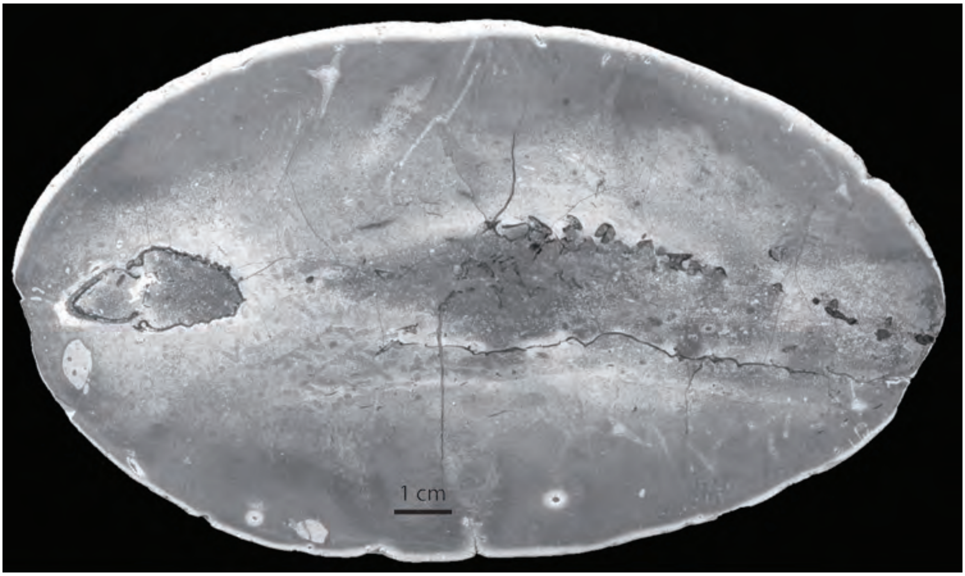


Fig. 10. Concretion containing *Palaeonephrops browni* (Whitfield, 1907), KSU D2068, with surrounding aureole. Adapted from Feldmann & others (2012, fig. 5).

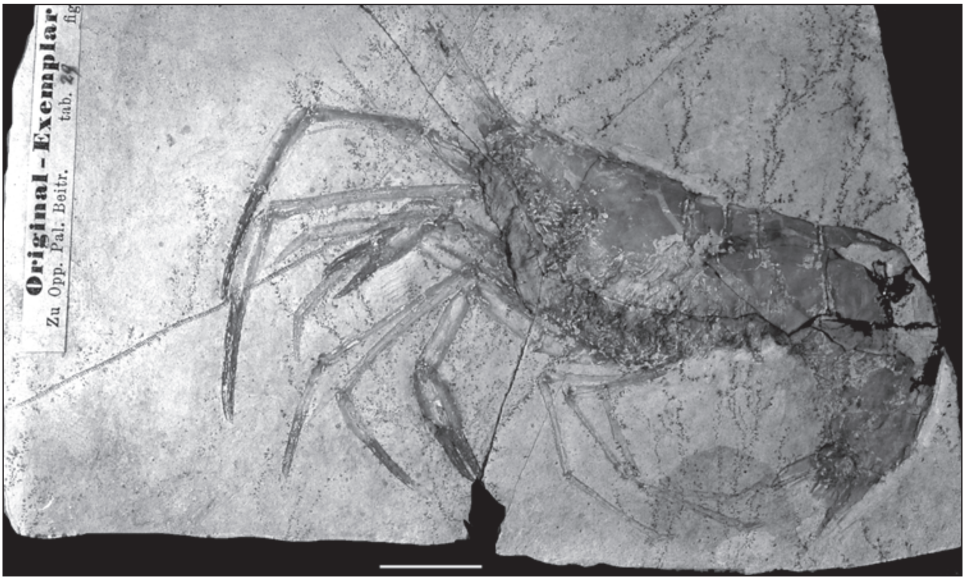


Fig. 11. Shrimp, *Bylgia spinosa* Münster, 1839, with superimposed pereiopods BSPG AS VII 713. Scale bar = 1 cm.

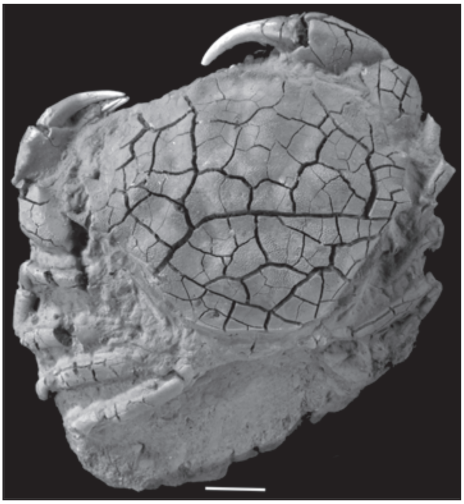


Fig. 12. *Lobulata lobulata* (Feldmann & others 1995), KSU D 3177, preserved in expandable clay, Danian, Argentina. Scale bar = 1 cm.

