

EKALAKIA (DECAPODA: BRACHYURA): THE PRESERVATION OF EYES LINKS CRETACEOUS CRABS TO JURASSIC ANCESTORS

RODNEY M. FELDMANN,¹ CARRIE E. SCHWEITZER,² AND WILLIAM R. WAHL³

¹Department of Geology, Kent State University, Kent, Ohio 44242, <rfeldman@kent.edu>; ²Department of Geology, Kent State University Stark Campus, 6000 Frank Avenue NW, North Canton, Ohio 44720, <cschweit@kent.edu>; and ³Wyoming Dinosaur Center, 110 Carter Ranch Road, Thermopolis, Wyoming 82443, <wwahl2@aol.com>

ABSTRACT—Description of a new species of crab, *Ekalakia exophthalmops*, brings to two the number of species within this Late Cretaceous genus from the upper mid-west in North America. Discovery of eyes and orbital structures in both species permits placement of the genus within the superfamily Glaessneropsioidea Patruilius, 1959 and family Glaessneropsidae Patruilius, 1959, extending the range of those taxa from the Late Jurassic into the Late Cretaceous. The extraordinarily large eyes relative to body size suggests that the Jurassic reef-dwelling crabs were adapted for a cryptic lifestyle which preadapted them for the deep-water, dysphotic, level-bottom habitat occupied by the Cretaceous descendants.

INTRODUCTION

THE GENUS *Ekalakia* Bishop, 1976 has been an enigmatic taxon of fossil crabs since its description because it bore no resemblance to other Cretaceous crabs from the mid-continent in North America. Instead, it more closely resembled primitive crabs known from the Jurassic of Europe. Unfortunately, the preservation of the type material was incomplete, and the surfaces of the specimens were highly abraded, so that detailed comparison with other taxa was not possible. The two additional specimens of the type species collected subsequently (Tucker et al., 1987) did little to supplement the knowledge of the morphology of the genus.

Chance collection of two new specimens, one from Wyoming and one from Montana, has provided necessary morphological details to profoundly enhance our understanding of *Ekalakia* and to place it in a much broader context. At the same time, these discoveries shed light on the morphology of an enigmatic Jurassic genus, *Glaessneropsis* Patruilius, 1959. Interpreting the relationship between these two genera was made possible by the description, for the first time, of the morphology of the eyes and the orbital structures surrounding the eyes.

The discovery of new specimens of *Ekalakia* spurred examination of uncatalogued material in the collections of the U.S. National Museum of Natural History, which revealed 24 specimens collected from a single locality in southwestern North Dakota, tentatively identified as *E. lamberti* by G. A. Bishop in 1976. Some, and possibly all, of that material was collected by Barnum Brown in August, 1931. This material is extremely important because it is not only better and more completely preserved than the types, but it also contains several specimens that retain parts of the eyes and the orbital rim structures. Another specimen of *Ekalakia*, identified as *?Prosopton* sp. by M. J. Rathbun and collected from the Bearpaw Shale in Montana, is questionably referable to the new species described herein.

Thus, the purposes of this work are to describe a new species of *Ekalakia* from the Upper Cretaceous of Wyoming and Montana; to amend the description of the type species; to document the placement of *Ekalakia* and *Glaessneropsis* within the same family, the Glaessneropsidae Patruilius, 1959; to describe the stratigraphic and geographic range extension of the family; and to discuss the functional morphology of the orbital structures in the two known species of *Ekalakia*. Discovery of the eyes and orbital structures permits the hypothesis that they evolved in the Jurassic as an adaptation to a cryptic lifestyle in reefs and were pre-adapted to life in dysphotic, deeper water environments in Cretaceous siliciclastic environments.

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations.—BSP, Bayerische Staatsammlung für Paläontologie und historische Geologie München, Munich,

Germany; C.C.M., Carter County Museum, Ekalakia, Montana; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Class MALACOSTRACA Latreille, 1802
Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Superfamily GLAESSNEROPSIOIDEA Patruilius, 1959
Family GLAESSNEROPSIS Patruilius, 1959

Included genera.—*Glaessneropsis* Patruilius, 1959; *Ekalakia* Bishop, 1976.

Genus EKALAKIA Bishop, 1976

Type species.—*Ekalakia lamberti* Bishop, 1976, by original designation.

