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GLYPHEA FORESTI N. SP. (DECAPODA) FROM THE CENOMANIAN OF
NORTHERN TERRITORY, AUSTRALIA

BY

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ABSTRACT

Examination of two well-preserved Cenomanian (Late Cretaceous) specimens of a glypheid lobster from Northern Territory, Australia, permits description of a new species, *Glyphea foresti*. The epistome of the new species and of *Glyphea alexandri* Taylor, 1979, and *G. regleyana* (Desmarest, 1822) is not fused to the cephalothorax. Southern hemisphere representatives of the genus *Glyphea* exhibit similarities in development of the carapace grooves suggesting that they are closely allied and that they may have been the rootstock of the living, tropical western Pacific *Neoglyphea inopinata* Forest & de Saint Laurent, 1975. The rounded margins of the abdominal pleura suggest that the paratype specimen is a female, based upon comparison with that region on *Neoglyphea inopinata*. Sexual dimorphism was previously recognized in *Glyphea regleyana* by Etallon (1858).

RÉSUMÉ

L'examen de deux spécimens bien conservés du Cénomaniens (Crétacé Supérieur) d'un glyphéide provenant de Northern Territory, Australie, a permis la description d'une nouvelle espèce, *Glyphea foresti*. L'épistome de la nouvelle espèce et de *Glyphea alexandri* Taylor, 1979, comme celui de *G. regleyana* (Desmarest, 1822) n'est pas soudé au céphalothorax. Les représentants de l'hémisphère Sud du genre *Glyphea* présentent des similarités dans le développement des sillons de la carapace, suggérant qu'ils sont étroitement apparentés et qu'ils pourraient être le groupe ancestral de l'espèce actuelle vivant dans le Pacifique tropical occidental, *Neoglyphea inopinata* Forest & de Saint Laurent, 1975. Les bords arrondis des pleurons abdominaux suggèrent que le spécimen paratype est une femelle, sur la base de la comparaison avec la région correspondante de *Neoglyphea inopinata*. Un dimorphisme sexuel avait été auparavant observé chez *Glyphea regleyana* par Etallon (1858).

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INTRODUCTION

In 1954, the National Geographic Society sponsored an expedition to the area of Melville and Bathurst islands, Northern Territory, Australia (fig. 1). As a result of that work, Dr. B. Daily collected a number of Cenomanian fossils including ammonite cephalopods and lobsters. The ammonites were subsequently sent to C. W. Wright, then at Phillimore Gardens, London, by M. F. Glaessner and were published (Wright, 1963). Glaessner retained two specimens of a glypheid lobster collected from Bathurst Island by Daily. Subsequently, Glaessner gave one of us (M. de S.L.) the material for description. Thus, the purposes of this paper are to describe these specimens as a new species, referable to *Glyphea*; to provide evidence bearing on the fusion of the epistome to the cephalothorax in this genus; to consider the significance of chelae and pseudochelae as the basis for distinguishing the Astacidea from the Palinura; and to comment on the systematic position of the Glypheoidea.