Fig. 13. *Austromunida casadioi* Schweitzer & Feldmann, 2000, KSU D 3179, preserved in volcanic ash, 25 de Mayo Formation, Argentina, with well-preserved sternal elements and appendages. Scale = 1 cm.

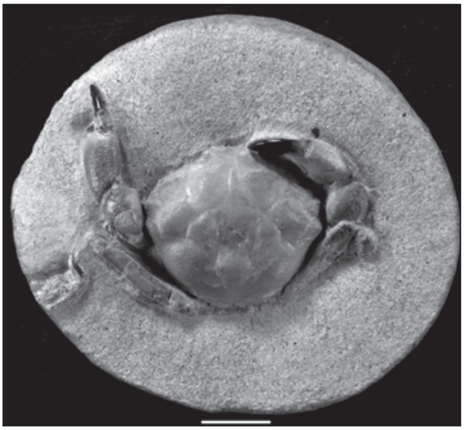


Fig. 14. *Pulalius vulgaris* (Rathbun, 1926), KSU D 3178, undegraded cuticle, Eocene, Washington, specimen donated to KSU by B. Thiel. Scale = 1 cm.

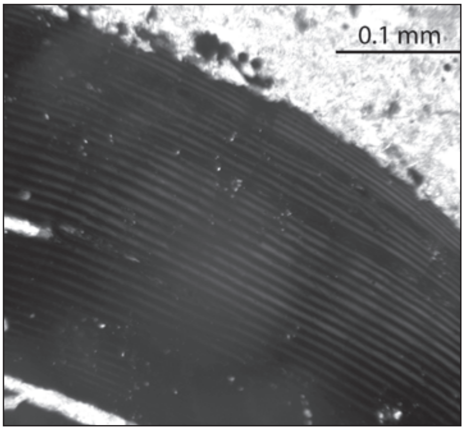


Fig. 15. Dark-colored replacement of cuticle of *Palaeonephrops browni* (Whitfield, 1907), KSU D2068 with endocuticular layers; thin-section under crossed nicols.

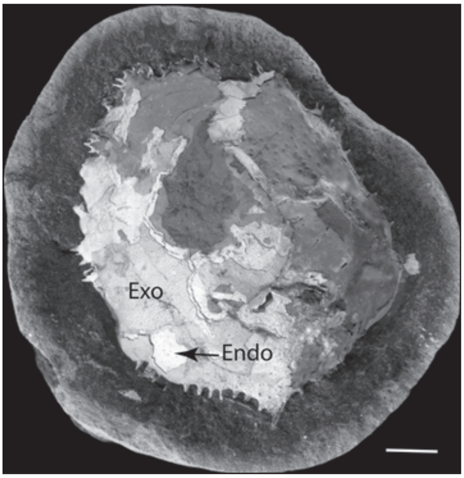


Fig. 16. Chalky endocuticle (Endo) and exocuticle (Exo) on *Trichopeltarion greggi* Dell, 1969, KSU D2106. Scale = 1 cm.

Fig. 17. Mold of interior of carapace, *Dromiopsis rugosus* (Schlotheim, 1820), KSU D801a. Scale bar = 1 cm.

Fig. 18. *Callinectes sapidus* Rathbun, 1896, remains after 8 years deployed in the Gulf of Mexico. V = V-notch in movable finger; M = mandibles; S = anterolateral spines. Adapted from Mutel & others (2008, fig. 3D).