Included species.—*Ekalakia lamberti* Bishop, 1976; *E. exophthalmops* new species.

Diagnosis.—Small crab, outline pentagonal to ovoid, longer than wide; with downturned, axially sulcate rostrum; prominent orbital rim surrounding inner and posterior margin of orbits; rim separated from remainder of carapace by deep groove; lower orbital margin extending laterally into spine or lobose projection extending beyond lateral margin of carapace; eyes large; regions well defined; mesogastric region triangular, separated into two sub-regions; metagastric region bilobate; cardiac region ovoid, strongly elevated; metabranchial region depressed below level of remainder of carapace; cervical and branchiocardiac grooves prominent, subparallel.

Discussion.—Discovery of a second species of *Ekalakia* permits identification of characters common to both species and, therefore, refinement of generic characteristics. Thus, the diagnosis given here emphasizes the characters visible on members of both species. Notable is the development of the prominent orbital rims that embrace very large, nearly circular eyes. Although the presence of eyes with apparently short eyestalks that protrude from beneath the rostrum and that are protected to a limited extent by an orbital rim is seen in all glaessneropsids, the rim is not known to extend onto the margin of the rostrum in any other member of the Glaessneropsidae. The outer, lower orbital spine or projection is unique in the family.

EKALAKIA LAMBERTI Bishop, 1976
Figure 1.1, 1.2, 1.4–1.10

Diagnosis.—Small carapace, outline ovoid; longer than wide; maximum width measured at distance of about 70% maximum length from front; carapace anterior to cervical groove relatively small; rostrum axially sulcate, downturned; termination unknown. Margins of rostrum strongly inflated and granular. Eyes large,

