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Systematic evaluation of raninid cuticle microstructure

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Abstract

Studies of decapod cuticle microstructure in both the paleontologic and neontologic literature generally focus on understanding cuticular construction and recognizing these features in fossil material. We examine the cuticle of 57 species in 26 genera within the Raninoidea. Within each genus cuticle microstructure of raninids is generally similar, but in successively higher taxonomic groups, greater variance is seen within and between groups. The subfamily Lyreidinae contains microstructures limited to pits and upright nodes. The Paleocorystinae contains species with predominantly upright nodes and cuticle that generally differs from the other subfamilies. The remaining subfamilies, including the Ranininae, Raninoidinae, Cyrtorhininae, and Notopodinae, are generally similar in their cuticle microstructure; they exhibit inclined nodes, and various combinations of pits, setal pits, depressions, and perforations. The Symethidae contains fungiform nodes, similar to those seen in *Cretacoranina*, a genus within the Paleocorystinae. Traditional taxonomic characters clearly separate the subfamilies of the Raninidae as well as separating the Raninidae from the Symethidae. Similar cuticle microstructures may appear in different subfamilies. Based upon cuticle microstructure alone, the Raninidae can be divided into three, morphotypes; the Paleocorystinae with upright and fungiform nodes, the Lyreidinae with pits and upright nodes, and the Ranininae, Raninoidinae, Cyrtorhininae, and Notopodinae with inclined nodes. Morphometric study of characters on the surface of the cuticle shows that features such as nodes and pits generally increase in size during the growth of the organism with a concomitant decrease in distribution density. Features of the cuticle change both across a single carapace and during growth of the organisms. Cuticle microstructures that are seen to grade into one another are considered to be part of a morphological continuum. Those structures that do not appear on the same carapace or during successive instars are not part of a morphological continuum.

Key words: Raninoidea, cuticle microstructure, systematics

Introduction

Cuticle microstructure has been examined from both biological and paleontological aspects. Most of these studies have examined the manner in which the cuticle is constructed (see Dennell, 1960; Hegdahl et al., 1977a, b, c; Roer and Dillaman, 1984) or attempted to recognize the structures in fossil material (see Neville and Berg, 1971; Vega et al., 1994; 2005; Guinot and Breton, 2006). Other studies have examined the functional morphology (Guinot, 1979; Savazzi, 1988, Haj and Feldmann, 2002) or taphonomic implications (Schäfer, 1951; Plotnick et al., 1988; Waugh et al., 2004). Few studies have attempted to use decapod cuticle microstructure for taxonomic purposes. The use of cuticle microstructure in taxonomic or phylogenetic studies has been difficult because there are few established characters and a small number of taxa with published data that includes information on the cuticle. Our previous work has concentrated on taphonomic aspects and the recognition of useful characters within cuticle. This study is the implementation of the characters we have recognized as applied to 57 species in 26 genera within the Raninoidea, including both fossil and extant species.

The purpose of this paper is to examine the cuticle morphology observed on the surface of raninid crabs, and to the extent possible in thin section, with the goal of determining biologically meaningful characters that can be both coded for future phylogenetic analysis and used in traditional systematic work. Observed cuticle microstructure is subdivided into basic structural components that are discussed broadly, followed by generic and species level descriptions of the cuticle. Morphometrics of cuticular features are also examined both on a single specimen and across a growth series.

Information on specimens examined, including author and date, age, museum and museum number, and type status are included in Table 1, and this information is excluded from the remaining text unless pertinent to the discussion. Figure 1 illustrates the cuticular layers and recognized characters, Figure 2 contains illustrations of taphonomic signatures, Figures 3–11 illustrate the cuticular structures of taxa examined in the systematic section, and Figures 12–13 pertain to the morphometrics of cuticle features.

Cuticle microstructure is studied by examining surface views, and when available, cross sections of the cuticle. Results presented here concentrate on surface features because observations of this type do not require destructive techniques and are therefore easier to obtain for a broad spectrum of taxa. Surface views are also more helpful for taxonomists who may not have the material or the facilities for making thin sections. Many of the microstructures described herein have been recognized by other workers, but generally the observations were inconsistent and lacked information on which layer of the cuticle was actually exposed.

For the purpose of this work, features less than 1 mm in diameter lie within our definition of microstructure. This definition is not absolute, and features that are commonly under 1 mm may attain larger sizes during ontogeny. Those features that may become larger due to growth remain within our broad definition of cuticle microstructure.

Structure of the cuticle: Construction of the cuticle has been extensively studied (see studies and reviews in Dennell, 1960; Hegdahl et al., 1977a, b, c; Roer and Dillaman, 1984; Plotnick, 1990). The following brief introduction of the major components is based on these studies. The cuticle of arthropods is generally divided into four major layers starting from the outer surface and moving inward, including the epicuticle, exocuticle, endocuticle, and the membranous layer (Fig. 1). Of these major layers, only the epicuticle does not have visible laminations. The epicuticle and exocuticle are formed underneath the existing cuticle before the animal molts; the endocuticle and membranous layer are formed following molting. All layers, with the exception of the membranous layer, may contain mineral components within the organic framework of the cuticle. The exocuticle and endocuticle that collectively make up the bulk of the cuticle's thickness are the most heavily mineralized.

The epicuticle (1 to 2 μm thick) is not considered further because it is too thin to differentiate from the exocuticle at the magnifications used in this work.

The exocuticle is composed of laminations and can be divided into upper and lower sections (Fig. 1.1–2). The lower section, or prismatic layer, contains so called prisms that appear as columns with domed tops in cross section and as close-packed polygons in tangential view. The walls of the prisms correspond to the boundaries of the cells that secreted the exocuticle. The upper exocuticle is thinner than the lower region, and is defined as the exocuticle above the prismatic layer (Fig. 1.1–2). Some of the smaller surface features that appear in raninid cuticle are formed exclusively within this layer. This layer is often damaged in fossil material, can be seen exfoliating from the surface, and may be erroneously confused with the epicuticle. The prisms in the lower exocuticle provide a useful marker to differentiate the exocuticle from the endocuticle in both cross section and tangential views.

The endocuticle (Fig. 1.1–2) is the thickest component of the cuticle. The laminations are coarser than those of the exocuticle, which is the basis most often used to visually differentiate the exocuticle from the endocuticle. In some cases, layers within the endocuticle are not altered to form features seen on the cuticle surface, so that when the exocuticle is lost and the top of the endocuticle is exposed, the carapace appears smooth.

The uncalcified membranous layer is the most basal feature of the cuticle and lies above the epidermis. This layer is not visible in all of the prepared thin sections, even in sections prepared from extant material. In these cases, it is possible that the membranous layer has not yet been formed, or it has been reabsorbed by the organism in preparation for formation of a new cuticle prior to the next molt. Regardless, the layer is ignored in this work, and the endocuticle is considered the most basal layer. This is not unreasonable considering that some authors consider the membranous layer to be a subdivision of the endocuticle (Dennell, 1960).

Characters Recognized in Raninid Cuticle

Microstructure: The most basic components of the cuticle surface are depressions, nodes, and perforations. Depressions are low areas of the cuticle; pits are a subdivision of depressions that are circular to ovate. Nodes, the opposite of depressions, are raised areas of the cuticle. Perforations are penetrations of the cuticle. These basic features have various forms and are found in various combinations that create the characters defined below.

Perforations: In this work, the term perforation is simply used to denote a penetration through the cuticle surface (Fig. 1.5). Perforations in extant decapod cuticle may, or may not, contain setae. In extant decapods, a perforation that does not contain setae has been typically described as a pore (Barnes, 1987, p. 475). In fossils this distinction cannot currently be made, hence our use of a strictly morphological term, perforation, throughout. Setal pits contain perforations, but are compound structures that include a perforation within a pit. Setal pits are defined separately below under their own subheading. Setae have not been observed in any fossil material to date. Setae observed in extant specimens such as *Umalia orientalis* (Fig. 7.6) would presumably, upon decay, result in perforations similar to those observed in the fossil *Eumorphocorystes sculptus*, because of their similar forms (Fig. 7.3). Thus, we hypothesize that many, if not most, of the perforations observed in fossil material would have contained setae before death of the crab. Some setal hairs also appear to have been lost during life or as a result of preservation in formalin or alcohol. A perforation, as we define it, is strictly a morphological structure and the function of the perforation, or its contents during life, has no bearing on the usage of the term. Realistically, the distinction between pores and perforations that contained setae and those that do not is unlikely to be of practical application to the study of fossil organisms. Examination of these features in thin section, and study during different stages of ontogeny may yield additional criteria to distinguish the function or morphology of perforations allowing refinement of this character.

When perforations are found alone, or without pits, they are typically distributed at densities over 50 per mm^2. The significantly higher densities of perforations not contained within pits suggests that the distinction between perforations and setal pits, as separate characters, has biologic significance.

Setal Pits: Setal pits are a combination of a pit, discussed below, and a perforation (Fig. 1.6). Our usage may differ from other workers in that we are making a distinction between what we call setal pits and perforations. As defined here, a setal pit is a circular to ovoid depression that contains a perforation. The term 'setal pit' is used with acknowledgement that the presence or absence of a setal hair during

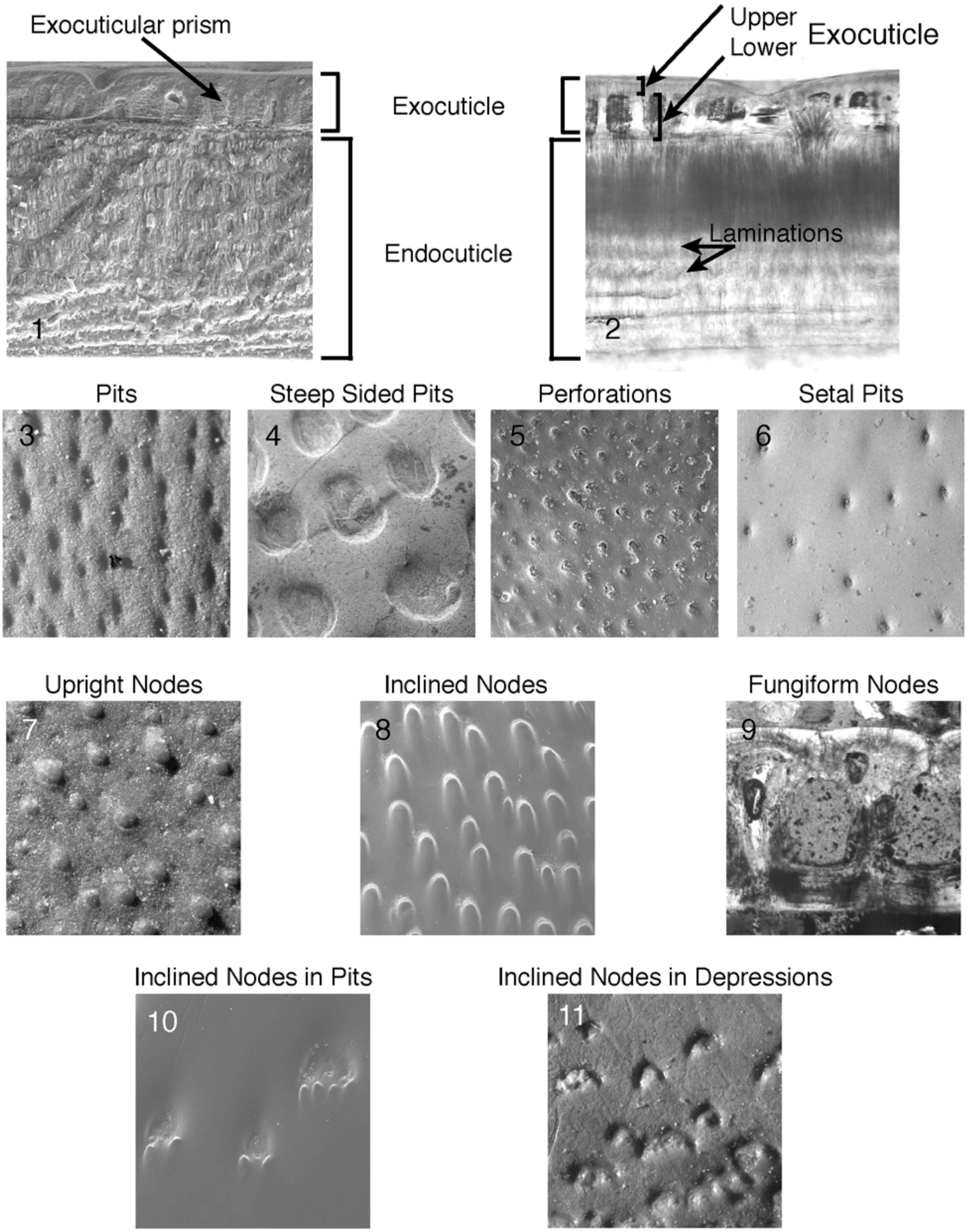

Fig. 1. Illustrations of cuticular layers and recognized microstructures. 1–2, *Raninoides louisianensis,* KSU K159, epicuticle and membranous layers are not discernable in the photographs and are not labeled. 3, *Lyreidus bairdii,* USNM 1000581. 4, *Macroacaena alseana,* KSU K254. 5, *Eumorphocorystes sculptus*, KSU K201. 6, *Ranilia* sp., FNHM UF117720, 7, *Notopocorystes stokesii,* BM, not cataloged, Lower Gault Clay. 8, *Umalia misakiensis*, SENK 7663. 9, *Cretacoranina testacea,* KSU K162. 10, *Cosmonotus grayi*, SENK 22380. 11, *Ranina americana*, KSU K169.

life cannot be verified in fossil material. However, the term is retained because it is so widely used.

Pits: Pits on the surface of raninids are circular to ovate depressions of the cuticle surface that generally have gently sloping walls (Fig. 1.3). They are either isolated on the carapace or found in conjunction with perforations and/or nodes. Pits in species of *Lyreidus, Raninoides,* and *Macroacaena* (the only taxa with pits available to thin section) observed in thin section or on fractured surfaces show that the pit is formed exclusively within the exocuticle. Laminations of the endocuticle are undisturbed and remain parallel to the surface of the cuticle (Figs. 4.2, 4.5). Laminations in the exocuticle are not truncated by the pit, but are reduced in thickness creating the depression. The boundary of the pit with the surrounding cuticle varies from relatively sharp to gradational, often making delimitation of the boundary for measurement difficult. If the pits are elongate, the long axis is generally parallel to the longitudinal axis of the carapace.

Steep sided pits: Pits with steep sides are wider than deep and have sharp boundaries with the cuticle (Fig. 1.4). They also have flattened bottoms. Steep sided pits have not been observed in association with perforations. These pits are further discussed under the genus *Macroacaena*.

Inclined nodes: Inclined nodes are positive features that project up from the cuticle surface and are directed toward the anterior of the crab (Fig. 1.8). Inclined nodes may appear in isolation or in pairs, triads or chains. The extent to which grouped nodes retain their lateral margins is variable. When nodes are laterally joined together, they form the "terraces" typified by *Lophoranina* (Fig. 3.6). In the Raninidae, all inclined nodes observed to date are directed in an anterior direction; consequently, their orientation is often not discussed in the systematic descriptions. Inclined nodes can be further subdivided to the extent that the node lies within a circular or ovate pit, is surrounded by a depression, or rises directly from the cuticle surface.

Inclined nodes in pits: Nodes associated with pits typically enter the posterior margin of the pit (Fig. 1.10). In cases where the nodes enter a setal pit, the number of nodes often corresponds to the number of setal hairs that emerge from perforations within the pit. The distinction made here between inclined and upright nodes holds relatively well for observations made on intact cuticle. When some inclined nodes are observed on damaged surfaces or in thin section, it becomes clear that the distinction is not so straightforward. The inclined nodes seen in *Cretacoranina broderipii* (Fig. 10.12) and *Raninella trigeri* (Fig. 2.6) are apparently constructed from upright nodes that are covered with exocuticle that is thicker on the posterior side of the node. The exocuticle in these cases results in an “upright node” appearing as an “inclined node”. This brings into question the homology of inclined nodes and may suggest that these features are strictly analogous. Further sampling of raninids that can be thin sectioned may help resolve this issue.