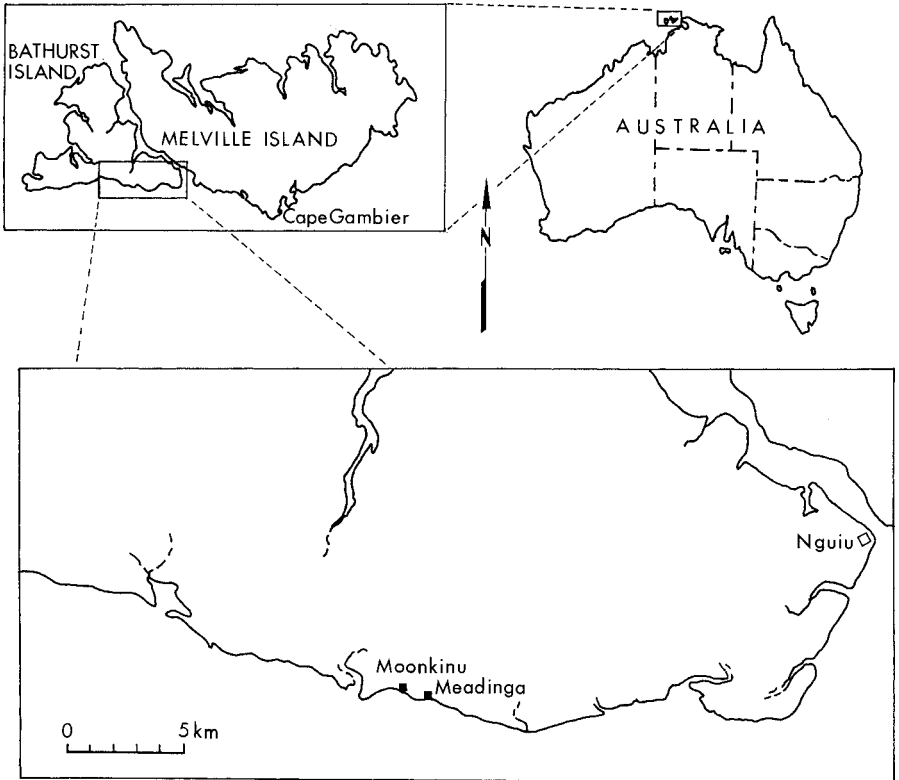


Fig. 1. Maps showing the locality, at Meadinga, on Bathurst Island, Australia, from which *Glyphea foresti* n. sp. was collected. Maps based upon locality data in Wright (1963).

SYSTEMATICS

Order DECAPODA Latreille, 1802

Superfamily GLYPHEOIDEA Winkler, 1882

Remarks. — The Glypheoidea have traditionally been placed within the infraorder Palinura, an infraorder characterized by the possession of pseudochelate, rather than truly chelate, pereiopods; the development of an epistomal plate that is inferred to have been fused to the cephalothorax; and the lack of a well-developed rostrum (Glaessner, 1969). Of these characters, the glypheoids were known to be exceptional in their possession of a well-developed rostrum. The discovery (Forest & de Saint Laurent, 1975) and subsequent detailed description (Forest et al., 1976; Forest & de Saint Laurent, 1981, 1989) of a living glypheid collected in the Philippines, *Neoglyphea inopinata* Forest & de Saint Laurent, 1975, provided anatomical comparisons that strongly suggested that the Glypheidae were more closely allied with the Astacidea than with the Palinura (Forest & de Saint Laurent, 1989). Although that position was supported by Feldmann & Maxwell (1999), they did not formalize the transfer of the Glypheidae into the Astacidea. Examination of new specimens forming the basis of a new species of *Glyphea* herein provides several lines of evidence essential to demonstrate the relationship of fossil glypheids to the extant *Neoglyphea* and to formalize the proximity of the Glypheoidea to the Astacidea.

In contrast to the view previously held, the differences between chelate, pseudo-chelate, and achelate pereiopods are simply those of gradation. For example, within the Glypheoidea, *Mecochirus* and *Pseudoglyphea* (Mecochiridae) and *Pemphix* (Pemphicidae) exhibit pseudochelate closures in which the distal edge of the propodus of at least the first pereiopod is drawn out into a spine closely resembling the fixed finger of true chelae (see Glaessner, 1969, fig. 271.2a, for example). Within the Astacidea, *Clytiopsis* (Erymidae) bears true chelae that are not substantially different from the pseudochelae seen in glypheoids. The claws of *Clytiopsis* have very short, rapidly tapering, edentulous fingers that distinctly resemble spines. If one compares the morphology of the pseudochelae of typical glypheids with the chelae of the raninid crabs (see Glaessner, 1969, fig. 311.8, for a good example), there is very little difference. Typical raninid claws have a dactylus that closes across the distal end of the propodus and the fixed finger resembles nothing as much as a hypertrophied spine. Achelate terminations of the first pereiopod(s) result from the lack of a pronounced spine on the propodus that serves as a fixed finger. None of these comments is intended to suggest that the taxa mentioned are closely related to one another on the basis of claw morphology. On the contrary, they simply demonstrate that the development of closures involving