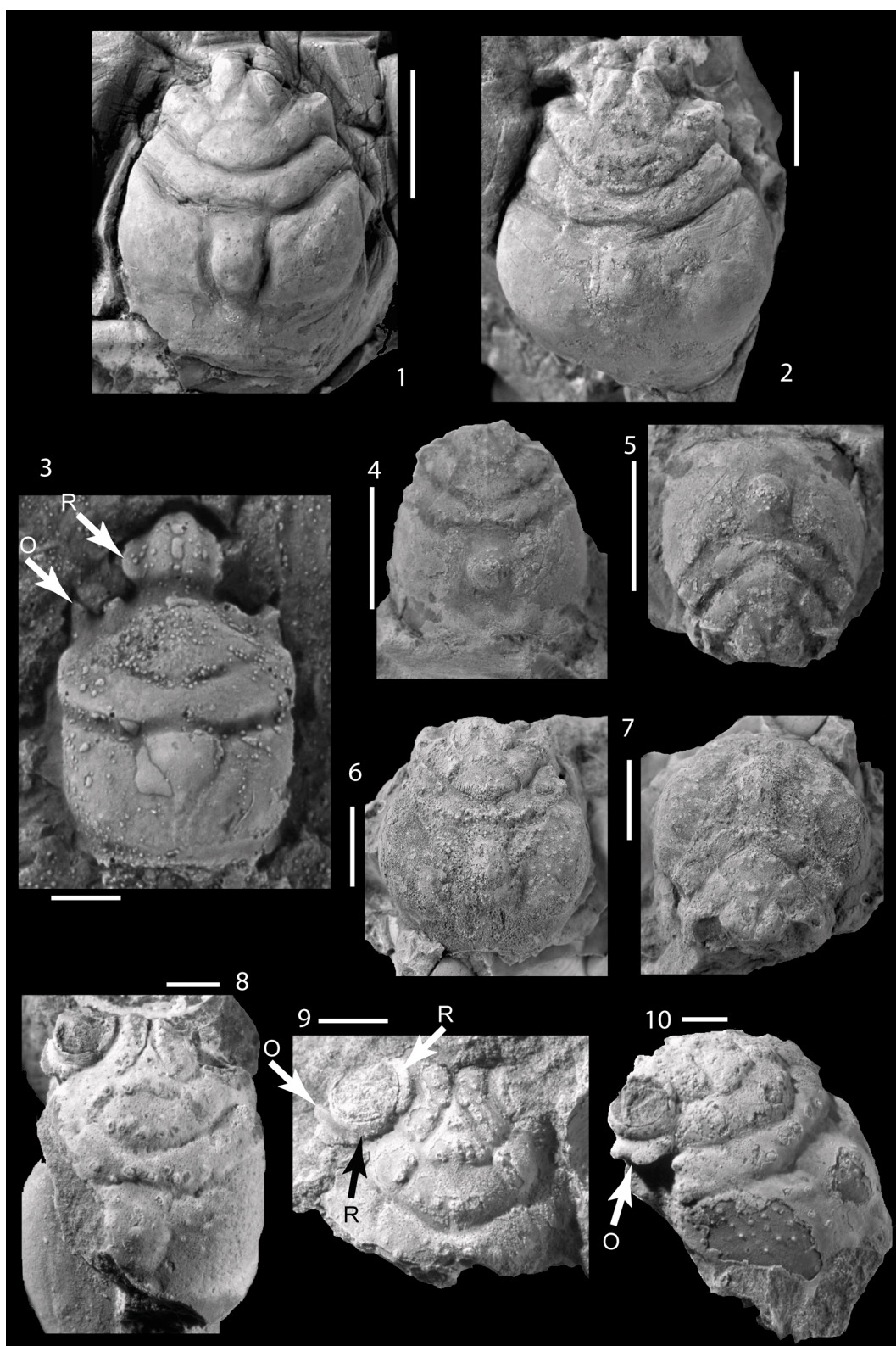


FIGURE 1—1, 2, 4–10, *Ekalakia lamberti* Bishop, 1976. 1, dorsal view of holotype, C.C.M. 5590; 2, dorsal view of paratype, C.C.M. 5571; 4, 5, dorsal and oblique frontal views of hypotype, CM 34559; 6, 7, dorsal and oblique frontal views of hypotype, CM 34558; 8, dorsal view of USNM 536306; 9, dorsal view of front part of carapace of USNM 536307; 10, oblique, left lateral view of USNM 536308. 3, *Glaessneropsis heraldica* (Moericke, 1897), cast of holotype, BSP AS III 306. Scale bar for 1, 2, 4–7 = 5 mm. Scale bars for 3, 8–10 = 1 mm. O = orbital projection; R = orbital rim.



FIGURE 2—*Ekalakia exophthalmops* new species. 1–3, Dorsal, frontal, and right lateral views of holotype, USNM 536328. 4, 5, dorsal and frontal views of paratype, USNM 536329. Scale bars = 1 mm. O = orbital projection; R = orbital rim.

circular, arising beneath rostrum, and directed forward and upward. Anterior orbital rim separated from rostrum by deep sulcus. Lateral termination of posterior orbital rim expanded into a broad plate bearing two blunt protuberances. Mesogastric region triangular with small anterior and larger posterior portions separated by subtle transverse groove; hepatic region strongly inflated. Cervical groove a smooth curve; branchiocardiac groove parallel to cervical groove. Cardiac region a prominent, circular swelling. Surface of cephalothorax moderately granular, becoming more finely granular on flanks of branchial region.

Occurrences.—All specimens of *Ekalakia lamberti* were collected from the uppermost part of the Campanian/Maastrichtian Pierre Shale (Bishop, 1976; Tucker et al., 1987). The type material, C.C.M. 5590 and 5571, was collected from two sites in southeastern Montana and deposited in the Carter County Museum in Ekalaka, Montana (Bishop, 1976). Subsequently described material, CM 34558 and 34559, was collected from southwestern North Dakota and deposited in the

Invertebrate Fossils collection of the Carnegie Museum, Pittsburgh, Pennsylvania (Tucker et al., 1987). These sites are all along the axis of the Cedar Creek Anticline. In addition to these sites, 22 additional specimens, USNM 536306–536327, were collected at USGS Locality 16003, 6½ miles (10.5 km) southwest from Marmarth, North Dakota, all presumably collected by Barnum Brown in August, 1931, and now deposited in the United States National Museum of Natural History, Washington, D.C. This locality, also on the Cedar Creek Anticline, is near locality A 1235 of Tucker et al. (1987).

EKALAKIA EXOPHTHALMOPS new species
Figure 2.1–2.5

Diagnosis.—Smaller and more quadrate than type species, with prominent outer orbital spine; cervical groove of two nearly straight elements; strongly granular ornamentation.