Inclined nodes with depressions: Nodes may also enter a depression which is typically crescentic (Fig. 1.11). Inclined nodes in depressions are often found toward the posterior of the carapace, and the depressions often disappear toward the anterior.

Upright nodes: Upright nodes are formed in the endocuticle and protrude into the exocuticle. The extent to which the nodes protrude above the surface of the animal varies from barely emergent to slightly higher than the node width. To accommodate the node originating from within the endocuticle, the exocuticle becomes extremely thin above the nodes. These nodes are often abraded so that the thin exocuticle that covered the node surface is often lost.

Fungiform nodes: First described in *Cretacoranina punctata* by Haj and Feldmann (2002), these upright nodes bear mushroomed tops that form flat sides when in contact with a neighboring node and remain circular when not in contact with other nodes. When closely packed, node tops appear as hexagonal plates when viewed tangentially (Figs. 1.9, 9.2). The exocuticle between fungiform nodes is thinner than seen in raninids lacking the structures; it also changes its appearance as it wraps up over the node formed from the endocuticle. The exocuticle over, and on the sides of, the nodes does not appear to contain the prismatic layer. In a number of taxa thin sectioned, the exocuticle is preserved in a different manner than the exocuticle lacking fungiform nodes suggesting that there are some chemical differences in the cuticle associated with these nodes.

The upright nodes and fungiform nodes described above appear to form a continuum from being simply upright to close-packed and fungiform (Fig. 1.9). Upright nodes are often lost either taphonomically or during exposure and preparation, leaving a circular stub, or sometimes a depression, both generally with a central dark spot. In cases where the nodes are lost, there is no way to determine if the node was simply upright or fungiform.

It is unclear if the fungiform nodes described by Haj and Feldmann (2002) are homologous or analogous to the “bolitimorphs” described by Blow (2003) in *Pterocarcinus baileyi* Blow, 2003, or the “forme de champignons” in *Actaea* and *Daira* described by Guinot (1979).

Straps and Terraces: The term strap is commonly used to describe the raised linear platforms found on raninids (Fig. 10.1). The extent to which these straps are homologous across taxa is unclear. Straps developed on species of *Eumorphocorystes* and *Eucorystes* are not constructed in similar fashions and can be easily distinguished in thin section. Straps of *Eumorphocorystes* are formed from thickened cuticle, whereas straps on *Eucorystes* spp. are composed of closely packed, but not fungiform, nodes. Care should be used when describing strap-like ornament on raninids because of the implied homology inherent in using one term for similar morphology. The difference between a strap and a terrace is also somewhat ambiguous. The term terrace tends to be used when the functional implications are stressed such as when the features are aligned transversely on the carapace. These terms are descriptive but should be used with caution if, in coding for phylogenetic analysis, a homology is implied.

High density nodes: Nodes are considered to be present at a high density when the internode space is too small to accommodate additional nodes of the same size.

Materials and Methods

Cuticle samples from extant and fossil raninids have been obtained in the course of an ongoing study of the role cuticle microstructures may play in constructing decapod phylogenies (Table 1). Cuticle was examined directly or was cast if the specimen was too rare for destructive sampling. Extant cuticle from museum spirit collections was cast or a section was extracted from the branchial region of the carapace. Casts and original specimens were examined using the SEM or whitened with ammonium chloride and photographed with a light microscope. In cases where samples could neither be cast nor borrowed, cuticle was examined with microscopes available in the museum. Sampling has been concentrated in the branchial region of the dorsal carapace to allow direct comparison across taxa. All illustrations and observations are based on features in this region unless otherwise stated.

Casts were made using Repliset F5™, a two-part industrial molding compound originally designed for use in the metallographic industry manufactured by Struers Inc. The casting compound is applied with a gun that extrudes the two materials through a disposable mixing nozzle. The compound can be applied directly to the dried specimen. Once the mold has cured, an epoxy cast is made using standard two-part epoxy. The resultant casts can be gold coated and examined with an SEM or whitened and photographed with a light microscope.

Measurements were made from optical and SEM photomicrographs using the Macintosh software package Image-J. The software was developed by, and is freely available from, the United States National Institutes of Health (NIH). Measurements were made by tracing the feature with the "freehand" selection tool and allowing the program to fit an ellipse onto the selected area. The program returns major and minor length measurement on the ellipse, providing paired length and width measurements for each pit or node.

Museum abbreviations: Bayerische Staatssammlung für Palaeontologie und Geologie, Munich, Germany (BSP); The Natural History Museum, London, UK (BM); Museo Civico "G. Zannato" di Montecchio Maggiore, Italy (MCZ); Regale Belgicum Institutum Scientiarum Naturalium, Brussels, Belgium (RBIS); The National Museum, Prague, Czech Republic (NMP); Kent State University Paleontological Collection, Kent, Ohio, USA (KSU); Florida Natural History Museum, Gainesville, Florida, USA (FNHM); Pink Palace, Memphis, Tennessee, USA (PP); Sedgwick Museum of Earth Sciences, Cambridge, UK (SM); Nationaal Natuurhistorisch Museum, Leiden, Netherlands, (NNM); United States National Museum of Natural History, Washington, DC, USA (USNM); Senckenberg Forschungsinstitut und Gesellschaft, Frankfurt, Germany (SENK).

Cuticle Taphonomy

The exocuticle/endocuticle boundary is often a plane of weakness that forms the zone of separation when a concretion containing a crab is split, entombing the true exterior of the crab in the counterpart (Waugh et al., 2004). Preparation of specimens that involves removing matrix from the surface of the crab can also damage cuticular layers, especially if friable. Either of these factors results in fossil material that does not exhibit the true exterior surface that was present during life, even in specimens that have otherwise survived the taphonomic processes.

The exocuticle and endocuticle of living decapods exhibit great variability in the density and distribution of mineralization (Waugh, 2002). This variation is both taxon specific and controlled by the molt cycle, both of which affect the likelihood and nature of preservation. Uncalcified layers of the cuticle are often lost, resulting in a void that remains open or alternatively, is filled with inorganic minerals. Weaknesses between layers that are inherent to the cuticle, or layers that are differentially affected by preservation, greatly increase the potential of the cuticle to exfoliate (Figs. 2.6–7), resulting in material loss. Regardless of how faithful the exposed layer of cuticle is to the condition during life of the organism, it is the layer available for study and must be assessed appropriately. Observation of damaged surfaces does contain useful information on cuticular microstructure because they reveal otherwise hidden surfaces. When specimens are not available for observation in thin section, these damaged surfaces may provide the only opportunity for internal examination of the cuticle.

A number of methods can be employed to expose or examine external surfaces of the cuticle on fossils. The most obvious method for observing the true exterior nature of the cuticle is to find material that displays excellent preservation. Careful examination of large sample lots often reveals patches of well-preserved cuticle. Surfaces with the best preservation may be found on incomplete or broken specimens; incomplete specimens should not be overlooked. It is also helpful to have material that has not been excessively handled after removal from the matrix. Cleaning and use of consolidants may mask or destroy the fragile surface, especially in cases in which some layers remain unmineralized. The most reliable way to ensure that the cuticle has not been extensively altered, or to determine if cuticular layers are missing, is to view the cuticle in thin section so that the presence or absence of layers may be assessed. If the exocuticle can be observed, it is likely that the cuticular surface contains useful data. If the cuticle cannot be observed in cross section, surface examination with the SEM or powerful light microscope may reveal the prismatic layer of the exocuticle. This indicates that a minimal, but not necessarily insignificant, amount of material has been lost. The prismatic layer is not the outermost layer of the exocuticle, and if visible, the epicuticle and part of the exocuticle has been lost, and possibly with it, fine detail cannot be observed.

Using the law of superposition, one can orient the order of the layers on a particular specimen. A damaged specimen may show multiple layers of the cuticle (Fig. 2.5–9), thus providing a key to what layer is exposed on apparently undamaged specimens. Epibionts and matrix on the specimen's surface often provide some protection to the cuticle immediately adjacent and underneath the foreign material (Fig. 2.8–9).

Casts of concretion counterparts have proven to be a reliable method to examine the exterior-most surface in cases where the cuticle has weathered on the outcrop, or in cases where the cuticle has exfoliated along internal planes. In these cases the cuticle can be removed with mechanical instruments such as dental tools, air scribes, or water

Table 1. List of species examined ordered by subfamily, including age, museum numbers, and type status. Specimens that were observed from only the literature contain the reference in place of the museum numbers. * additional material from the Kent State collection was used.

Ranininae			
Lophoranina bishopi Squires and Demetrion, 1992	Eocene	KSU K170	non-type
Ranina americana Withers, 1924	Miocene	BM 23798	Holotype*
Ranina ranina (Linnaeus, 1758)	Extant	USNM 106160	non-type
Lyreidinae			
Hemioon cunningtonii Bell, 1863	late Albian	BM 60137, BM In29965 and SM B23289	Syntypes
Lyreidina pyriformis Fraaye and van Bakel, 1998	late Maastrichtian	Fraaye and van Bakel, 1998	Holotype
Lyreidus antarcticus Feldmann and Zinsmeister, 1984	Eocene		non-type
Lyreidus channeri (Wood-Mason, 1885)	Extant	SENK 22367	non-type
Lyreidus nitidus (A. MilneEdwards, 1880)	Extant	KSU K70	non-type
Lyreidus tridentatus De Haan, 1841	Extant	KSU K252	non-type
Macroacaena alseana (Rathbun, 1932)	Oligocene	KSU K254	non-type
Macroacaena naselensis (Rathbun, 1926a)	late Eocene–Oligocene	USNM 413255	non-type
Macroacaena schencki (Rathbun, 1932)	late Eocene	USNM 371921	Holotype
Macroacaena willapensis (Rathbun, 1926a)	late Eocene	USNM 494641	non-type
Raninella oaheensis Bishop, 1978	Maastrichtian	USNM 173589	Holotype
Raninella trigeri A. Milne Edwards, 1862	Cenomanian	BM 63689	non-type
Raninella eocenica Rathbun, 1935	Eocene	USNM 335984A, B	Paratypes
Rogueus orri Berglund and Feldmann, 1989	early middle Eocene	KSU K278	Holotype
Raninoidinae			
Notopoides latus Henderson, 1888	Extant	SENK 22364	non-type
Notosceles ecuadorensis (Rathbun, 1935)	Extant	USNM 173372	non-type
Quasilaeviranina ovalis (Rathbun, 1935)	Paleocene	USNM 371689	Cotype
Quasilaeviranina simplicissima (Bittner, 1883)	Eocene	MCZ 1210	Holotype
Raninoides bouvieri Capart, 1951	Extant	NNM 38618	non-type
Raninoides glabra (Woodward, 1871)	Eocene	SM C7739	non-type
Raninoides louisianensis Rathbun, 1933	Extant	USNM 120617	non-type
Raninoides vaderensis Rathbun, 1926a	Eocene	KSU K165	non-type
Raninoides washburnei Rathbun, 1926a	Eocene	USNM 353336	Holotype
Notopodinae			
Cosmonotus eocaenicus Beschin et al., 1988	middle Eocene	MCZ 1105-1107	Holotype
Cosmonotus grayi Adams and White, 1848	Extant	SENK 22380	non-type
Eumorphocorystes sculptus Binkhorst, 1857	late Maastrichtian	KSU K46	non-type
Lianira beschini Beschin et al., 1991	Eocene	MCZ 1231 and 1537	Holotype
Lianira convexa Beschin et al., 1991	Eocene	MCZ 1317, 1912	Holotype
Lovarina cristata Beschin et al., 1991	Eocene	Beschin et al. (1991)	non-type
Notopus dorsipes (Linnaeus, 1758)	Extant	SENK 22373	non-type
Pseudoraninella vahldieki Förster and Mundlos, 1982	late Eocene	BSP 1981XI31	Holotype
Ranila muricata H. Milne Edwards, 1837	Extant	USNM 121656	non-type
Ranilia constricta (A. Milne Edwards, 1880)	Extant	SENK 17019	non-type
Ranilia sp. Portell and Agnew, 2004	Pliocene	FNHM UF117720	non-type
Raniliformis baltica (Segerberg, 1900)	middle Danian	Jagt et al., 1993	non-type
Raniliformis prebaltica Fraaye and van Bakel, 1998	late Maastrichtian	Fraaye and van Bakel, 1998	Holotype
Umalia misakiensis (Sakai, 1937)	Extant	SENK 7663	non-type
Umalia orientalis (Sakai, 1963)	Extant	SENK 18661	non-type
Paleocorystinae			
Cretacoranina broderipii (Mantell, 1844)	Albian	BM 61249	Type Series
Cretacoranina dichrous (Stenzel, 1945)	Cretaceous	KSU K174	non-type
Cretacoranina fritschi (Glaessner, 1929)	Senonian	NMP O4296/CL.6979	Lectotype
Cretacoranina ornatus Wright and Collins, 1972	Cenomanian	BM 61111	Holotype
Cretacoranina punctata (Rathbun, 1935)	late Albian	Haj and Feldmann, 2002	non-type
Cretacoranina schloenbachi (Schlüter, 1879)	Coniacian	Jagt et al. (2003)	non-type
Cretacoranina syriacus (Withers, 1928)	Cretaceous	BM I.8407	Holotype
Cretacoranina testacea (Rathbun, 1926b)	Campanian	KSU K162	non-type
Cretacoranina trechmanni (Withers, 1927)	Cretaceous	BM 26011	Holotype
Eucorystes carteri (McCoy, 1854)	Albian	BM 29830	non-type
Notopocorystes normani (Bell, 1863)	Cenomanian	SDG B8823	Holotype
Notopocorystes stokesi (Mantell, 1844)	Albian	BM 29618	non-type
Cyrtorhininae			
Cyrtorhina fusseli Blow and Manning, 1996	Eocene	Tessier et al., 2004	Holotype
Cyrtorhina globosa Beschin et al., 1994			
Cyrtorhina oblonga Beschin et al., 1988	middle Eocene	MCZ 1394	Holotype
Symethinae family, Symethidae			
Symethis johnsoni Rathbun, 1935	Paleocene	USNM 371691	Paratypes
Symethis variolosa (Fabricius, 1793)	Extant	USNM 273180	non-type

Table 2. Coding of characters observed in the cuticle of raninids. When characters are divided by a backslash, the first marking represent the posterior half of the carapace and the later for the anterior. "High Density Perfs" are perforations that are present in densities over 50 per mm^2. The "Pit-Node-Perf" column is checked if both inclined nodes are present in setal pits. Characters marked with an "h" are found only in the hepatic region. Because the coding does not describe the full morphology of the cuticle, or all locations, refer to the text for details on each specimen.