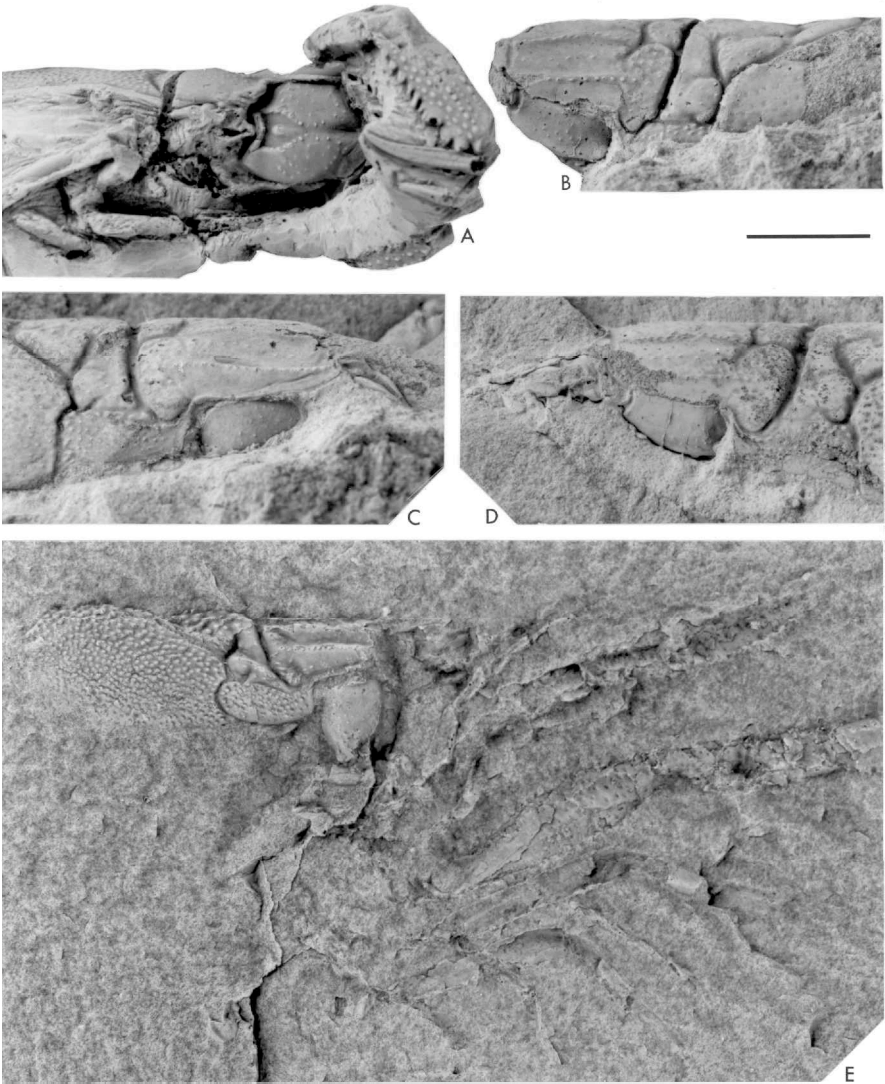


Fig. 2. Displacement of epistomes in *Glyphea* spp. A, ventral view of holotype, MNHN R.63537, of *Glyphea foresti* n. sp., showing epistome displaced within carapace. B, C, D, lateral views of three specimens of *Glyphea regleyana* (Desmarest, 1822) (uncatalogued specimens, MNHN), showing differing degrees of breakage and displacement of the epistome. E, latex mold of holotype, KG.18.46, British Antarctic Survey, of *Glyphea alexandri* Taylor, 1979, showing separation and 90 degree rotation of epistome, relative to the carapace, on a molted specimen. Scale bar equals 1 cm.

the propodus and dactylus can be quite variable and gradational. The fixed finger is simply a distal extension of the propodus, and thus, “true” chelae may have arisen independently within several, different decapod lineages.