Description.—(Note: measurements and percentages are those determined on holotype; those taken on paratype are enclosed in brackets.) Small carapace, pentagonal outline, longer, 5.8 [6.2] mm than wide, 4.7 mm

width at outer orbital spine, 4.7 mm. Carapace width excluding eyes and spine, 4.5 [5.0] mm, measured at position 67 [71] % total length from front. Carapace anterior to cervical groove small; regions variable in expression; cervical and branchiocardiac grooves well defined; surface granular.

Rostrum broad, 40 % maximum width, downturned, axially sulcate, inflated on either side of sulcus, bounded on either lateral edge by orbital rim; termination not known. Frontal width, including inner orbital rims, 1.8 [2.4] mm; fronto-orbital width approximately equals maximum width.

Orbits large, semicircular, defined by thick orbital rim consisting of two parts; inner, anterior part extends longitudinally along anterior part of epigastric region and rostrum and is separated from it by broad sulcus. Narrow fissure in orbital rim separates anterior part of rim from posterior and lateral part of orbital rim. Fissure may serve as point of articulation of ocular peduncle. Posterior part of orbital rim paralleling anterior margin of protogastric and hepatic regions, separated from remainder of carapace by a sulcus. Rim flairs out laterally, at position of intersection of cervical groove with lateral margin, into rimmed platform that bears a sharp, anterolaterally directed, outer orbital spine marking widest part of carapace. Lateral margin between cervical and branchiocardiac grooves bears two strong, apparently blunt, spines. Posterolateral margin smoothly convex, becoming more strongly convex as it merges with rimmed, concave posterior margin.

Epigastric regions elongate, arcuate, extending onto rostrum, separated anteriorly from one another by axial sulcus extending onto rostrum and posteriorly by anterior part of mesogastric region. Distinct sulcus separates epigastric region from rectilinear protogastric region. Hepatic region distinct, moderately inflated. Mesogastric region more or less triangular; divided into triangular, coarsely pustulose anterior portion, and more weakly pustulose, posterior portion by transverse depression. Posterior portion of metagastric region bears domed swelling axially. Cervical groove consists of two nearly straight elements converging on midline at about 115° angle.

Metagastric region widest axial region, 60 [55] % maximum width; narrow axially, widens laterally; separated from bulbous, weakly pustulose epibranchial region by subtle sulcus. Urogastric region rectangular, about 3 times as wide as high, depressed. Cardiac region ovoid, longer than wide, about 24 [28] % maximum width, domed. Branchiocardiac groove with straight lateral elements converging on midline at about 130° angle to margin of cardiac region, then curving around cardiac region. Intestinal region narrow, straight-sided, indistinct.

Epibranchial region well-defined, quadrate, defined by cervical and branchiocardiac grooves and distinct longitudinal groove between it and mesogastric region. Mesobranchial region large, inflated; with triangular, somewhat more coarsely pustulose, branchial swellings on and separated from remainder of mesobranchial region by subtle arcuate depression. Metabranchial region with depressed surface bearing two broad, low elevations on each side.

Eyes very large, about 1 mm in diameter, nearly circular, nested within ocular ring so that ocular peduncle must have been short. Entire carapace surface pustulose or granular. Ventral surface, abdomen, and appendages not known.

Etymology.—The trivial name is the Greek word, *exophthalmops*, meaning bulging or protruding eyes in reference to the extremely large, circular eyes exhibited by the holotype specimen. The gender is female.

Types.—The holotype, USNM 536328, was collected in a roadcut along Wyoming Highway 270, SW corner, SW¼, sec. 34, T36N, R63W, Telephone Draw 7.5 minute Quadrangle, near Redbird, Niobrara County, Wyoming. The paratype, USNM 536329, was collected from NE corner, sec. 2, T13N, R55E, Upper Magpie Reservoir 7.5 minute Quadrangle, Dawson County, Montana. The specimens are deposited in the U.S. National Museum of Natural History, Washington, DC. A third specimen, which is incompletely preserved, lacking the front and orbits, may be referable to the species, as well. This specimen, USNM 536330, was collected from USGS Locality 22972, in the Bearpaw Shale 20 miles southwest from Mingsville (now Wibaux), Montana. It was tentatively identified as *?Prosopon* sp., presumably by M. J. Rathbun. Although the specimen is definitely assigned to *Ekalakia*, the species identification is tentative and, therefore, it should not be considered as part of the type series.