Species	Inclined Node	High Density Nodes	Inclined Node in pit	Node in depression	Upright Node	Fungiform Node	Pits	Steep-sided Nodes	Setal Pits	High Density Perfs	Perforations	Pit-Node-Perf
Ranininae												
Lophoranina bishopi	y	n	n	y	n	n	n	n	n	n	n	n
Ranina americana	y	n	n	y	n	n	n	n	n	n	n	n
Ranina ranina	y	n	n	n	n	n	n	n	n	n	n	n
Lyreidinae												
Hemioon cunningtonii	n	?/y	?	?	?/y	?	?	?	?	?/y	?/y	?
Lyreidina pyriformis	?	n	n	?	n	n	n/y	?	?	n	?	?
Lyreidus antarcticus	n	n	n	n	n	n	y	n	n	n	n	n
Lyreidus channeri	n	n	n	n	n	n	y	n	n	n	n	n
Lyreidus nitidus	n	n	n	n	n	n	y	n	n	n	n	n
Lyreidus tridentatus	n	n	n	n	n	n	y	n	n	n	n	n
Macroacaena alseana	n	n	n	n	y	n	y	y	n	n	n	n
Macroacaena naselensis	n	n	n	n	y	n	y	y	n	n	n	n
Macroacaena schencki	n	n	n	n	y	n	y	y	n	n	n	n
Macroacaena willapensis	n	n	n	n	y	n	y	y	n	n	n	n
Raninella oaheensis	n/y	n	n	n	n	n	y	n	?	n	?	n
Raninella trigeri	y	y	n	n	n	n	n	n	n	n	n/y	n
Raninella eocenica	y/?	n	?	?	y/?	?	?	?	?	?	?	?
Rogueus orri	n	n	n	n	y	n	y	y	n	n	n	n
Raninoidinae												
Notopoides latus	y	n	n	y/n	n	n	y	n	n	n	?/y	n
Notosceles ecuadorensis	y	y	n	y/n	n	n	n	n	y	n	y	n
Quasilaeviranina ovalis	y	y	n	y	n	n	n	n	n	n	n	n
Quasilaeviranina simplicissima	y	y	n	n	n	n	n	n	n	n	n	n
Raninoides bouvieri	y	n	y	y	n	n	n	n	n	n	y	y
Raninoides glabra	y	n	n	y	n	n	n	n	y	n	y	n
Raninoides louisianensis	y	n	y	n	n	n	n	n	n	n	n	n
Raninoides vaderensis	y	n	y	n	n	n	n	n	n	n	n	n
Raninoides washburnei	n	n	n	n	y	n	y	y	n	n	n	n
Notopodinae												
Cosmonotus eocaenicus	y	n	y	n	n	n	n	n	y	n	y	y
Cosmonotus grayi	y	n	y	n	n	n	n	n	n	n	y	y
Eumorphocorystes sculptus	y	n	n	n	n	n	n	n	n	y	y	n
Lianira beschini	n	n	n	n	n	n	n	n	y	n	n	n
Lianira convexa	n	n	n	n	n	n	n	n	y	n	n	n
Lovarina cristata	?	n	n	n	n	n	n	n	n	n	n	n
Notopus dorsipes	n/h	n	n	n	n	n	y	n	n	n	n	n
Pseudoraninella vahldieki	n/h	n	n	n	n	n	y	n	n	n	n	n
Ranila muricata	y	n	y	n	n	n	n	n	y	n	y	y
Ranilia constricta	y	n	y	n	n	n	n	n	y	n	y	n/y
Ranilia sp.	n/y	n	n/y	n	n	n	n	n	y	n	y	n/y
Raniliformis baltica	n/y	n	n	?/y	n	n	n	n	n	n	?	?
Raniliformis prebaltica	n/y	n	n	?/y	n	n	n	n	n	n	?	?
Umalia misakiensis	y	n	n	y/n	n	n	n	n	n	n	n	n
Umalia orientalis	y	n	n	n	n	n	n	n	n	y	y	n
Paleocorystinae												
Cretacoranina broderipii	y	n	n	y	n	n	y	n	?	n	n	n
Cretacoranina dichrous	n/y	y	n	n	y	y	?	n	?	n	n	n
Cretacoranina fritschi	n	y	n	n	y	y	n	n	n	n	n	n
Cretacoranina ornatus	?	n	?	?	?	?	n	?	?	?	?	?
Cretacoranina punctata	n	y	n	n	y	y	n	n	n	n	?	n
Cretacoranina schloenbashi	n	y	n	n	y	y	n	n	n	n	n	n
Cretacoranina syriacus	?	n	n	?	?	n	y	n	?	n	?	n
Cretacoranina testacea	n	y	n	n	y	y	n	n	n	n	n	n
Cretacoranina trechmanni	n	n	n	n	y	y	n	n	n	n	n	n
Eucorystes carteri	n	y	n	n	y	y	n	n	n	y	y	n
Notopocorystes normani	y	n	n	n	?	n	n	n	n	n	y	n
Notopocorystes stokesi	y	n	n	n	?	n	n	n	n	n	y	n
Cyrtorhininae												
Cyrtorhina fusseli	y	n	n	?	n	n	n	n	?	n	?	n
Cyrtorhina globosa	n/y	n	n	?	n	n	n	n	?	n	?	n
Cyrtorhina oblonga	n/y	n	n	?	n	n	n	n	?	n	?	n
Symethinae, family Symethidae												
Symethis johnsoni	n	n	n	n	y	n	y	y	n	n	n	n
Symethis variolosa	n	y	n	n	y	y	n	n	n	n	n	n

blasters, which will remove any remaining cuticle from the counterpart (Jakobsen, 2003). When concretions split along the external cuticle boundary, no preparation of the surface is needed. A positive cast of the surface can then be made and examined.

Because arthropod cuticle has potential as a phylogenetic character, the description of its true morphology is a worthwhile pursuit. To observe this morphology, an understanding of cuticular degradation is necessary. A collection of *Cretacoranina testacea* from the Ripley

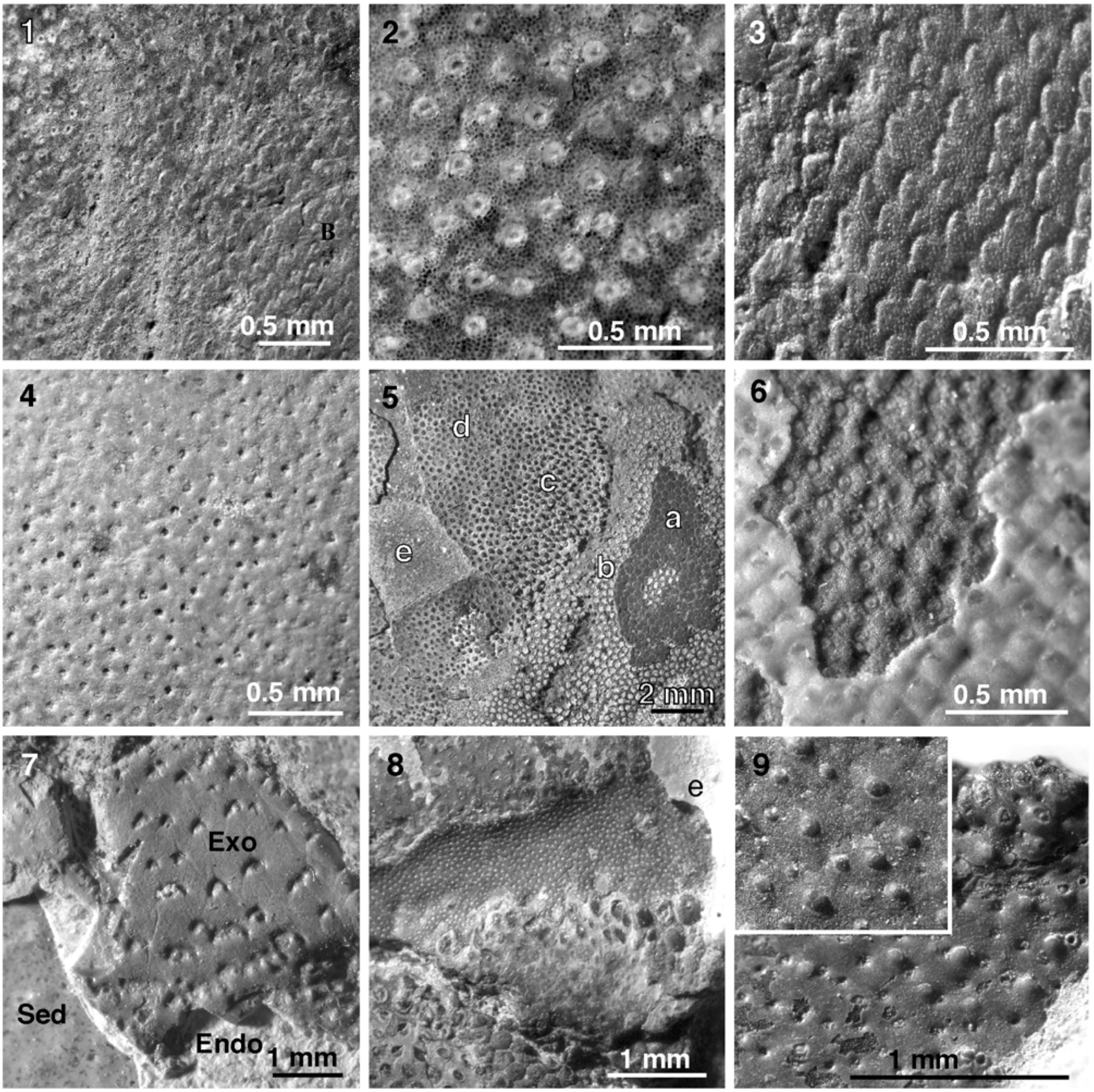

Fig. 2. 1–4, *Quasilaeviranina ovalis*, cuticle from the branchial region of the carapace showing different preservational styles. 1–2, USNM 371692. 1, Gradation of preservational conditions from excellent (lower right) to poor (upper left). 2, Close-up of poorly preserved exocuticle seen in the upper left of Fig. 1, nodes are broken revealing dark central cores and exocuticular prisms are visible between broken nodes. 3, USNM 371689, close up of cuticle from Fig. 1, note inclined nodes defined by shallow depressions on the anterior and lateral parts of the node. 4, USNM 371689, contrasting preservation style showing nodes in which the central portions of the nodes are absent, contrast to Fig. 2.2, USNM 371689. 5, *Cretacoranina testacea*, surficial view showing effects of weathering and/or preservation of cuticle surface, a, complete fungiform nodes; b, node cap missing, but sediment remaining; c, node cap and sediment missing, cylindrical part of node remains; d, only node bases remain; e, sediment surface, all cuticle missing. 6, *Raninella trigeri*, BM 63689, damaged cuticle showing exfoliation of the exocuticle, or possibly just the upper exocuticle, note that underneath the inclined nodes, bases of what appear to be upright nodes can be seen in pockets. 7, left most frontal spine of *Ranina americana*, KSU K169, one of the few remaining patches of cuticle on the specimen, exocuticle in center “exo”, top of the endocuticle lower right “endo”, and sediment lower left. 8, Depressed area of cuticle above cervical groove and just below first “strap” on *Eucorystes carteri*, BM 29830, note preservation of the cuticle containing a dense field of perforations that were protected from abrasion by the epibiont seen on the far right “e”. 9, *Notopocorystes stokesi*, BM, not cataloged, Lower Gault Clay, inset shows typical preservation style on the same specimen, foreground shows cuticle with exocuticle.

Formation housed in the Pink Palace Museum contains a series of degraded cuticle surfaces that provide a case study of how preservation and exposure can alter arthropod cuticle. The pebbled surface of *Cretacoranina* is formed from closely packed fungiform nodes (Haj and Feldmann, 2002). This structure can be observed in *C. testacea* found in the Coon Creek Formation. Variation in preservation, exposure, or preparation of the material examined can mask these fungiform nodes. In some examples, the bulbous node tops are abraded or broken leaving only their supporting pillars (Fig. 2.5c). In other cases these pillars are lost, leaving what appears to be low nodes (Fig. 2.5d). The tops of the hexagonal caps can also be lost, leaving a partial exposure of the infilling material that resided beneath the plates (Fig. 2.5b). A number of specimens had to be examined in this case to reveal the true morphology and range of degraded surface types. Examination of damaged surfaces does provide data on construction of the cuticle, and if recognized and matched with the undisturbed structures, becomes a guide to inferring morphology in other specimens.

Specimens of *Quasilaeviranina ovalis* provide an example of how degraded surfaces can provide misleading interpretations of the cuticular structure. One specimen in this series shows a surface that contains exocuticular prisms and the bases of broken columnar nodes (Fig. 2.1–2). Upon closer examination of the specimen, comparatively less damaged surfaces show that the broken nodes are in fact inclined, not upright (Fig. 2.3). Another specimen with extremely poor preservation has a surface covered with what would be described as perforations (Fig. 2.4) These perforations are in fact formed from loss of the endocuticle that was folded up into the exocuticle, forming the nodes. Without careful examination of multiple specimens, the true surface morphology often cannot be inferred.

Systematic Paleontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Superfamily Raninoidea de Haan, 1839
Family Raninidae de Haan, 1839
Subfamily Ranininae de Haan, 1839

Discussion: All members of the subfamily possess inclined nodes covering the dorsal carapace and lack both pits and perforations in the branchial regions. Cuticle of *Ranina americana*, with paired nodes, could be considered as intermediate between the isolated nodes of *Ranina ranina* and the laterally joined, terrace-forming nodes of *Lophoranina* spp.

Genus *Ranina* Lamarck, 1801

Discussion: *ranina ranina* has a distinctive carapace bearing evenly distributed, forward-directed, inclined nodes (Fig. 3.1–3). Unlike other raninids outside the subfamily, the distal tips of the nodes are not connected to the dorsal carapace and extend unsupported (Fig. 3.3) in an anterior direction parallel to the dorsal carapace. Smaller nodes are inserted between existing nodes at specific times during ontogeny (Fig. 3.2). Nodes of *R. ranina* are strictly positive features, and no depressions or pits surround the anterior portions as seen in other species of raninids, including *Ranina americana*.

Nodes on *R. americana* do not have unsupported tips, are defined by slight depressions, and are often paired laterally (Fig. 2.7; 3.5). Depressions surrounding the nodes of *R. americana* become more prominent toward the anterior of the dorsal carapace. The nodes in *R. ranina* and *R. americana* are constructed from both the exocuticle and endocuticle. *Ranina americana* can be easily distinguished from *R. ranina* based on the presence of depressions in the former.

Genus *Lophoranina* Fabiani, 1910

Discussion: *Lophoranina* is easily distinguished from other raninids by its oft-mentioned terraces that extend transversely across the dorsal carapace (Fig. 3.6). Terraces are formed by lateral linkage of both nodes and their associated depressions. In *Lophoranina bishopi,* nodes are constructed such that all layers of the cuticle are altered (Fig. 3.7; see also illustrations in Vega et al., 2005). Terrace width appears to vary across species. Not observed in the study material, but reported by Feldmann et al. (1996) and others, are spines that extend from the nodes in an anterior direction. The strong ornamentation of the surface of *Lophoranina* makes characterization of the cuticle possible even from photographs in the literature.

Subfamily Lyreidinae Guinot, 1993

Discussion: With the exception of *Raninella* and possibly *Lyreidina,* the Lyreidinae is characterized by carapaces covered in pits and an absence of inclined nodes. *Rogueus* and *Macroacaena* exhibit steep sided pits and upright nodes. Species of *Lyreidus* have non-emergent nodes that are formed within the endocuticle, but do not penetrate the surface. These nodes may be analogous to the emergent nodes present in *Rogueus* and *Macroacaena.* Pending further work, results presented here suggest that *Raninella* and *Lyreidina* may not fit within the Lyreidinae.

Genus *Lyreidina* Fraaye and van Bakel, 1998

Discussion: Based on photographs and descriptions in Fraaye and van Bakel (1998), the branchial regions of *Lyreidina pyriformis* are covered in transversely elongate depressions; anterior to the widest point of the carapace, the cuticle is covered in pits. It is unclear if the elongate depressions described as "incised terraces" by Fraaye and van Bakel (1998) contained laterally joined, inclined nodes posterior to the depressions that have been subsequently abraded. Without examination of the sole specimen, assessment of the surface condition and therefore its true morphology is difficult. Based on the tentative observations above, the cuticle differs significantly from other members of the subfamily.