Fusion of the epistome with the carapace in the glypheoids has largely been inferred by the observation that, in the Glypheidae, the epistome is often preserved and presumed to be in place. To be sure, the large and well-developed epistome is a hallmark of the Glypheidae. However, careful preparation of the Australian material (fig. 2A) and of specimens of the type species, *Glyphea regleyana* (Desmarest, 1822) (fig. 2B-D), confirm that the epistome is not fused to the carapace and that a suture separates the epistome from the carapace. In some cases, for example, it can be observed that the epistome is not actually in place but is displaced dorsally beneath the lower margin of the carapace. Displacement is even more obvious in the holotype specimen of *Glyphea alexandri* Taylor, 1979, in which the epistome is entirely dissociated from the carapace and is rotated 90 degrees to its original position (fig. 2E). Forest & de Saint Laurent (1989) noted that the epistome was, in fact, a separate plate in *Neoglyphea inopinata*. There does not seem to be any evidence of a fused epistomal plate in any of the other Glypheoidea.

Finally, the rostrum in all glypheoids, when preserved, is a prominent, well-developed structure. Thus, the criteria distinguishing the Palinura from the Astacidea do not apply to the Glypheoidea and the superfamily most appropriately can be assigned to the Astacidea. The Glypheoidea include the Glypheidae, Mecochiridae, and Pemphicidae.

Family GLYPHEIDAE Winkler, 1882

Included genera. — *Glyphea* Von Meyer, 1835; *Litogaster* Von Meyer, 1847; *Neoglyphea* Forest & de Saint Laurent, 1975; *Trachysoma* Bell, 1858.

Diagnosis. — Carapace subcylindrical, laterally compressed, anterior part of carapace with longitudinal carinae, cervical groove steeply inclined, branchiocardiac groove well-developed, postcervical groove present but variably developed, first pereopods well-developed, pseudochelate or achelate.

Genus *Glyphea* Von Meyer, 1835

Type species. — *Palinurus regleyanus* Desmarest, 1822, by original designation.

Included species. — *Glyphea alexandri* Taylor, 1979; *G. arborinsularis* Etheridge Jr., 1917; *G. australensis* Feldmann, Tshudy & Thomson, 1993; *G. bathonica* De Ferry, 1865*; *G. bohémica* Fritsch, 1887*; *G. calloviensis* H. Woods, 1927; *G. carteri* Bell, 1863; *G. christeyi* Feldmann & Maxwell, 1999; *G. crassa* Oppel, 1861*; *G. cretacea* McCoy, 1854; *G. georgianus* Taylor, 1979; *G. gussmanni* Schütze, 1907*; *G. jeletzkyi* Feldmann & McPherson, 1980; *G. liasina* Von Meyer, 1840*; *G. lyrica* Blake, 1876; *G. muensteri* (Voltz, 1835)*; *G. oculata* J. Woods, 1957; *G. prestwichi* H. Woods, 1929; *G. pseudoscyllarus* (Schlothheim,

1822)*; *G. regleyana* (Desmarest, 1822); *G. reticulata* Feldmann & Gazdzicki, 1997; *G. robusta* Feldmann & McPherson, 1980; *G. rostrata* (Phillips, 1829); *G. squamosa* (Münster, 1839)*; *G. stilwelli* Feldmann, 1993; *G. tomesi* Woodward, 1868; *G. udressieri* Von Meyer, 1840; *G. vectensis* H. Woods, 1927; *G. willetti* (Woodward, 1878). Those taxa denoted by an asterisk (*) were taken from Glaessner (1929) and have not been verified.

Diagnosis. — Carapace with simple, pointed rostrum; anterior longitudinal carinae well-developed, tuberculate; cervical groove steeply inclined to long axis of carapace but not perpendicular to it; postcervical and branchiocardiac grooves oblique, converge posteriorly, and joined medially and, in some species, laterally; epibranchial region inflated and with long, narrow anterior extension; epistome large, swollen; telson rounded, complete; uropods with diaeresis; first pereopods strong, pseudochelate.