Occurrence.—Both type specimens were collected from the Late Cretaceous Pierre Shale. The holotype was collected from a silty limestone concretion within massive to finely laminated gray-brown mudstone and shale, bearing local ironstone and sparse phosphatic nodules. The sequence lies within the Western Interior Ammonite Taxon Range Zone of *Baculites grandis*, which is early Maastrichtian in age. *Baculites grandis* has a range of 70 ± 0.45 Ma (Cobban et al., 2006, Fig. 1). The stratigraphic details of the paratype are not known.

Discussion.—Bishop (1976, p. 400) described *Ekalakia lamberti*, based upon two specimens collected from two different locations in southeastern Montana (Fig. 2.4–2.5). Subsequently,

Tucker et al. (1987) noted the occurrence of two additional specimens of the species (Fig. 2.6–2.9) from two localities in southwestern North Dakota, quite near the localities from which the types were collected. The type material is completely decorticated and, as noted by Bishop (1976, p. 400), the surfaces of the specimens are severely scratched, ruling out the possibility of determining surface ornamentation. Further the fronts of both specimens are missing. Comparison of the type specimens to the two specimens collected from North Dakota supports the decision that they are conspecific. Again, the fronts of the specimens are missing but the comparison of the conformation of carapace grooves and development of regions is similar enough to warrant assigning the North Dakota specimens to *E. lamberti*. These specimens are somewhat better preserved and exhibit a finely granular surface sculpture.

The two specimens herein assigned to *Ekalakia exophthalmops* differ from *E. lamberti* in several significant ways that justify erecting a new species. The type species exhibits a more ovoid outline, has parallel, arcuate cervical and branchiocardiac grooves, bears a more inflated hepatic region, and has a very subdued branchial swelling on the mesobranchial region. In contrast, *E. exophthalmops* has a more quadrate outline, a cervical groove that is comprised of two straight elements converging on the midline at a more acute angle than the branchiocardiac groove, a more subtle hepatic region, and more prominent branchial swellings.

SUPRAGENERIC REASSIGNMENT

Presence of the front and orbital regions on both species of *Ekalakia* permits reassessment of the suprageneric placement of the genus. Bishop assigned the genus to the family Prosopidae von Meyer, 1860, which was consistent with the view of the primitive crabs at the time (Glaessner, 1969). *Ekalakia* is the first of the taxa previously assigned to the Prosopidae (sensu Glaessner, 1969) to have eyes preserved. This is significant because it permits, for the first time, describing the form of the eye in relation to the orbital structures. Recent re-examination of the Jurassic representatives of the Prosopidae (sensu Glaessner, 1969) resulted in major revision of the group (Feldmann et al., 2006; Schweitzer et al., 2007; Schweitzer and Feldmann, 2008a [imprint 2007]; Schweitzer and Feldmann, 2008b). Several of the morphological features that were significant in the re-classification were related to the form of the rostrum and the configuration of the orbits and accessory orbital features. One of the genera that was removed from the Prosopidae and assigned to a different superfamily and family was *Glaessneropsis* Patruilius, 1959. The Glaessneropsidae exhibit a broad, downturned, often sulcate rostrum bounded laterally by swellings (Fig. 1.3). The eyes arise from beneath the rostrum and lie within well-developed orbital rims. Because of the incomplete preservation of the orbital region, the swellings along the margin of the rostrum that are seen on specimens of *Glaessneropsis* were not interpreted as being part of the orbital rim. Presence of nearly complete rims enclosing the eyes on the holotype of *E. exophthalmops* now makes it possible to understand the nature of the morphology of that area and to ally *Ekalakia* with *Glaessneropsis*.

FUNCTIONAL MORPHOLOGY OF THE EYES

The orbital morphology is particularly significant. In contrast to most of the decapods that have traditionally been assigned to the Prosopidae s.l., the Glaessneropsidae are characterized by limited development of protective structures for the eyes. Most of the “prosopid” decapods other than the Glaessneropsidae have deep eye sockets into which the eyes can be retracted or some kind of augenrest surrounded at least partially by spines or nodes. In contrast, the eyes exhibited by *Ekalakia* spp. are extremely large and are exposed over a majority of their surface. Their position adjacent to the rostrum and surrounded on two sides by an orbital rim indicates that they would be exposed at all times; there

is no means by which the eyes could retract in times of stress. Although eyes have not been observed on the Jurassic members of the family, the similarity of rostrum shape, development of a similar orbital rim, and lack of protective structures strongly supports the conclusion that the eyes of Jurassic glaessneropsids were similar to those of *Ekalakia*.