Genus *Lyreidus* de Haan, 1841

(=*Lysirude* Goeke, 1985)

Discussion: All species of *Lyreidus* examined (see Table 1), including species previously assigned to its junior synonym *Lysirude*, possess pits covering the entire dorsal carapace (Fig. 4.1). These pits are formed

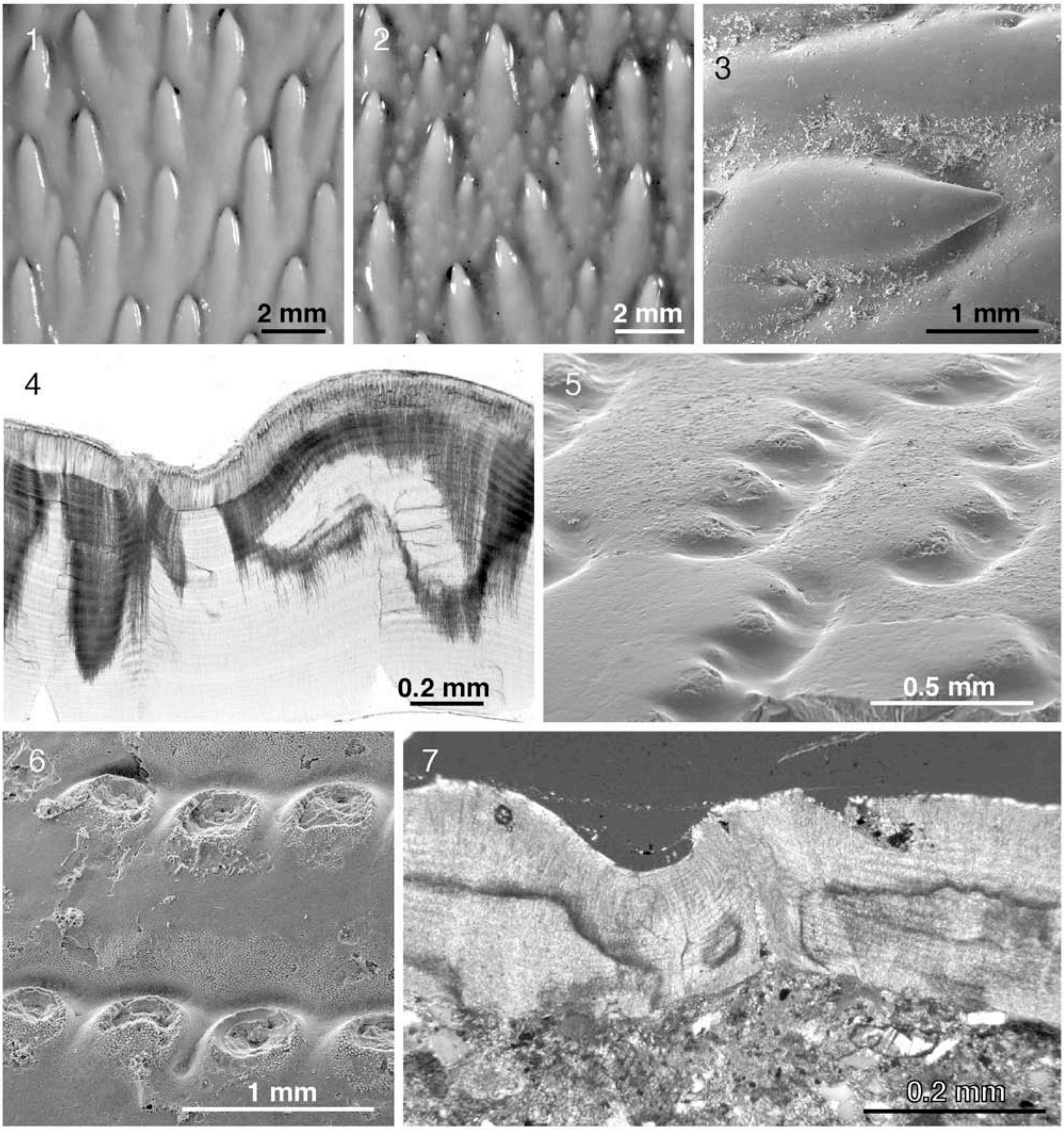

Fig. 3. 1–4, *Ranina ranina*, 1, USNM 5230, branchial surface. 2, USNM 18874, note introduction of smaller nodes. 3, USNM 106160, SEM photomicrograph. 4, USNM 106160, thin section perpendicular to long axis of nodes. 5, *Ranina americana*, KSU K169, oblique view of branchial surface. 6–7, *Lophoranina bishopi*, KSU K170, 6, tangential view, tops of nodes are broken, nodes are slightly raised above cuticle surface, but are mostly defined by depressions, top of prismatic layer partially exposed on cuticle surface and on the fractured nodes. 7, thin section cut perpendicular to terraces, exocuticle missing, photomicrograph taken under cross polars.

within the exocuticle; in some cases, the endocuticle is subtly deflected upward under the pit (Fig. 4.2–3). Unlike pits found on *Raninoides*, those of *Lyreidus* lack associated nodes. Setal hairs have not been observed on the carapace except on some frontal and lateral regions. In thin section, this seemingly simple morphology becomes more complex. In cross section, the pits are often observed in association with non-emergent, upright nodes formed from within the endocuticle (Fig. 4.3). These non-emergent nodes may be analogous to the nodes observed in *Macroacaena* (Fig. 4.4, 4.6), or may be related to the node-pit combination commonly observed in other raninids.

Genus *Macroacaena* Tucker, 1998

(= *Carinaranina* Tucker, 1998)

Discussion: Steep sided pits characterize the *Macroacaena* specimens

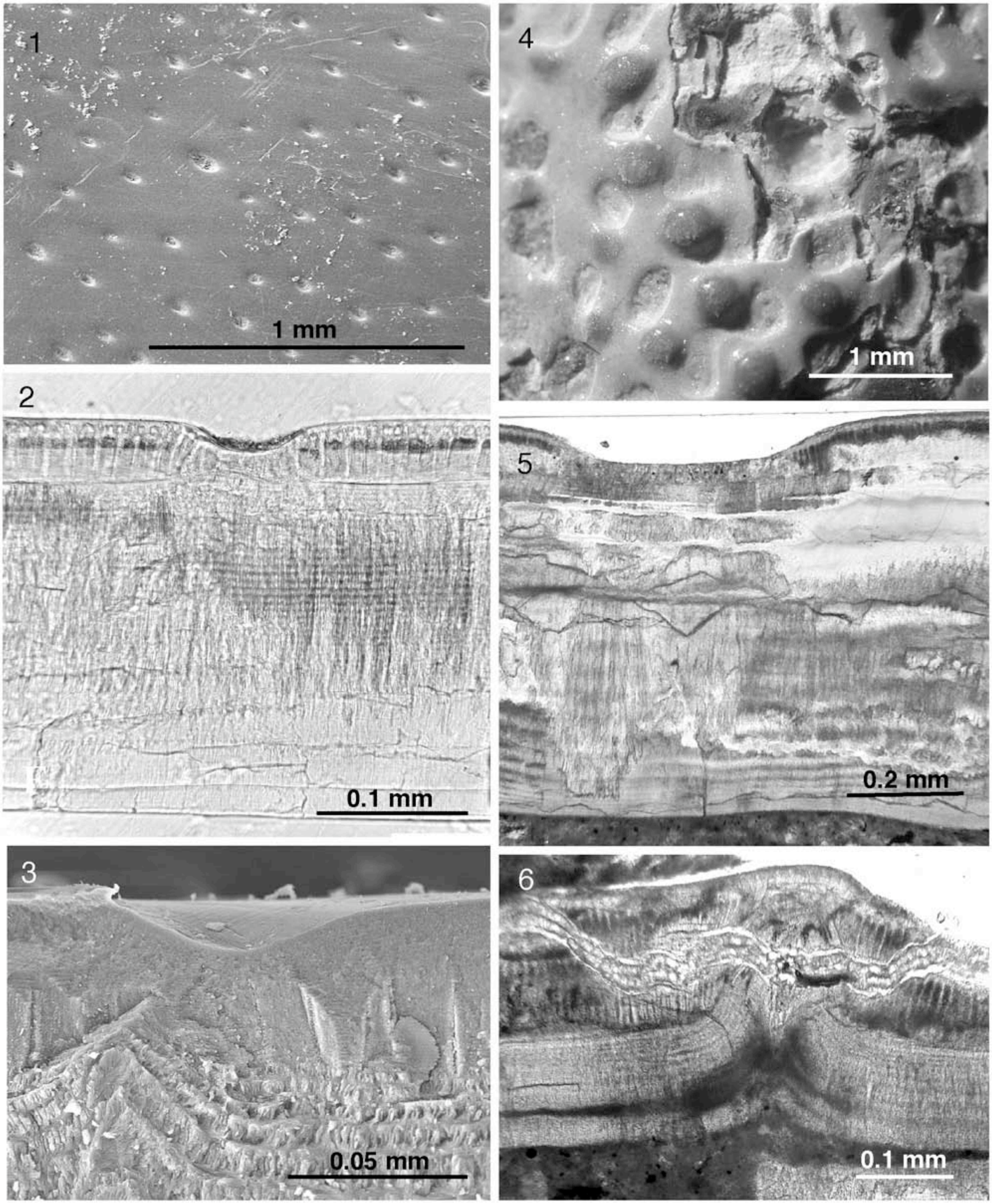

Fig. 4. 1, *Lyreidus tridentatus*, KSU K252, branchial surface. 2, *Lyreidus nitidus*, NNM 22469, thin section showing pits and slight rise of the endocuticle into the exocuticle adjacent to the pit. 3, SEM micrograph of specimen in Fig. 4.2, showing endocuticle protruding into the exocuticle. 4–6, *Macroacaena alseana*, KSU K254. 4, branchial surface. 5, thin section of steep sided pit. 6, thin section of upright node; note filled crack running horizontally though the thin section.

available for careful study including *Macroacaena naselensis, Macroacaena schencki,* and *Macroacaena alseana* (Fig. 4.4–6). Upright nodes are observed in association with the pits, especially on the medial parts of the dorsal carapace (Fig. 4.4). The upright nodes observed in a specimen of *M. alseana*, the only member of the genus available for thin sectioning, are covered with a thinner layer of exocuticle than the remaining carapace (Fig. 4.6). Presence of the exocuticle indicates that these nodes are truly emergent and project above the carapace surface. These nodes are formed entirely from laminations of the endocuticle (Fig. 4.6). The pits are completely contained within the exocuticle and are formed by thinning of the prismatic layer (Fig. 4.5). Observation of other species assigned to *Macroacaena*, based on photographs from the literature, suggest that other species are not typified by the large, steep sided pits and upright nodes described here.

In species of *Lyreidus*, pit size increases with increasing carapace dimensions (Fig. 12). It is likely that the steep sided pits in species of *Macroacaena* also exhibit this growth trend. An informal survey of the literature suggests that specimens possessing the larger, steep sided pits are larger than specimens with smaller carapace dimensions. These larger pits may not represent a distinct type of pit, but rather are the result of increasing carapace dimensions. The pit size on ***M. alseana*** shows a progression of increasing pit size that corresponds to the increasing width of the carapace measured at points along a longitudinal transect (Fig. 12.2). Pits toward the posterior margin are more like the smaller pits of *Lyreidus*. The progression of pit size and the surficial expression of upright nodes that are seen on a single specimen of *M. alseana* may be mirrored during growth, providing a model for the surface features of other species within the genus. A similar growth trend is seen in *Ranilia***.** Examination of *Symethis johnsoni,* (described with *Symethis*)**,** shows that the cuticle is similar to *Macroacaena* (Fig. 12.3). The nodes of *Symethis johnsoni* appear to be smaller versions of those seen in *Macroacaena*, which seems contrary to the observation

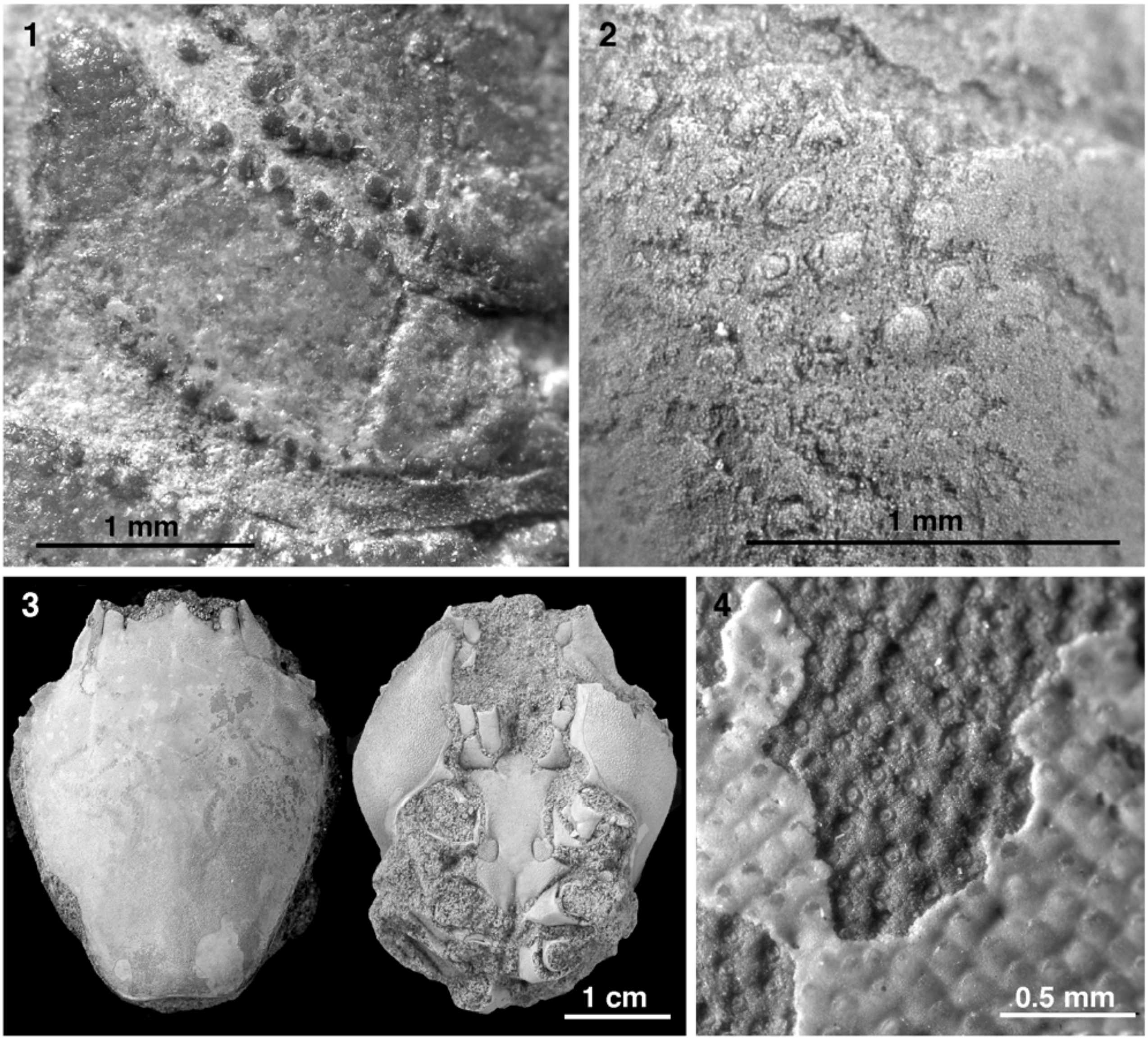

Fig. 5. 1–2, *Hemioon cunningtonii*, SM B23289. 1, cuticle between straps showing densely packed perforations, upright nodes only visible on upper strap. 2, branchial region showing damaged nodes of uncertain morphology. 3–4, *Raninella trigeri*, BM 63689, dorsal and ventral views. 4, partially exfoliated cuticle revealing prismatic layer and bases of upright nodes.

that the pits of *Lyreidus* and *Macroacaena* form a continuum. Further sampling will help determine the true nature and taxonomic distribution of these steep sided pits.

Genus *Hemioon* Bell, 1863

Discussion: There are three syntypes of *Hemioon cunningtonii*: BM 60137, BM In29965 and SM B23289 (Wright and Collins, 1972). Of these three specimens, only SM B23289, illustrated in plate 2, fig. 7 of Bell (1863), has cuticle preserved; it is also the most complete specimen within the type series. Anterior to the cervical groove, upright nodes are closely packed to form straps like those of *Eucorystes carteri*, and closely spaced perforations cover the depressed surface between the straps like those observed in *E. carteri* (Fig. 5.1). In addition to being damaged, the posterior of specimen SM B23289 is infested with a bopyrid making characterization of the surface difficult, but upright nodes are apparent in the branchial region (Fig. 5.2). The damage in the branchial region makes the nature of these upright nodes unclear. They could be the remains of upright nodes, fungiform nodes, or inclined nodes.