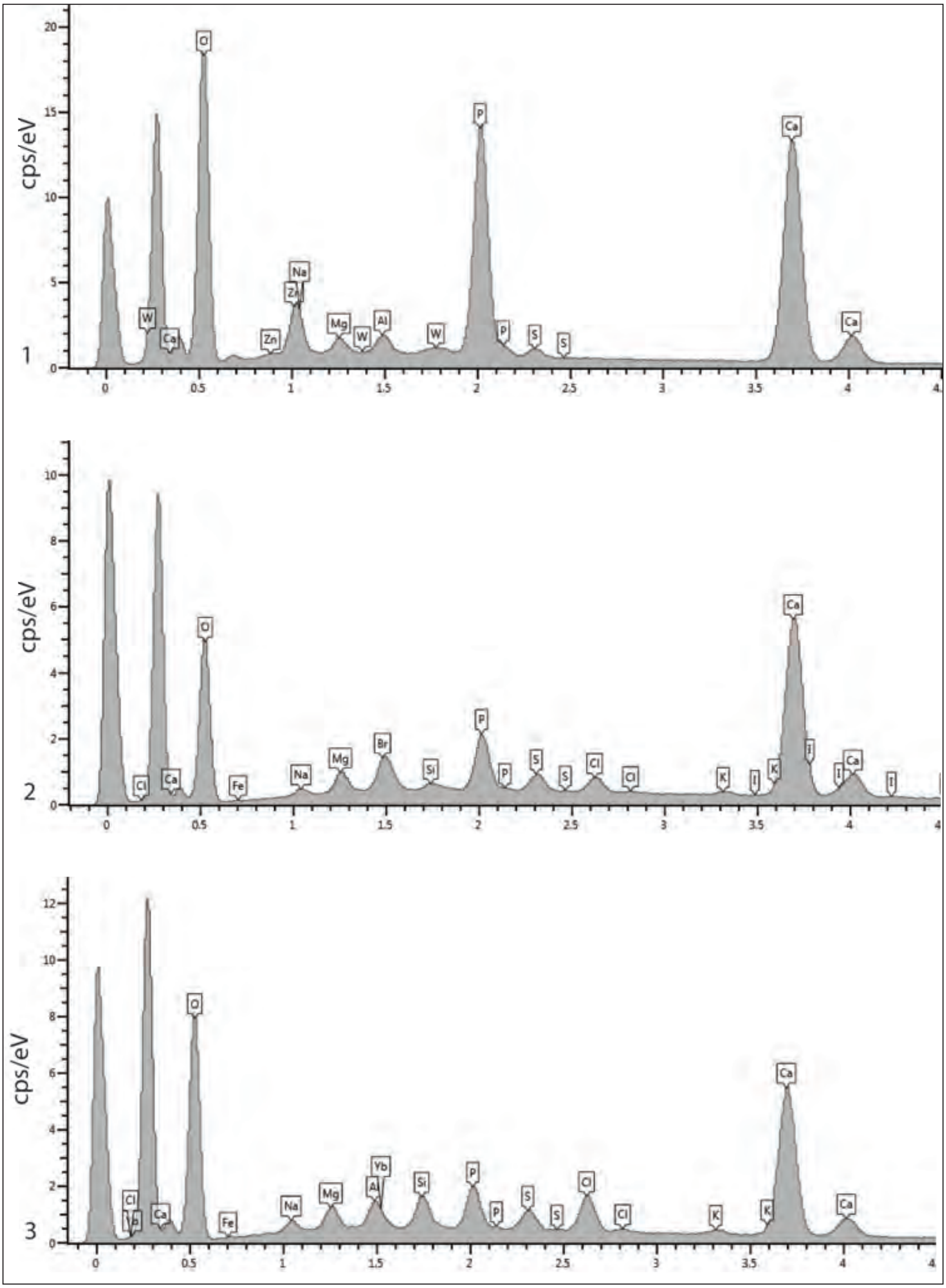


FIG. 19. Elemental spectra (EDS) of surface of cuticle of *1*, *Penaeus* sp. (Dendrobranchiata, shrimp); *2*, *Homarus americanus* H. MILNE EDWARDS, 1837 (Astacida, lobster); *3*, *Callinectes sapidus* RATHBUN, 1896 (Eubrachyura, crab).

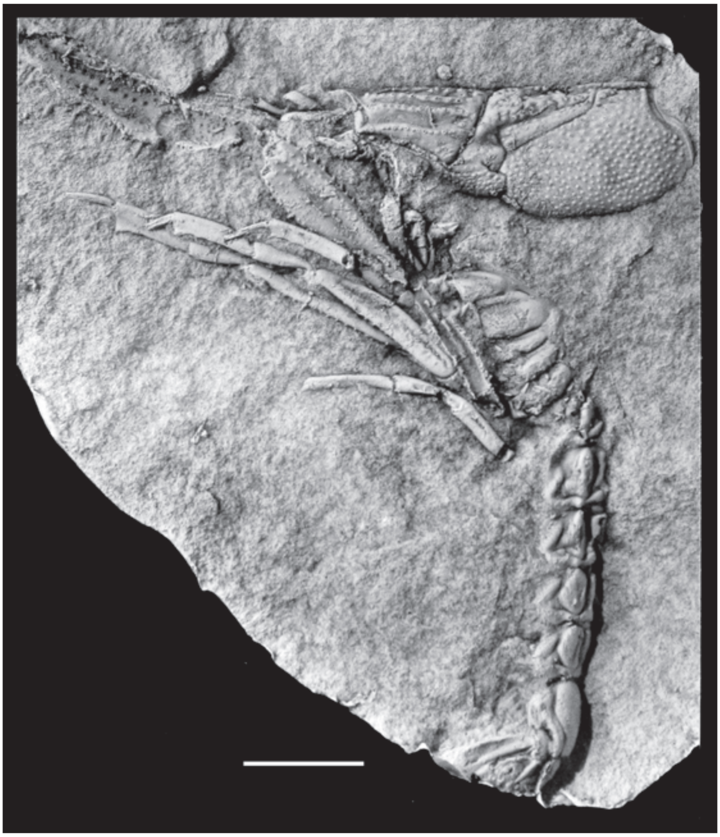


Fig. 20. *Trachysoma robusta* (Feldmann & McPherson, 1980), in Salter's position, Jurassic, Canada. Scale bar = 1 cm.