Research on the structure and function of compound eyes in arthropods is voluminous; however, relatively little has been devoted specifically to eyes in brachyurans. Land (1984) described the compound eyes of the brachyurans that were then known to be of the apposition type. Apposition compound eyes are those in which each lens forms an independent image (Land, 1984). Subsequent and more comprehensive work on eye structure in the decapods (Gaten, 1998) demonstrated that only the more derived brachyurans exhibited apposition eyes and that the primitive, podotreme, crabs as well as many heterotremes were characterized by superposition compound eyes. Superposition compound eyes are those in which several lenses focus to form a single image (Land, 1984). *Ekalakia*, within the Glaessneropsidae, lies near the basal brachyuran stock and is likely a podotreme. Because discrete facets are not visible on the known specimens of *Ekalakia*, it is not possible to be more precise in the definition of the eye structure. Furthermore, the distinction between apposition and superposition eyes cannot be determined by an examination of the facets so that it may never be possible to determine the true nature of the eyes in fossils except by analogy with extant descendants. Thus, it is likely that *Ekalakia* had superposition compound eyes.

Several studies do bear directly on the interpretation of the size of eyes in *Ekalakia*. Hiller-Adams and Case (1985) observed that eye size increases with increased depth and that in superposition compound eyes, the larger the eye, the more sensitive it is. Hiller-Adams and Case (1985) demonstrated that not only do deep-water taxa have larger eyes than their shallow-water relatives, the growth rate of eye diameter, relative to body growth, increased with depth. Land (1999) noted that superposition eyes can be 2–3 times as sensitive to light as apposition eyes. This combination of observations regarding the relationship between eye size and sensitivity coupled with the probable possession of superposition compound eyes with their greater sensitivity leads to the conclusion that *Ekalakia* was adapted to an environment characterized by low light levels.

The lack of protective structures for the eyes, the very large size of the eyes relative to the body size of the crab, and the small size of the crabs, support the notion that representatives of the family were adapted to cryptic habitats where they could seek shelter in times of stress and forage successfully under limited light conditions. The Jurassic representatives of the family are preserved in reefal rocks, and the tiny size of the organisms would be ideal for hiding within reentrants in the reefs. Feeding might have been limited to night time when the large eyes would serve them well. Although *Ekalakia* spp. probably inhabited level-bottom rather than reef communities, it is possible that the eyes were pre-adapted for this lifestyle. The Pierre Shale was deposited in offshore, moderately deep settings, below wave base, and it is possible that the small size would, again, be suited for seeking shelter under mollusk shells or in other available nooks. The small size would also make the crab light-weight which would permit it to forage on a soft substrate. The large eyes would serve the animal under dysphotic conditions and during nocturnal foraging.

PALEOGEOGRAPHY

Placement of *Ekalakia* within the Glaessneropsidae significantly extends the geographic and geological range of the family. Previously, all representatives of the family have been described from central and southern Europe, in rocks of Jurassic age (Schweitzer and Feldmann, accepted). The occurrence of *Ekalakia* in Campanian

to Maastrichtian rocks of the midcontinent of North America suggests that further collecting in rocks spanning that time interval may yield more material and elucidate the dispersal pathway. One might tentatively suggest a Tethyan dispersal route owing to the occurrence of the Jurassic forms in reefal carbonate rocks. It is also important to note that the North American occurrences of *Ekalakia* occur in fine-grained siliciclastic sediments, rather than carbonate rocks. This may suggest that representatives of the family may have radiated from warm water, cryptic reefal habitats to temperate water, level bottom communities below wave base.

ACKNOWLEDGMENTS

Study of Jurassic decapods in Romania was supported by NSF INT 0313636 to Feldmann and Schweitzer. Examination of museum collections was supported by NSF EF 0531670 to Feldmann and Schweitzer. The holotype of *Ekalakia exophthalmops* was collected by R. Eason, Casper, Wyoming, and was donated to the non-profit Big Horn Basin Foundation associated with the Wyoming Dinosaur Center, Thermopolis, Wyoming. The Foundation generously consented to deposit the specimen in the U.S. National Museum of Natural History. The paratype specimen was collected by D. Hansen, Bismarck, North Dakota, who agreed to have the specimen deposited in the U.S. National Museum of Natural History. W. White, Director, Carter County Museum, Ekalaka, Montana, loaned the type material of *E. lamberti* to RMF and CES. A. Kollar, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, made the specimens of *E. lamberti* from North Dakota available for study. J. Thompson and the late W. Blow loaned comparative material from the U.S. National Museum of Natural History. Our thanks to these individuals.