Glaessner (1969, p. R627) synonymized *Hemioon* with *Raninella* based on the advice of Wright and Collins (1972). They maintained that Bell's *H. cunningtonii* represented juvenile specimens of *H. elongata* (Wright and Collins, 1972). *Hemioon* then became available for *H. elongata*, and Wright and Collins (1972) revised the generic description and re-illustrated two of the three Bell specimens (BM 60137, BM In29965).

Based on two specimens of *Eucorystes* that we have sectioned, the straps and especially the cervical groove are constructed with all layers of the cuticle, which would leave an impression on the resulting steinkern. These features cannot be seen on the other two specimens within Bell's type series which are preserved as molds of the interior. It is probable that Bell's type material is not monospecific. Given these complications and others mentioned above, it is clear the *Hemioon* is in need of reevaluation. The observations contained here are only valid for the one specimen with preserved cuticle, SM B23289.

Genus *Raninella* A. Milne Edwards, 1862

Discussion: A specimen in the British Museum, BM 63689 (Fig. 5.3–4), collected from Cenomanian rocks in France, contains labels assigning it to *Hemioon elongatum* and *Raninella trigeri*. Pending further work, we assign the specimen to *Raninella trigeri* based on features of the dorsal carapace, especially the front. The specimen is exceptional, preserving cuticle, claws, and sternum. The dorsal carapace is densely covered by inclined nodes with slightly swollen tips (Fig. 5.4). Perforations are present, most notably posterior to the post-frontal margin. The perforations gradually disappear about one quarter of the way toward the posterior of the carapace. The cuticle on the dorsal surface is most comparable to that of *Notosceles ecuadorensis* (Fig. 6.5). The front and sternum resemble *Ranina americana*. Wright and Collins (1972) recognized the similarity of the front of *Raninella* with that of *Ranina*. The cuticle is inconsistent with all taxa we have observed in the Lyreidinae. Assuming we are correct in assigning BM 63689 to *R. trigeri*, *Raninella* is in need of reassignment.

Raninella oaheensis is covered in either pits or perforations. Based on observation of Bishop's (1978) illustrations, nearly upright nodes are present in the hepatic region. These observations must be considered tentative until better material can be examined, but the cuticle is unlike that of the specimens of *R. trigeri*.

Genus *Rogueus* Berglund and Feldmann, 1989

Discussion: *Rogueus orri* has steep sided pits and upright nodes on the dorsal carapace. These steep sided pits and nodes are almost identical to *Macroacaena*.

Subfamily Raninoidinae Lőrenthey, 1929 *in* Lőrenthey and Beurlen, 1929

Discussion: All species within the Raninoidinae contain inclined nodes.

Genus *Raninoides* H. Milne Edwards, 1837

(= *Laeviranina* Lőrenthey *in* Lőrenthey and Beurlen, 1929 = *Pseudorogueus* Fraaye, 1995)

Discussion: *Raninoides louisianensis*, extant, and *Raninoides vaderensis*, Eocene, have a consistent pattern of pits with narrow, inclined nodes entering the posterior margins of the pits (Fig. 6.1–2). Extant forms appear to have narrower nodes with slightly raised sides, whereas the fossil forms possess wider, inflated nodes. It is unclear whether this difference in node morphology is a result of evolution or simply loss of the epicuticle and/or the upper exocuticle during fossilization. *Raninoides bouvieri* and *Raninoides glabra* have similar inclined nodes compared to *R. louisianensis* and *R. vaderensis*, but in addition they exhibit setal pits that appear either in isolation or in association with a node (Fig. 6.2). In cross section small upright nodes are present next to the pits. These nodes are not emergent and their connection to the nodes present on the surface is unclear because too few of these features have been sectioned.

Genus *Notopoides* Henderson, 1888

Discussion: The branchial regions of *Notopoides latus*, are covered by inclined, blunt nodes without depressions and sparsely distributed pits (Fig. 6.4). It is unclear if the pits are setal, except in the frontal regions where setal hairs are visible in the cast of the surface. Toward the posterior the nodes are in subtle depressions. The nodes become more erect toward the anterior of the carapace with the addition of setal hairs just posterior to, and anterior to, the postfrontal ridge. The nodes are most comparable to *Umalia misakiensis*, although the nodes of *U. misakiensis* are noticeably longer and have comparatively more domed surfaces (Fig. 7.7).

Genus *Notosceles* Bourne, 1922

Discussion: *Notosceles ecuadorensis* is densely covered with low, sharply pointed, triangular nodes on the branchial region that grade into more swollen and upright nodes toward the front (Fig. 6.5 and 13.4–6). Nodes in the branchial regions are partially defined by slight depressions; these depressions diminish in size toward the anterior of

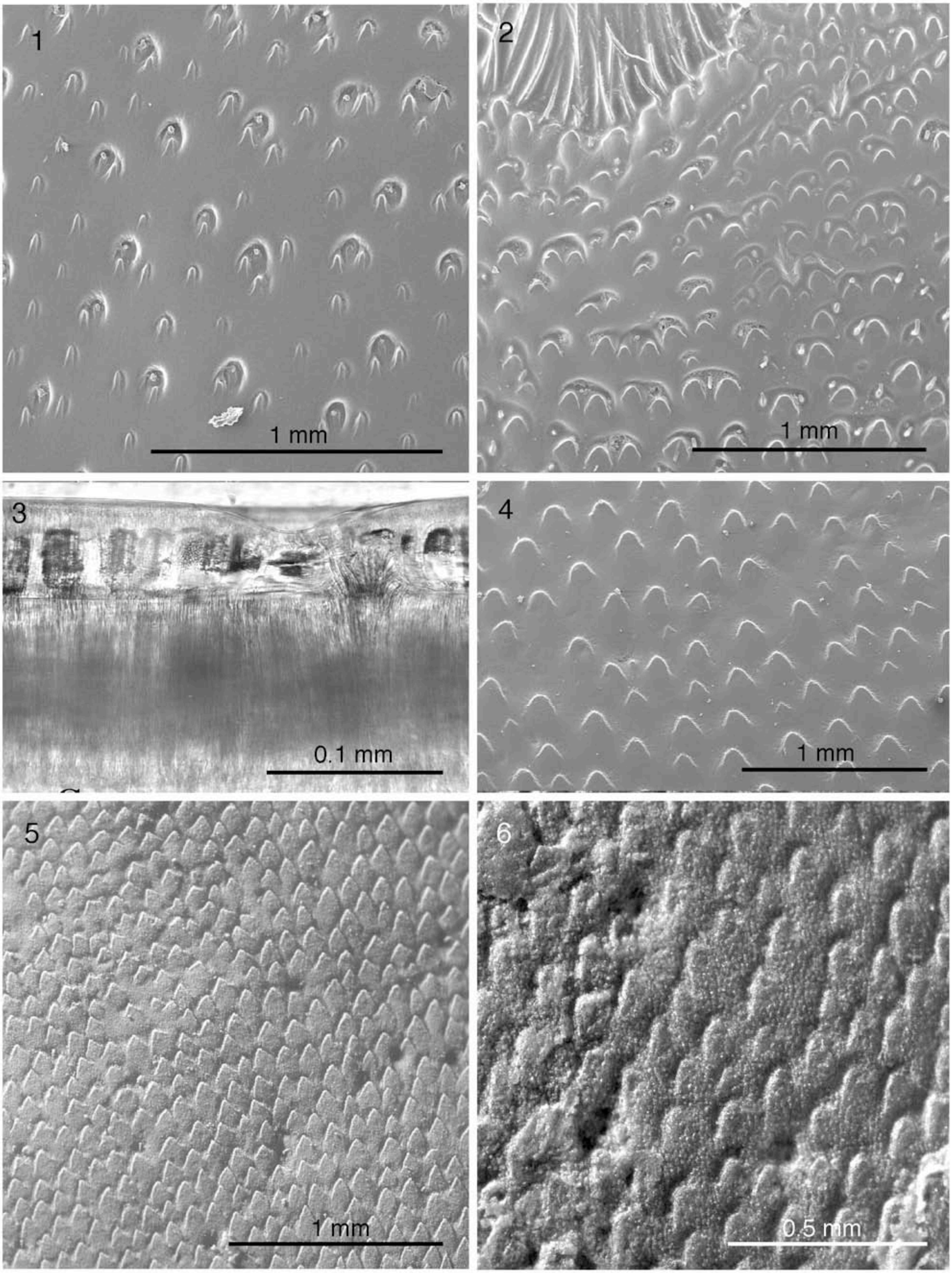

Fig. 6. 1–2, *Raninoides bouvieri*, NNM 38618. 1, cast of frontal region. 2, branchial surface. 3, *Raninoides louisianensis*, KSU K159, thin section of pit and non-emergent node originating from the endocuticle. 4, *Notopoides latus*, SENK 22364, branchial surface. 5, *Notosceles ecuadorensis*, USNM 173372, branchial surface. 6, *Quasilaeviranina ovalis*, USNM 371692, branchial surface, note exposure of the prismatic layer.

the carapace where they almost disappear. In addition to the nodes, setal pits are present on the dorsal carapace at a significantly lower density than the nodes (Fig. 6.5). In thin section, the nodes of the branchial region have little relief and are hardly noticeable. These nodes are apparently formed from the upper exocuticle and may not be readily preserved in fossil material. The larger nodes toward the anterior of the carapace are of unknown construction, but their larger size could indicate involvement of more cuticle layers. The larger width and much higher density of the nodes easily separate *N. ecuadorensis* from species of *Raninoides*. The cuticle of *N. ecuadorensis* is most comparable to that of *Quasilaeviranina ovalis* (Fig. 6.6). Both *N. ecuadorensis* and *Q. ovalis* can be distinguished from *Notopoides latus* based on the higher density of nodes in the former two species.

Genus *Quasilaeviranina* Tucker, 1998

Discussion: The cotypes of *Quasilaeviranina ovalis* are evenly and densely covered with inclined nodes defined by depressions on the anterior and lateral portions (Fig. 6.6). The specimen illustrated (Fig. 6.6) clearly shows the top of the prismatic layer, indicating that the upper exocuticle is missing.

A specimen, MCZ 1210, referred to *Quasilaeviranina simplicissima* displays sharp, low, inclined nodes, becoming more upright toward the anterior of the carapace. This cuticle is very similar in appearance to *Q. ovalis*.

One specimen, assigned to *Quasilaeviranina omboni*, MCZ 1131, has preserved cuticle on the branchial region, which appears to be covered in pits. As discussed above, and specifically in species of *Quasilaeviranina*, it can be difficult to interpret a poorly preserved surface. Because of the limited number of specimens of *Q. omboni* available, the observation of pits on the surface is in need of further verification.

Based on the specimens examined, *Quasilaeviranina* and *Notosceles* can be easily distinguished from *Notopoides* based on the extreme density of their nodes. *Quasilaeviranina* and *Notosceles* are both characterized by low inclined nodes that are densely packed, almost to the point of eliminating the internodal space. Lower densities of nodes, and the presence of pits on the branchial regions, separates *Quasilaeviranina*, *Notosceles*, and *Notopoides* from *Raninoides*.

Subfamily Notopodinae Seréne and Umali, 1972

Genus *Notopus* de Haan, 1841

Discussion: *Notopus dorsipes* (Fig. 7.2), as observed from a cast of the branchial surface, is covered in pits without perforations or nodes (Fig. 7.1). In the region of the postfrontal ridge and within small patches of the hepatic regions, sharp, inclined, and conical nodes appear. These sharp, conical nodes are unlike those we have observed in other raninids. The pits and nodes in the hepatic regions are like those seen in the holotype of *Pseudoraninella vahldieki*, although the holotype of *P. vahldieki* is missing the frontal region, preventing more detailed comparison with *N. dorsipes*.

Genus *Cosmonotus* Adams and White, 1848

Discussion: The dorsal surface of *Cosmonotus grayi* is unevenly covered in inclined nodes associated with setal pits (Fig. 8.1). Nodes are joined laterally in sets of two to five. The number of setal hairs roughly corresponds to the number of nodes in the grouping. The inclined nodes associated with setal pits described above are both more densely distributed and contain nodes that are more upright than in the branchial region, moving toward the medial and anterior regions of the carapace. The frontal region contains similar inclined nodes, but the pits are lost and the setal hairs emerge from perforations just anterior to the laterally joined nodes.

The cuticle of *Cosmonotus eocaenicus* is similar to *C. grayi* although the nodes on the branchial region are not as fully developed or were poorly preserved in the material examined.

Genus *Ranilia* H. Milne Edwards, 1837

(=*Notopella* Lőrenthey in Lőrenthey and Beurlen, 1929)

Discussion: *Ranilia constricta* has branchial regions evenly covered with setal pits (Fig. 8.2). Medially, and toward the anterior of the dorsal carapace, inclined nodes are introduced in conjunction with the setal pits (Figs. 8.3–4). The inclined nodes are present in laterally joined pairs medially and triads toward the front. Nodes near the front do not project into the pits, but rather lie in transversely elongate depressions (Fig. 8.4).

Specimens of *Ranilia muricata* have cuticle that is comparable to *R. constricta*. *Ranilia muricata* possesses not only setal pits in the branchial region, but also contains inclined nodes associated with the setal pits. The nodes become increasingly larger toward the medial and anterior regions of the carapace (Fig. 13.1–3). The sample lot of *R. muricata* examined contains a range of sizes, and the prominence of nodes on a given region increases with successively larger carapace sizes. The smallest specimen of *R. muricata* examined in fact did possess setal pits without nodes like those observed in *R. constricta*. These observations suggest that the inclined nodes of species within *Ranilia* become more prominent with increasing carapace size, forming a progression in the branchial region, starting with simple setal pits into which larger nodes are successively introduced.

The cuticle of *Ranilia* sp. (see Portell and Agnew, 2004) is consistent with that of the extant members of the genus. The surface is covered in setal pits that only grade into setal pits with inclined nodes toward the anterior. The specimen examined did not contain nodes within the branchial and medial parts of the carapace like those seen in *R. constricta* and *R. muricata*. Inclined nodes do begin to appear toward the frontal region (Portell, personal communication). Based on these observations, it appears that the cuticle of *Ranilia* is consistent across species, and differences are more highly correlated with carapace size.