Remarks. — Genera within the Glypheidae are distinguished from one another largely on the orientation and relative development of the primary carapace grooves. *Litogaster* Von Meyer, 1847, and *Trachysoma* Bell, 1858, bear parallel postcervical and branchiocardiac grooves. Those grooves converge posteriorly, and the postcervical groove is often incompletely developed in *Glyphea* and *Neoglyphea*. Of these genera, considerable confusion has surrounded the identification of *Glyphea* and *Trachysoma*. Quayle (1987) considered the two genera to be synonymous, a view that was not sustained by Feldmann & Gazdzicki (1997). In addition to the convergence of the postcervical and branchiocardiac grooves in *Glyphea*, two other morphological landmarks would seem to unequivocally distinguish the two genera. In all authentic representatives of *Glyphea* the cervical groove approaches the dorsal surface at an angle ranging from about 60 to 80 degrees, whereas in *Trachysoma* that angle approaches 90 degrees. Further, the inflated epibranchial region of authentic *Glyphea* extends anteriorly from the inferior groove, passes beneath the ventral-most extension of the cervical groove, and tapers out at approximately the position of the posterior margin of the epistome.

The epibranchial region is thus quite distinct and is not similarly developed in either *Trachysoma scabrum* Bell, 1858 (see Quayle, 1987, text-fig. 5b), the type species of the genus, or *T. ornatum* (Quenstedt, 1858) (see Glaessner, 1969, fig. 269-2b). That same extension of the epibranchial region is apparent on *Neoglyphea inopinata* and in that species appears to accommodate movement of the 2nd maxillipeds (see Forest & de Saint Laurent, 1981, fig. 23). Thus, there seem to be sufficient characters of the cephalothorax that distinguish *Glyphea* from *Trachysoma* to warrant retaining each as a distinct genus.

***Glyphea foresti* n. sp. (figs. 2A, 3A-E, 4A-D)**

Types. — The holotype, MNHN R.63537, and paratype, MNHN R.63538, are deposited in the Muséum national d'Histoire naturelle, Paris. Both specimens were collected by Dr. B. Daily, 1954, and were presented to Dr. M. F. Glaessner.

Occurrence. — The specimens were collected from the Moonkinu Member of the Bathurst Island Formation, from 3 m above to 5 m below "Tapara Bed" in association with *Acanthoceras* sp., among other ammonites (Wright, 1963: 612) at Meadinga, east of Moonkinu Creek, on the south coast of Bathurst Island, Northern Territory, Australia (fig. 1). The age of the rocks is Upper Cenomanian.