REFERENCES

- BISHOP, G. A. 1976. *Ekalakia lamberti* n. gen., n. sp. (Crustacea: Decapoda) from the Upper Cretaceous Pierre Shale of eastern Montana. *Journal of Paleontology*, 50:398–401.
- COBBAN, W. A., I. WALAXZCZYK, J. D. OBRADOVICH, AND K. C. MCKINNEY. 2006. A USGS zonal table for the Upper Cretaceous Middle Cenomanian-Maastrichtian of the Western Interior of the United States based on ammonites, inoceramids, and radiometric ages. U.S. Geological Survey Open-File Report, 2006–1250:47 p.
- FELDMANN, R. M., I. LAZÁR, AND C. E. SCHWEITZER. 2006. New crabs (Decapoda: Brachyura: Prosopidae) from Jurassic (Oxfordian) sponge bioherms of Dobrogea, Romania. *Bulletin of the Mizunami Fossil Museum*, 33:1–20.
- GATEN, E. 1998. Optics and phylogeny: is there an insight? The evolution of superposition eyes in the Decapoda (Crustacea). *Contributions to Zoology*, 67:223–235.
- GLAESSNER, M. F. 1969. Decapoda, p. R400–R533, R626–R628. In R. C. Moore, (ed.), *Treatise on Invertebrate Paleontology*, Pt. R4(2), Geological Society of America and University of Kansas Press, Lawrence.
- HILLER-ADAMS, P. AND J. F. CASE. 1985. Optical parameters of the eyes of some benthic decapods as a function of habitat depth (Crustacea, Decapoda). *Zoomorphology*, 105:108–113.
- LAND, M. F. 1984. Crustacea, p. 401–438. In M.-A. Ali (ed.), *Photoreception and vision in Invertebrates*, Plenum Press, New York.
- LAND, M. F. 1999. Compound eye structure: Matching eye to environment, p. 51–71. In S. N. Archer (ed.), *Adaptive Mechanisms in the Ecology of Vision*, Kluwer Academic Publishers, Dordrecht, The Netherlands.
- LATREILLE, P. A. 1802–1803. *Histoire naturelle, générale et particulière, des crustacés et des insectes*, Volume 3, DuFart, Paris, 468 p.
- MEYER, H. VON. 1860. Die Prosoponiden oder die Familie der Maskenkrebse. *Palaeontographica*, 7:183–222.
- PATRULIUS, D. 1959. Contributions à la systématique des décapodes néojurassiques. *Revue de Géologie et Géographie*, 3:249–257.
- SCHWEITZER, C. E. AND R. M. FELDMANN. 2008a [imprint 2007]. A new classification for some Jurassic Brachyura (Crustacea: Decapoda: Brachyura: Homolodromioidea): Families Goniidromitidae Beurlen, 1932 and Tanidromitidae new family. *Senckenbergiana lethaea*, 87:119–156.
- SCHWEITZER, C. E. AND R. M. FELDMANN. 2008b. Revision of the Prosopinae sensu Glaessner, 1969 (Crustacea: Decapoda: Brachyura) including 4 new families and 4 new genera. *Annalen des Naturhistorischen Museums Wien*, series, 110.
- SCHWEITZER, C. E., R. M. FELDMANN, AND I. LAZÁR. 2007. Decapods from Jurassic (Oxfordian) sponge megafacies of Dobrogea, Romania and reconsideration of *Nodoprosopon* Beurlen, 1928. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 244:99–133.
- TUCKER, A. B., R. M. FELDMANN, F. D. HOLLAND JR., AND K. F. BRINSTER. 1987. Fossil crab (Decapoda: Brachyura) fauna from the Late Cretaceous (Campanian-Maastrichtian) Pierre Shale in Bowman County, North Dakota. *Annals of Carnegie Museum*, 56:275–288.

ACCEPTED 21 FEBRUARY 2008