Genus *Eumorphocorystes* Binkhorst, 1857

Discussion: *Eumorphocorystes* sculptus might be considered the archetype for the "straps" often described in raninids. The straps, as seen in cross section, are formed from a thickening of the laminations within the exocuticle and endocuticle (Fig. 7.4–5). Inclined nodes present on the leading edge of the straps are formed within both the

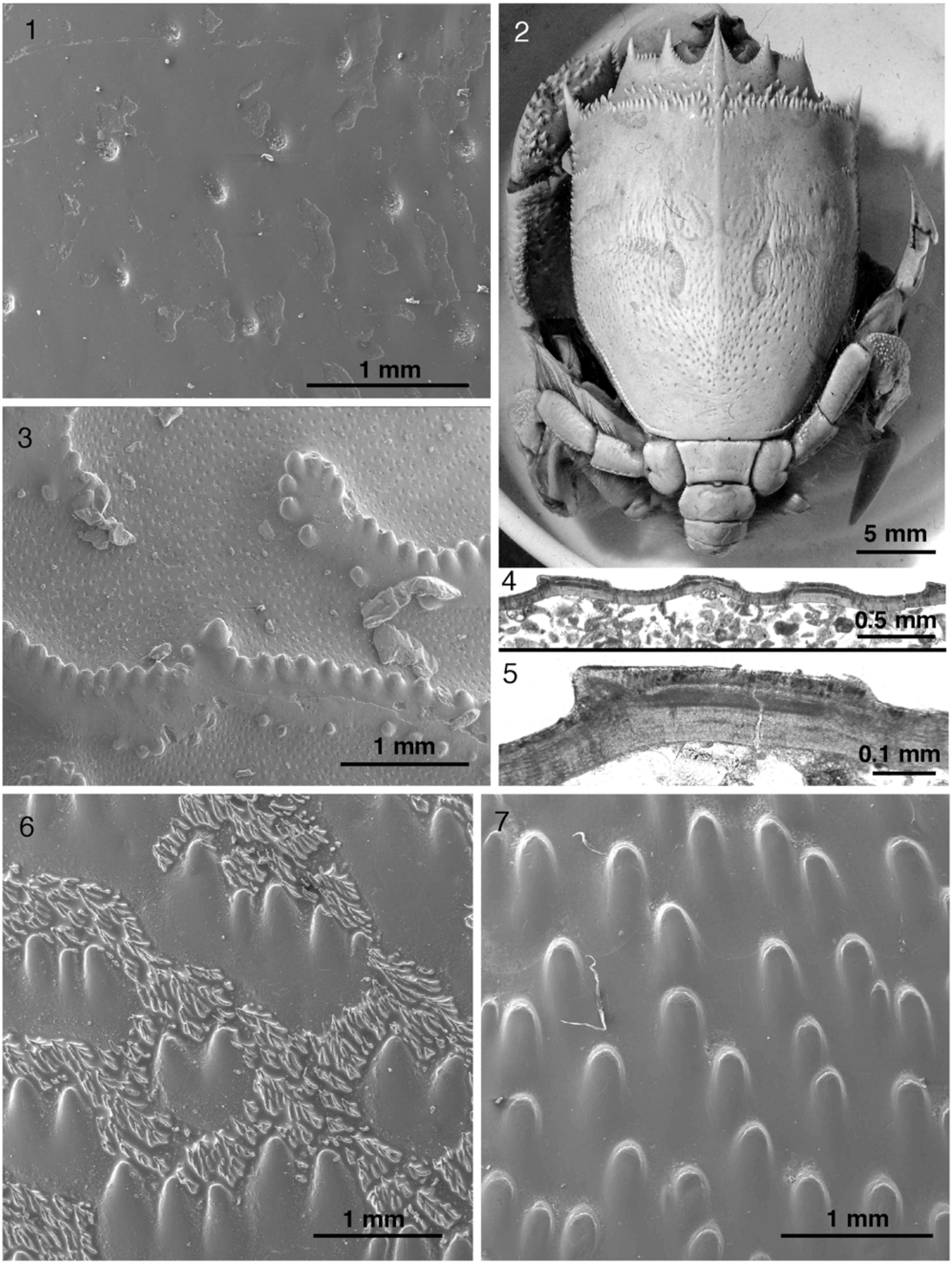

Fig. 7. 1–2, *Notopus dorsipes*, SENK 22373. 1, branchial surface. 2, dorsal carapace. 3–5, *Eumorphocorystes sculptus*, KSU K46, branchial surface, 4–5, thin sections perpendicular to straps. 6, *Umalia orientalis*, SENK 18661, cast of branchial surface, setae between rows of nodes have lost some definition due to molding and casting. 7, *Umalia misakiensis*, SENK 7663, cast of dorsal surface.

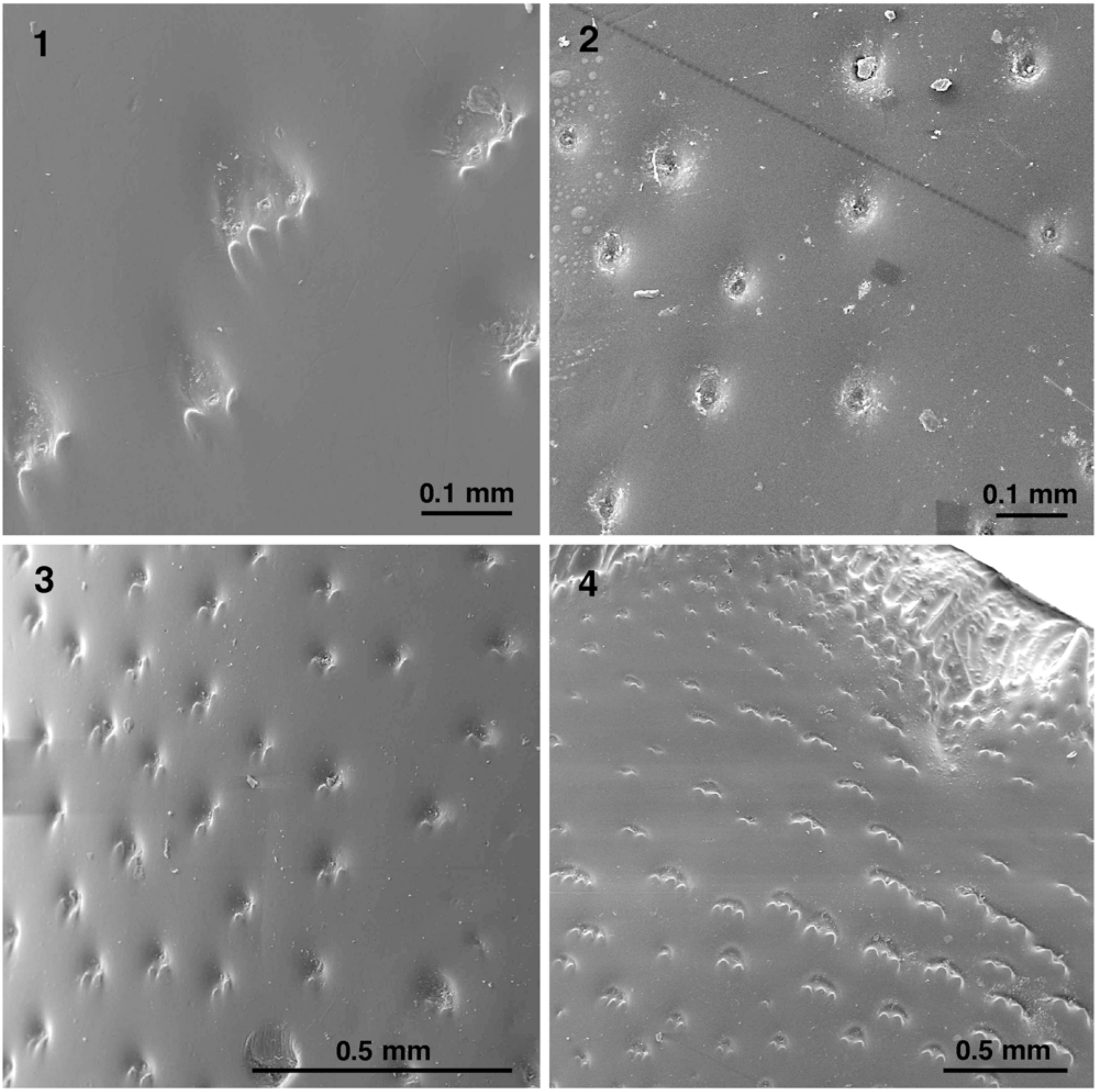

Fig. 8. 1, *Cosmonotus grayi*, SENK 22380, cast of branchial surface. 2–4, casts of *Ranilia constricta*, SENK 17019. 2, branchial surface. 3, cardiac region. 4, frontal surface.

endocuticle and exocuticle, but do not disrupt the laminations of the entire strap width. In plan view, the straps have flat tops that pitch toward the posterior, with nodes arrayed primarily on the anterior edge (Fig. 7.3). Nodes are occasionally present on the posterior of the straps, and commonly on lateral portions, when the straps are oriented longitudinally. Between the straps, the surface is covered with a dense field of perforations never observed on the strap or nodes surfaces (Fig. 7.3). With the exception of the wider straps, the cuticle surface is comparable to *Umalia orientalis*. Discussed under the genus *Umalia*, *U. orientalis* also possesses a dense field of setal hairs and perforations between the nodes, which are also laterally-joined forming straps, but that do not attain the width of the straps seen in *E. sculptus* (Fig. 7.3). The similarity of the cuticle between these two species suggests that *U. orientalis* serves as a modern analog for *E. sculptus*.

Genus *Pseudoraninella* Lőrenthey and Beurlen, 1929

Discussion: Examination of the holotype of *Pseudoraninella vahldieki*, although it is missing the front, shows large pits lacking perforations spaced roughly 1 mm apart on the dorsal surface. Patches of inclined nodes are present in pockets of depressed cuticle of the hepatic regions. The pits present on the dorsal carapace are unlike the perforations of *Eumorphocorystes*. Presence of pits and the lack of laterally joined inclined nodes suggests that *Pseudoraninella vahldieki* is in need of reassignment, possibly within *Notopus* which possesses both the pits and nodes in depressed portions of the hepatic regions. other species that were contained in the genus *Pseudoraninella* have not been examined.

Genus *Lovarina* Beschin, Busulini, De Angeli, Tessier, and Ungaro, 1991

Discussion: Based on photographs and line drawings of *Lovarina cristata*, the cuticle of the dorsal carapace, as noted by Tucker (1995), is most similar to *Lophoranina*. In contrast, the chelae and frontal regions are more similar to *Umalia*. *Umalia orientalis*, especially toward the anterior half of the carapace, does possess linked nodes, but they are not the terrace forming nodes seen in *Lovarina* and *Lophoranina*. Without examination of the sternum, *Lovarina* seems best placed within the Notopodinae. A similar cuticle bauplän and the functional requirements of burrowing could result in convergent cuticular forms between subfamilies or higher taxonomic levels.

Genus *Raniliformis* Jagt, Collins, and Fraaye, 1993

Discussion: Based on photographs of *Raniliformis baltica* in Jagt et al. (1993), the dorsal carapace is covered with a series of transversely elongate depressions that may contain muted or eroded nodes that grade into what are clearly inclined nodes with depressions toward the anterior. The anterior portion of the carapace is characterized by nodes linked to form terraces, such as those seen in *Umalia orientalis* and to a lesser extent in *Ranilia muricata*.

Illustrations of *Raniliformis prebaltica*, along with their original description, indicate that the cuticle of *R. prebaltica* is similar to that of *R. baltica*, although the nodes in the hepatic region are not as noticeably joined forming terraces, but rather are freestanding and isolated.

Genus *Umalia* Guinot, 1993

Discussion: Species of *Umalia*, including *Umalia orientalis* and *Umalia misakiensis* were removed from *Ranilia*. This reassignment was based on carapace shape, configuration of the front, eye placement, and carapace ornamentation (Guinot, 1993). Our observations of the cuticle support this generic reassignment. Casts made from the branchial regions of *Umalia orientalis* and *Umalia misakiensis* show surfaces with inclined nodes generally without pits or depressions. The exception to this statement is if that in *U. misakiensis* some nodes enter depressions near the lateral margins at the posterior of the carapace (Fig. 7.6–7). Depressions and paired nodes do appear in the lower part of the branchial regions of *U. misakiensis* where the carapace slopes toward the lateral and posterior margins. The cuticle between these two species is easily distinguished by the presence of densely spaced perforations and their associated setal hairs covering the internodal regions of *U. orientalis* (Fig. 7.7) and the pairing of nodes to form short terraces in *U. orientalis*. Nodes of *U. misakiensis* are not joined laterally and no perforations are present between the nodes (Fig. 7.6). Cuticle of *Ranilia*, in contrast, contains inclined nodes associated with setal pits. Inclined nodes and the complete absence of setal pits characterize species of *Umalia*.

Genus Lianira Beschin, Busulini, De Angeli, Tessier, and Ungaro, 1991

Discussion: Examination of both type and non-type material of *Lianira beschini* and *Lianira convexa*, shows that the branchial surfaces are covered in setal pits; anterior to the post-frontal margin, inclined nodes are introduced into the setal pits.

Subfamily Palaeocorystinae Lőrenthey *in* Lőrenthey and Beurlen, 1929

Discussion: The Palaeocorystinae is the only subfamily that typically exhibits upright nodes. Species of other families may have nodes that toward the front or hepatic regions are more upright than typical of the remaining dorsal carapace, but they never attain the truly upright position of the Palaeocorystinae. The extent that the nodes in *Macroacaena* are an exception is unclear.

Cretacoranina Mertin, 1941

Discussion: Haj and Feldmann (2002) translated the original description of *Cretacoranina schloenbachi* (Schlüter, 1879), the type species for the genus, and concluded that *C. schloenbachi* does have fungiform nodes. Jagt et al. (2003) concurred. We agree with Haj and Feldmann (2002) that the presence of fungiform nodes is a significant character of species within the genus. All species of *Cretacoranina* examined (Table 1) in this study with the exception of *Cretacoranina broderipii* (Fig. 10.11–12), *Cretacoranina ornatus*, and *Cretacoranina syriacus* possess these fungiform nodes. Based on this diagnostic feature of the cuticle, we suggest that *C. broderipii*, *C. ornatus*, and *C. syriacus* do not fit within *Cretacoranina*. Haj and Feldmann (2002) correctly identified the presence of fungiform nodes within *Eucorystes* (Fig. 10.1–3), and we report similar nodes in *Symethis* (Fig. 9.7–9). Clearly the presence of fungiform nodes is not limited to *Cretacoranina*.

The holotype of *Cretacoranina ornatus* is poorly preserved. Based on our examination of the specimen, fungiform nodes are not present on the surface. The upright nodes present on the surface are larger and less densely spaced than typical for raninids with fungiform nodes. In addition, some of the nodes appear to be paired. The high relief of the observed nodes is most likely a result of preferential loss of cuticle surrounding the nodes; the result is nodes with exaggerated relief. Based on these observations, we suggest that *C. ornatus* is in need of reassignment.

The holotype of *Cretacoranina syriacus*, BM I.8407, has a dorsal carapace covered with small upright nodes that are flush with or slightly below the surface in a density of about 8 per mm^2, often with a raised rim encircling the base of the nodes. The branchial region contains larger pits, possibly with perforations in a density of about 2 per mm^2. Although this specimen is incomplete, and the cuticle is not fully preserved for study, fungiform nodes were not present. *Cretacoranina syriacus* lacks the cuticular morphology typical of the genus as currently understood. The cuticle may well be similar to that of *Cretacoranina broderipii*, but the poor preservation prevents a full comparison.