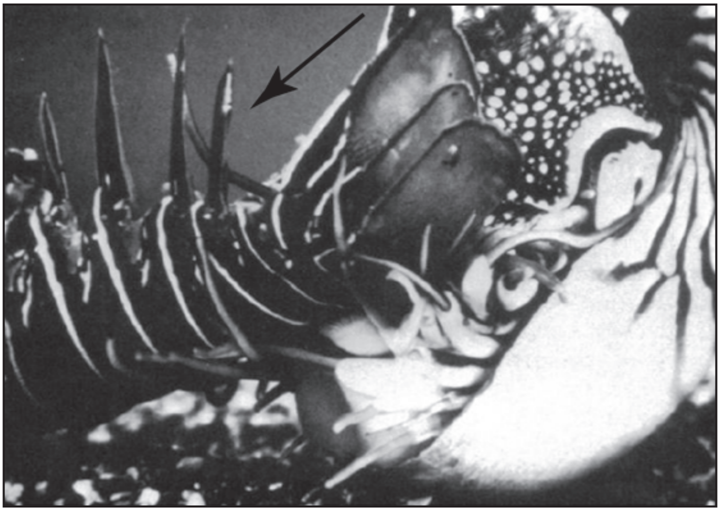
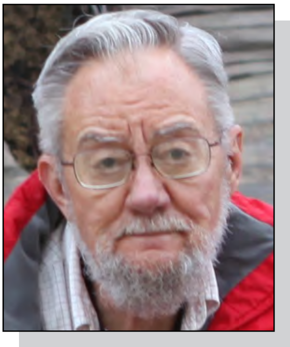
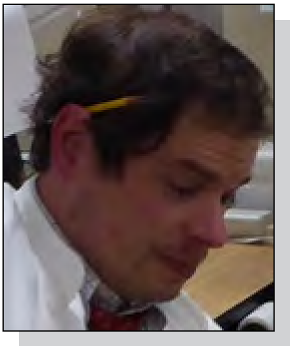


Fig. 21. *Nautilus macromphalus* Sowerby, 1849, eating pleon of *Panulirus longipes* A. Milne-Edwards, 1868 (arrow). Adapted from Tshudy & others (1989, fig. 1).

ABOUT THE AUTHORS



Rodney M. Feldmann (1939-2024) received his B.S., M.S., and Ph.D. from the University of North Dakota in the 1960s. Rod taught geology and paleontology at Kent State University for 59 years, mentoring 58 graduate students and countless undergraduates. He published more than 500 articles, books, and other publications mostly on fossil crustaceans. Rod's work on fossil decapods has formed the basis for the entire *Treatise on Invertebrate Paleontology*, Part R, Decapoda, Revised, volume. He was an outstanding mentor and role model for students and colleagues, and his research continues to influence scientists worldwide.



David Waugh got a BA at St Lawrence University and an M.S. and Ph.D. at Kent State University. He works primarily on microstructure of hard-tissues (is that hyphenated?), although as an undergraduate he studied bryozoan colony morphology. From bryozoans, he branched out to decapod cuticle microstructure, and lately has been working on cetacean teeth, focused on aspects of determining animal age (with the ultimate goal of learning more about the other signals teeth record). Starting with his work on decapods, and now extended to whale teeth, his work has been split almost evenly between examining living and fossil material, which is clearly an important aspect of studying the past. Besides hard tissues, he has also studied cetacean brain size, body size, and hearing through time.

Roy E. Plotnick has been at the University of Illinois at Chicago since 1982 and is currently Professor Emeritus. He was educated at Columbia University, the University of Rochester, and the University of Chicago. He is a Research Associate at the Field Museum and worked as a consultant for Texaco and Chevron oil companies. During his career, he also conducted research at Oak Ridge and Argonne National Laboratories, the National Center for Evolutionary Synthesis, the National Museum of Natural History, and Yale University. He works across a wide range of paleontological, geological, and ecological subjects, including the fossil record of the Sixth Extinction and the Anthropocene, Geoheritage of the Chicago region, paleobiology of eurypterids, sensory biology in the fossil record, and fractal methods in stratigraphy.

Carrie E. Schweitzer got a B.A. in biology from Hiram College and an M.S. and Ph.D. in geology from Kent State University. She has been a professor in the Department of Earth Sciences since 2000, teaching a variety of courses in geology, paleontology, and sedimentary geology. Her research has focused on the systematics, evolution, and paleobiology of decapod crustaceans and relatives of all geological ages.