Most specimens of *Cretacoranina broderipii* appear to have cuticle similar to *C. syriacus*; we were able to find specimens of *C. broderipii* in the collections of The Natural History Museum, London, with their original exterior surfaces present. The surface is covered in small, narrow inclined nodes (Fig. 10.12). In typically preserved specimens

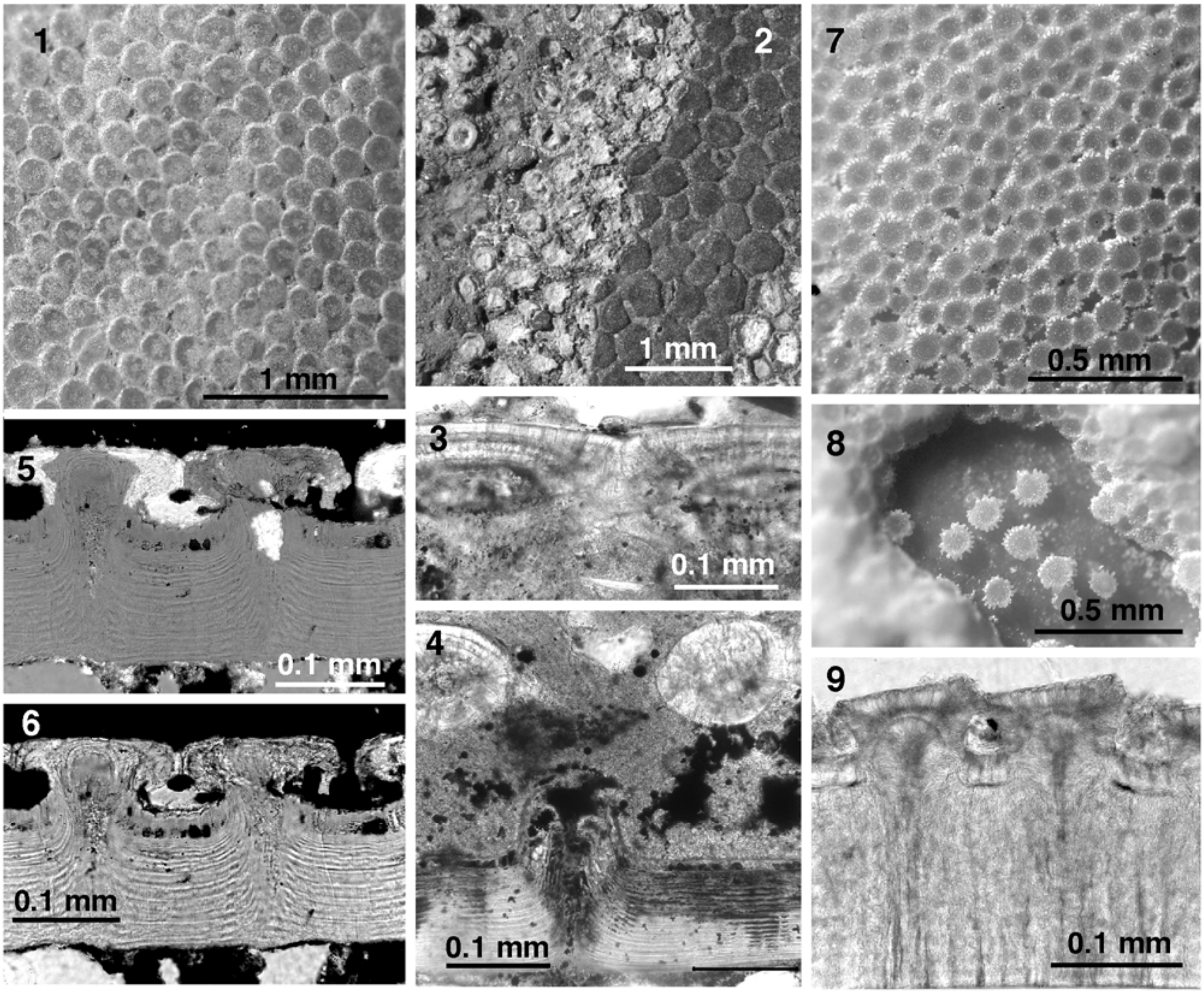

Fig. 9. 1, *Cretacoranina punctata*, KSU K272 branchial surface. 2–4, *Cretacoranina testacea*. KSU K162. 2, branchial surface, dark strip to right is the only undamaged region. 3, thin section, cross section of two node tops touching creating a planar surface, that when viewed tangentially (Fig. 9.2), forms the sides of a polygon. 4, neighboring nodes have not come into contact, nodes have curved margins, contrast with Fig. 9.3. 5–6, *Cretacoranina dichrous*, KSU K174, 5, thin section, cross polarized light. 6, thin section, plain polarized light. 7–9, *Symethis variolosa*, USNM 273180. 7, branchial surface. 8, surface on anterior half of carapace showing pockets with drastically reduced node density. 9, thin section, plain polarized light, showing fungiform nodes.

of *C. broderipii* the inclined nodes appear circular in plan view, and typically show varying levels of abrasion. Pits appear on the surface at a significantly lower density than the nodes; the presence of perforations within these pits is uncertain.

Haj and Feldmann (2002) described the fungiform nodes on the surface of *Cretacoranina punctata* (Fig. 9.1). *Cretacoranina punctata* has the fungiform nodes of *Cretacoranina*, but its sternum and frontal arrangement do not conform with the genus. Not observable on the other specimens of *Cretacoranina* that we examined because of poor exposures, but apparent in the illustrations of Haj and Feldmann (2002), are upright, possibly fungiform nodes covering the entire cuticle of the venter; a similar pattern is seen in Symethis. The placement of *Cretacoranina punctata* must also be reexamined.

Genus *Eucorystes* Bell, 1863

Discussion: Our examination of *Eucorystes carteri* confirms the observation of Haj and Feldmann (2002) that the dorsal surface, posterior to the cervical groove, contains the same fungiform nodes as does *Cretacoranina*. Anterior to the cervical groove, the surface is covered in straps composed of upright nodes of similar densities to those of the branchial region but not fully developed into fungiform nodes (Fig. 10.1). The straps are formed from both a change of thickness of the cuticle and deflections of the entire thickness (Fig. 10.3). The depressed regions between straps are devoid of nodes and covered in densely packed perforations (Fig. 10.4).

Genus *Notopocorystes* McCoy, 1849

Discussion: The dorsal surface of *Notopocorystes stokesi* (Fig. 10.6–10) and *Notopocorystes normanii* is covered in upright, but not fungiform, nodes. Regions between nodes are interspersed with

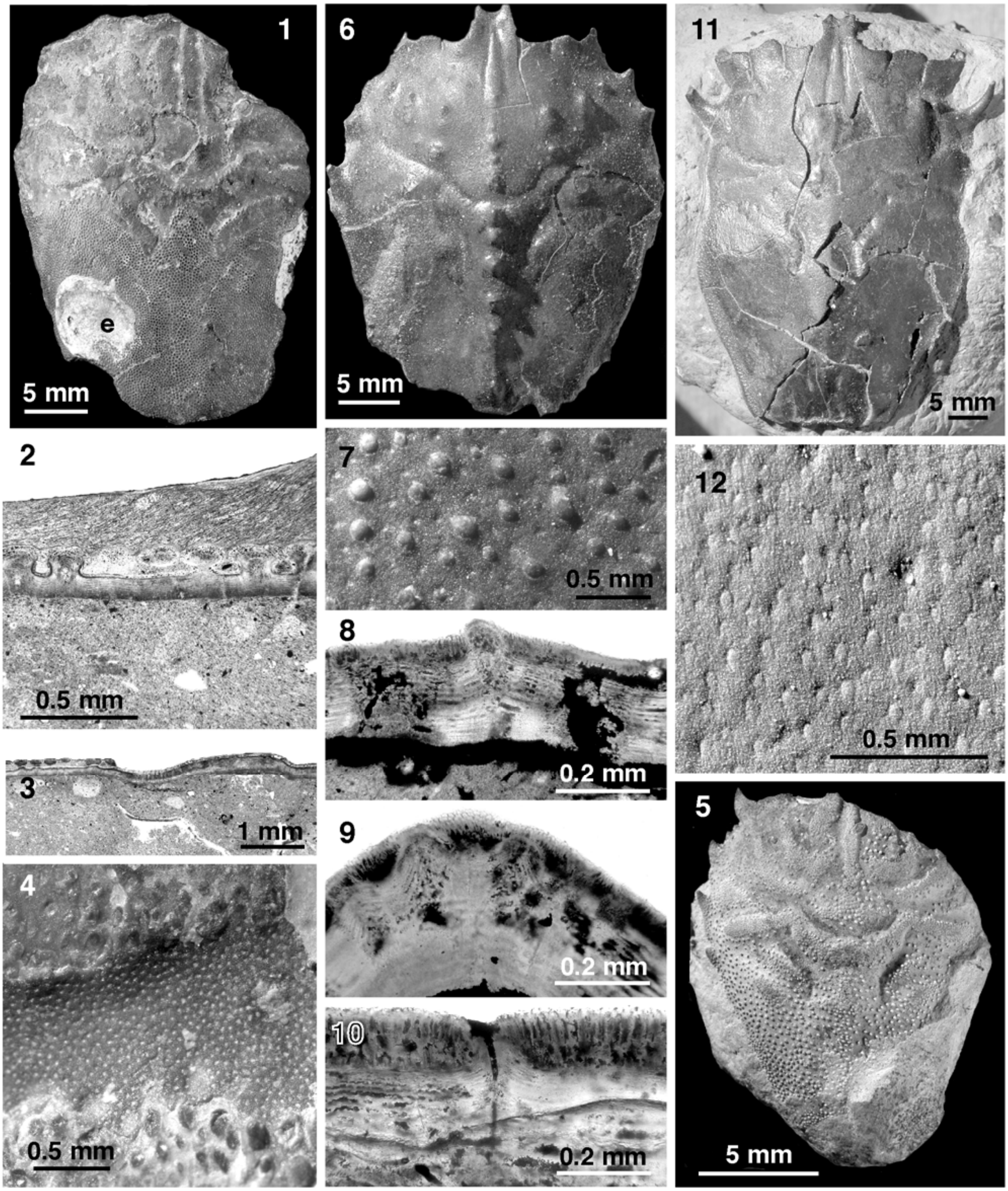

Fig. 10. 1–4, *Eucorystes carteri*. RBIS 8968. 1, dorsal carapace, note epibiont to the lower left "e". 2, thin section of branchial region, fibrous structure above nodes is epibiont seen in Fig. 10.2, note fungiform nodes with various degrees of fusion between neighboring nodes. 3, thin section, perpendicular to a "strap", note undulation of the entire cuticle thickness and thinning of the cuticle between straps. 4, zone of high-density perforations between straps. 5, *Eucorystes* sp., KSU K47, note that upright nodes of the branchial surface are apparently not close enough to form close-packed hexagonal nodes. 6–10, *Notopocorystes stokesi*. BM not cataloged, Lower Gault Clay. 6, dorsal carapace. 7, typical preservation of cuticle, branchial surface. 8, thin section through upright node, note that the upper exocuticle is missing and the whole exocuticle has been lost from the node top. 9, thin section through one of the larger nodes on the carapace midline, note that there are smaller upright nodes also contained in the larger nodes, exocuticle can be seen to cover two of the three nodes. 10, thin section through a perforation, note upright non-emergent node under perforation and canal, filled with an opaque substance, that penetrates the cuticle. 11–12, *Cretacoranina broderipii*, BM 29980. 11, dorsal carapace. 12, branchial surface.

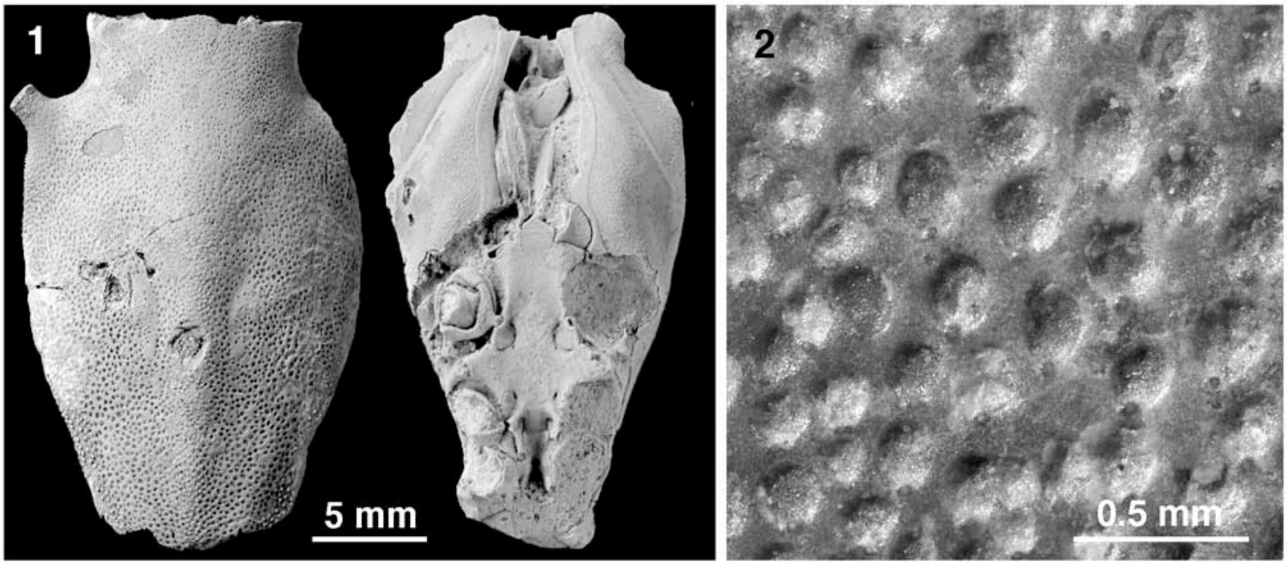

Fig. 11. 1–2, *Symethis johnsoni*, USNM 273180, 1, dorsal and ventral views of carapace, two specimens from the type series. 2, branchial surface.

perforations (Fig. 10.7). When the upper exocuticle is missing from the surface, the nodes appear upright. When the upper exocuticle is present, the nodes take on a slightly inclined appearance, at least as observed on the hepatic region which was the only well preserved part of the cuticle available for study. The inclination of these nodes does not reach the extent seen in species outside the subfamily. More pristine material is needed to fully evaluate the surface of *Notopocorystes*. Larger nodes on the surface of *Notopocorystes*, especially anterior of the cervical groove and carapace midline, contain the same upright nodes observed on the surface of other regions (Fig. 10.8). The perforations appear to vary in their density across populations collected from different localities and across different regions of the carapace, these may serve to distinguish the subspecies of *Notopocorystes stokesi* described by Wright and Collins (1972). The perforations are widest in the exocuticle and narrow within the endocuticle. Underneath the perforations are non-emergent nodes formed within the endocuticle that extend half the way up into the prismatic layer of the exocuticle (Fig. 10.10).

Subfamily Cyrtorhininae Guinot, 1993

Genus *Cyrtorhina* Monod, 1956

Discussion: Cuticle of *Cyrtorhina oblonga*, the only specimen examined directly, shows inclined nodes just posterior and anterior to the post-frontal ridge and apparently no surface features in the branchial regions, except near the lateral margins. Specimens illustrated in Tessier et al. (2004) of *C. fusseli* and *C. globosa* show inclined nodes covering the dorsal carapace. This suggests that *Cyrtorhina* has some variability in surface features or in preservation. Extant specimens of this subfamily have not been examined, thus, it may be premature to make generalizations about the cuticle of the Cyrtorhininae.

Family Symethidae Goeke, 1981
Subfamily Symethinae Goeke, 1981

Genus *Symethis* Weber, 1795

Discussion: With the exception of small outgrowths that radiate from the upper rim of the nodes (Fig. 9.7–8), the cuticle of *Symethis variolosa* is almost identical to that of *Cretacoranina* in possessing fungiform nodes (Fig. 9.9). Two important features that differentiate *Symethis variolosa* from those *Cretacoranina* that posses fungiform nodes are the depressed pockets of the cuticle on the anterior half of the carapace (Fig. 9.8) and grooves of depressed cuticle on either side of the midline. The depressions lack fungiform nodes and are therefore as deep as the nodes are high.

Although limited sampling of cuticle microstructure has been performed outside of the Raninoidea, the structures exhibited by *Symethis* and *Cretacoranina* are comparable to *Camarocarcinus arnesoni* Holland and Cvancara, 1958, and *Cancer* Linnaeus, 1758, which have large pillars within the exocuticle that originate from layers of the endocuticle. *Camarocarcinus arnesoni* has cuticle that is most similar to that of *Symethis* and *Cretacoranina* because the nodes on its surface are somewhat enlarged or bulbous at their tops. Recently, Feldmann et al. (2008) suggested that *Camarocarcinus* be assigned to a new family within the Raninoidea.

Symethis johnsoni, based on its sternum and cuticle (Fig. 11.1–2), clearly does not belong in the Symethidae. *Symethis johnsoni* should be reassigned to a genus in the Lyreidinae. The dorsal carapace of the holotype is covered in steep sided pits with upright nodes barely emergent on the posterior of the pit rim (Fig. 11.2). The cuticle is similar to that of *Macroacaena* (Fig. 4.4).

Morphometrics

Twenty species in eight raninid genera have been examined to determine the size and density of distribution of pits and nodes in relation to carapace size (Fig. 12.1). The trends seen within this data are an increase in feature size with increasing carapace dimensions and a decrease in the density of the features with increasing carapace size.

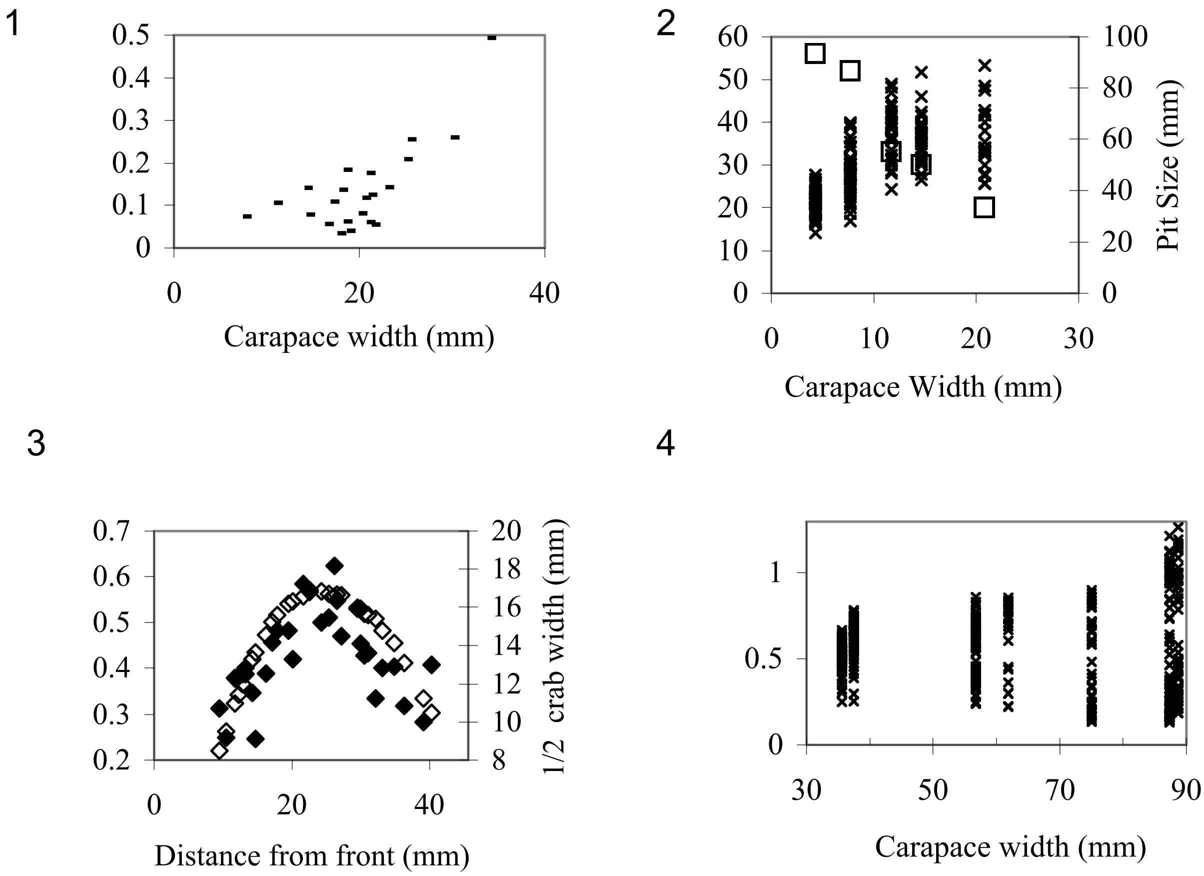

Fig. 12. 1, Pit size plotted against carapace width for raninids sampled from the KSU collection. Data points are averages of all measurements taken from the branchial region of each specimen. 2, pit size and density vs. carapace width of *Lyreidus tridentatus*; open boxes are density measurement taken on each specimen; × indicates individual measurements of pit sizes measured on the branchial region. 3, size distribution of pit size along a transverse transect on *Macroacaena alseana*, KSU K254, solid diamonds represent maximum pit size, open diamonds represent carapace width at each point along the transect that a pit measurement was taken. 4, carapace width plotted against node size in specimens of *Ranina ranina*, USNM 268504, 268510, 64628, 18874, 5230, and 106160, × indicates individual measurements of node width measurements taken on the branchial region of each crab, note that when the carapace width becomes greater than about 75 mm, new nodes are introduced between the smaller ones, causing the lower end of the node size distribution to decrease, while the maximum continues to increase.

Although a general trend can be seen in the sampled taxa, only *Ranina ranina* and *Lyreidus tridentatus* have been sampled with a significant number of specimens within a population to show this same trend during ontogeny. *Lyreidus* demonstrates a trend of increasing feature size and decreasing feature density with increased carapace size (Fig. 12.2). Samples from a population of *Ranina ranina,* were not measured for feature density, but do show increasing node size with increased carapace dimensions (Fig. 12.4). Also observed in *Callinectes sapidus* Rathbun, 1896, smaller nodes are introduced between the larger existing nodes during ontogeny in *Ranina ranina*. We have not examined enough raninid population samples to conclude that the introduction of smaller feature between larger ones during ontogeny is unique to *Ranina ranina,* but it is the only species that obviously exhibited this feature.

The link between the expanding size and decreasing density of pits and nodes can be expected from a simple model in which a portion of cuticle starts out with a given number and size of features that expands with each molt. This model of growth is too simplistic to apply uncritically, and the introduction of smaller nodes on the surface of *Ranina ranina* clearly does not follow this pattern (Fig. 12.4). Future work will examine the allometric relationship of all cuticle features with the expectation that certain features will show static growth, others will expand with growth, and some features may be introduced during growth. These patterns will likely provide important characters in their own right and help to clarify homology of features across taxa.

Although there is no expectation that all raninids should show an identical growth pattern of increasing cuticle feature size and decreasing density for strictly biological reasons, subtle differences in carapace vaulting and geometry will affect the surface area of the cuticle that cannot be reflected in the simple length and width measurements that were used to demonstrate overall growth trends. This more complex geometric relationship was tested across the carapace of a single individual of *Macroacaena alseana*. The dimensions of pits measured on a longitudinal transect clearly show a correlation with the changing dimensions along this axis (Fig. 12.3). A simple length or width measurement may capture the gross area of the cuticle, but will never show the true area causing feature dimensions to appear more variable when plotted against carapace dimensions. Although only quantified in *Macroacaena,* most taxa that we have examined show a similar trend of

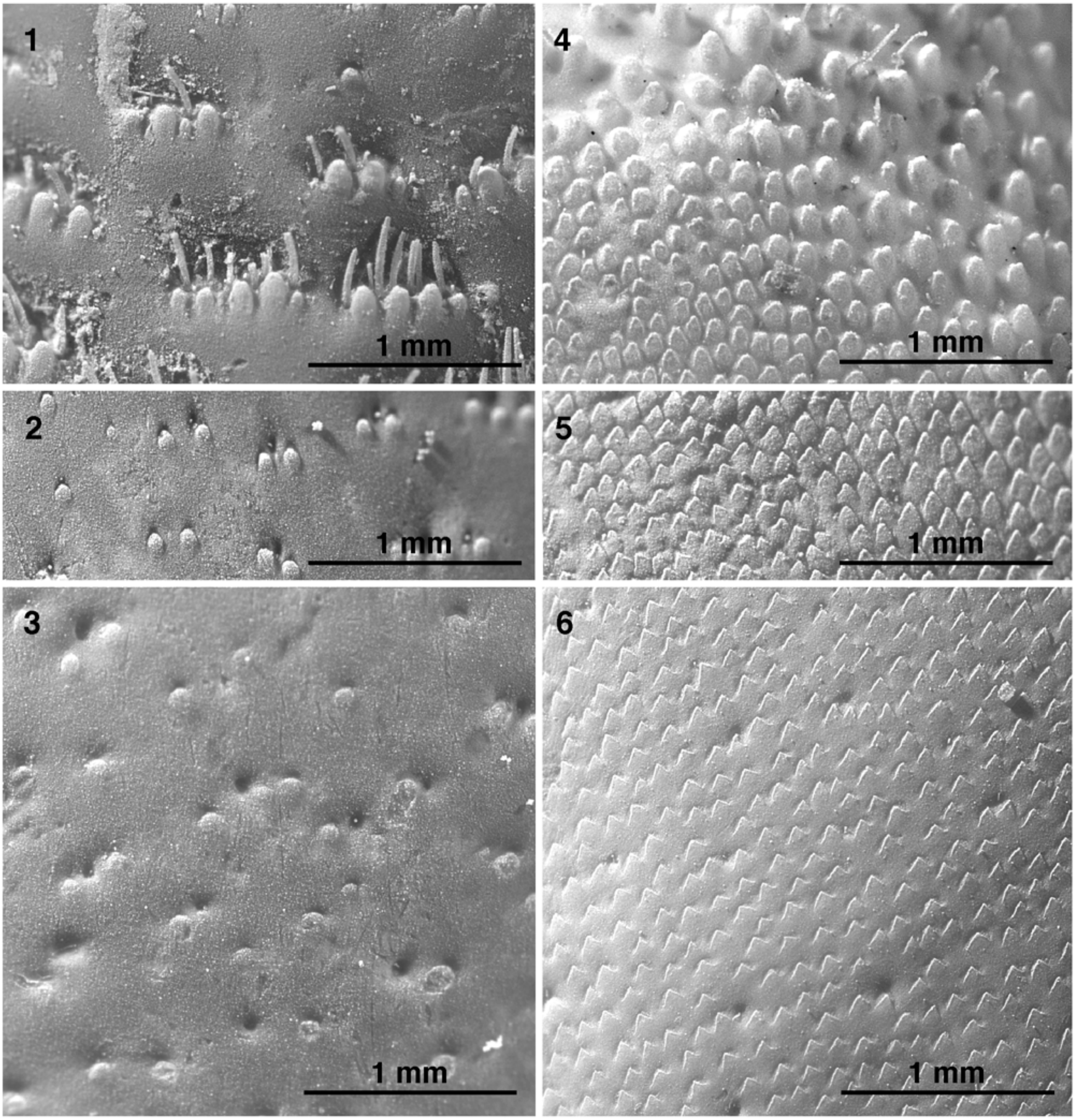

Fig. 13. Gradations of inclined node morphology on the carapace. 1–3, *Ranila muricata*, USNM 121656. 1, anterior of post-frontal ridge. 2, just lateral to carapace center. 3, lower branchial region. Nodes become more upright, and the pits lose definition, on the carapace posteriorly to anteriorly. 4–6, *Notosceles ecuadorensis*, USNM 173372. 1, anterior to post-frontal ridge. 2, just lateral to carapace center. 3, lower branchial region. Note that the nodes become less pointed and more upright from the posterior to the anterior of the carapace.

increasing feature size toward the widest part of the carapace.

In addition to increasing character size toward wider parts of the carapace, the characters of the features may change. Photographs taken of the posterior, middle, and anterior portions of the carapace on single specimens of *Ranilia* and *Notosceles* show nodes that are small and low toward the posterior and increase in size toward the front (Fig. 13). Nodes of *Notosceles* are sharply pointed toward the posterior and become more rounded and inflated, losing their sharp edges, toward the front. Species of *Ranilia* show an even stronger trend to the extent that the characters are coded differently. Toward the posterior, only setal pits are present, small nodes are introduced about one third of the way toward the front, and these nodes then increase in size and the pits grade into depressions moving toward the front.

These trends of feature size, density, and morphology that occur during ontogeny and across regions of the carapace indicate that the cuticle of crabs may not be sufficiently sampled by examining the cuticle from one location. Understanding these transitions can both help select how encompassing a character should be and at what taxonomic level that character is useful. Within a subfamily the presence or absence of depressions that surround inclined nodes may be significant; at the family level, the presence of absence of nodes, regardless of the presence or absence of depressions, may be the operative form of the character.

Progressions of feature morphology may also suggest a phylogenetic pattern. If species show a progression, either during growth or across the carapace, it is likely that closely related species would have cuticle that falls within the progression, rather than cuticle features that are never found on the same specimen or in a growth series. For example, inclined nodes are never found on species that also contain upright nodes, although species with upright nodes may also have fungiform nodes.

Discussion and Conclusions

Transitions of cuticle microstructures seen on the dorsal surface of the cuticle are observed on both single specimens and in monospecific populations with individuals of differing sizes. These transitions, such as nodes in pits becoming nodes in depressions and finally inclined nodes, appear to be correlated to increasing size of the carapace, or in the case of an individual specimen, the increase in carapace width along the longitudinal axis. Variation within an individual is typically the strongest near the lateral margin of the posterior and in the hepatic regions close to the lateral margins; these are areas in which the cuticle is forced into rapid changes of geometric shape. Because these transitions are observed in populations, or in individuals that presumably have a similar genotype, the transitions may be an expression of resultant morphotypes controlled by variation in the amount, or geometry, of expansion during a single molt or in a series of successive molts. From these transitions we may be able to infer the phylogenetic similarity of cuticle microstructures. Different taxa that possess features observed in a single species or on an individual are more likely to have closer phylogenetic similarities than two taxa with cuticle microstructures never seen in association.

Cuticle surface features are relatively stable within genera, excluding species discussed in the taxonomic section that are clearly in need of reassignment. Of the genera examined, *Umalia* contains the highest level of variation observed between two species within the same genus. *Umalia orientalis* has inclined nodes that are laterally joined to create terraces with closely spaced perforations containing setal hairs. In contrast, *Umalia misakiensis* only contains inclined nodes. *Eumorphocorystes sculptus*, a Cretaceous raninid, has cuticle remarkably similar to that of *U. orientalis*. *Eucorystes carteri* also has dense patches of perforations between its straps. These invariably low and perforated areas of cuticle show no indications of merging or grading into other features. It seems plausible that these low areas of cuticle containing dense fields of setae are the result either of some kind of phenotypic expression that reoccurs within raninids or from some kind of controlled tearing or over-extension of the cuticle during molting. If this speculative hypothesis is true, these features could come and go in lineages without resulting in a continuous signature in the fossil record. An ability to increase the expansion capability of the cuticle would allow increased growth rates which might be an advantage under certain selection pressures.

The general stability of surface features in raninid genera suggests that cuticle microstructures are conservative enough to provide a phylogenetic signal. Although the cuticle does not seem to have strong signals unique to each subfamily, utility of the microstructure is clear in solving taxonomic problems at the generic level. The greatest utility of this study may be the addition of newly recognized taxonomic characters. These additional characters will help to support generic placement of existing and yet undiscovered specimens based upon traditional morphological criteria. Placement of fragmentary and incomplete fossil specimens is most likely to benefit as they are lacking many of the currently recognized characters such as those of the front and sternum. Fossil material, including those specimens that are incomplete or fragmentary, must be described and placed within a taxonomic framework if our understanding of decapod phylogenetics is to advance. Paleogeographic and temporal distribution data based on fossil taxa all rely on correct taxonomic placement. Fine tuning of currently recognized taxa and correct placement of newly discovered specimens in a taxonomic framework has great implications for the construction of phylogenies at higher levels. Categorizing the microstructure of the cuticle can help place new taxa, and help identify misplaced taxa, and therefore improve the accuracy of taxon age ranges and biogeography which are ultimately the only available test of phylogenies or cladistic analyses.

At higher taxonomic levels within the Raninoidea, the phylogenetic signal of cuticle microstructure may not be clear within each currently recognized taxonomic grade. This does not suggest that characters of cuticle microstructure are not useful. A study based on one character, or group of related characters, is unlikely to formulate a reasonable phylogeny and certainly will not necessarily mirror one based on a diverse array of characters. Because the focus of this work is solely on cuticle microstructure, we have chosen not to make formal taxonomic changes, but rather we suggest areas that the characters of the cuticle indicate possible inconsistencies.

The Lyreidinae contains a fairly simple set of microstructures limited to pits and upright nodes. Cuticle of the Paleocorystinae is apparently very different from that of the other subfamilies, but more work is needed within this subfamily to understand relationships within and to other taxonomic groups. The remaining subfamilies within the Raninoidea, including the Ranininae, Raninoidinae, Cyrtorhininae, and Notopodinae, are generally similar to one another in their cuticle microstructure. They exhibit inclined nodes and various combinations of pits, setal pits, depressions, and perforations. The Symethinae contains fungiform nodes that are similar to those seen in *Cretacoranina*. Collectively, traditional taxonomic characters clearly separate these subfamilies indicating that cuticle microstructure, like many other characters, is best used in conjunction with other, unrelated characters. Working within the framework of other taxonomic characters, the Raninoidea can be divided into three groups based on cuticle microstructure, the Lyreidinae with pits and upright nodes, the Paleocorystinae with upright and fungiform nodes, and the Ranininae, Raninoidinae and Notopodinae with inclined nodes. As our work on decapod cuticle microstructure expands into other families, affinities with these three cuticle types within the Raninoidea will hopefully be established.

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