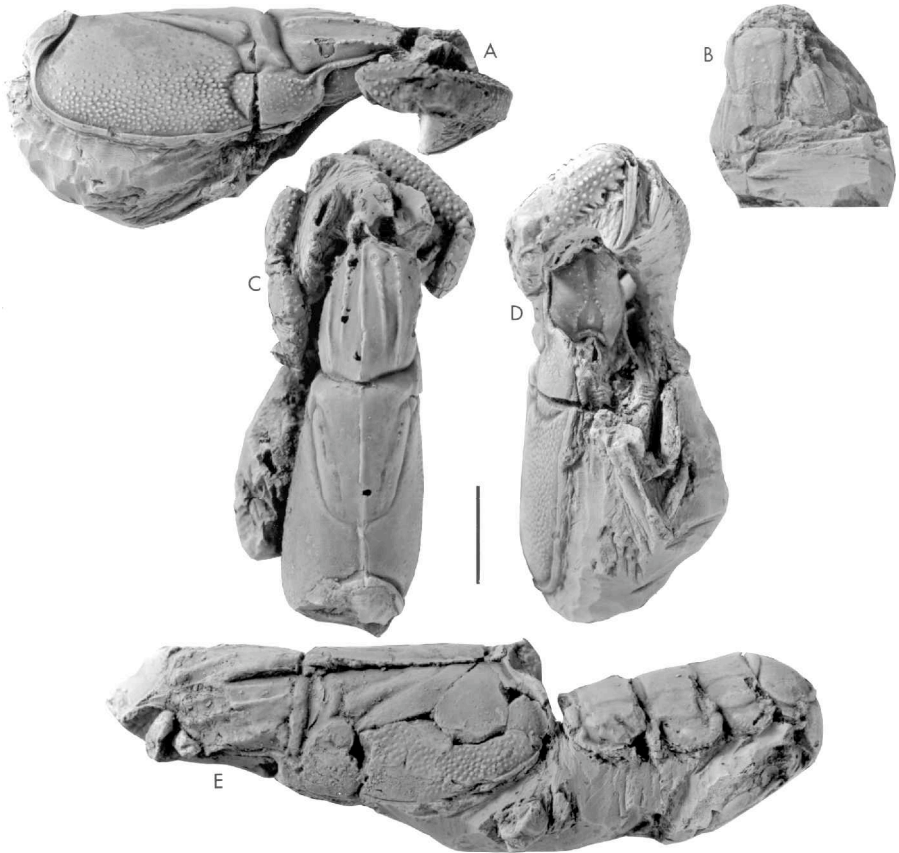


Fig. 3. *Glyphea foresti* n. sp. A, C, D, right lateral, dorsal, and ventral views of holotype, MNHN R.63537; B, telson and right uropod of paratype, MNHN R.63538; E, left lateral view of paratype, MNHN R.63538, showing details of abdominal pleura of presumed female specimen, and a portion of the endophragmal skeleton. Scale bar equals 1 cm.

Diagnosis. — Glypheid with three pairs of cephalic carinae becoming spinose anteriorly; deeply impressed cervical groove bounded posteriorly by a broad, smooth collar; smooth region between branchiocardiac and cervical grooves; abdominal pleura with finely beaded margins.

Description. — Cephalothorax average size for genus. Height about 2.75 times length, excluding rostrum. Dorsal margin slightly convex in cephalic region, nearly straight in thoracic region; posterior margin concave dorsally and smoothly convex ventrally; ventral thoracic margin gently convex, greatest depth at about midlength; ventral cephalic margin nearly straight, inclined posteroventrally, strongly downturned at base of cervical groove; anterior margin poorly preserved, nearly vertical; rostrum short, triangular, sulcate distally in advance of termination of smooth axial crest.

Cervical groove weakly sinuous, steeply inclined, intercepting dorsal midline at 65 degree angle at distance of 0.4 length measured along dorsum and excluding rostrum; very deeply impressed and bordered by smooth, broad flanks. Branchiocardiac groove well defined, deep, with smooth flanks; steeply inclined, approaching dorsal margin at about 15 degrees and curving abruptly to cross midline at 70 degree angle. Postcervical groove weak, shallow, discontinuous; defined anteriorly by deeply depressed, convex curve at junction with branchiocardiac groove, defined medially by series of shallow, elongate pits, converging with branchiocardiac groove, and joining it near midline. Hepatic groove biconvex, most deeply impressed posteriorly, merges anteriorly with base of cervical groove at point of origin of anterior groove which parallels ventral margin. Inferior groove well defined, convex posteriorly.

Cephalic region with three well defined carinae on flanks; carinae generally smooth posteriorly, becoming spinose anteriorly; supraorbital and orbital carinae more closely spaced than orbital and antennal carinae. Dorsal midline with smooth axial ridge; ventral border of cephalic region finely beaded; remainder of cephalic region smooth.

Region between branchiocardiac and cervical grooves lacking spines; epi-branchial region anterior to inferior groove covered by small outward-directed spines; extension of beaded rim bordering cephalic region extends onto this region and disappears posteriorly. Branchiostegite with coarse, forward-directed spines ventrally grading into smaller spines and then setal pits dorsally. Marginal rim and sulcus well defined, smooth on posterior and ventral margins, broad and sharply upturned in the position of inflection on posterior margin, terminates anteriorly at inferior groove.

Epistome inflated, with axial groove narrowing posteriorly to behind midlength at which point axial region broadens to about 33 percent total width; single spine

situated in middle of broad field. Axial region defined by finely beaded ridge. Lateral fields of epistome finely spined.

Abdomen of female (?) well developed. Somite 1 not preserved. Somite 2 with generally smooth tergum, tergal flanks set down from axial portion along longitudinal step; pleura separated from tergum by inflection connecting points of articulation; pleural margin smoothly arcuate with very fine spines and broad, inflated border. Somites 3 and 4 similar to 2. Somites 5 and 6 with smooth terga and reduced pleura. Telson trapezoidal, proximal region transversely inflated; tapering, lateral inflated areas extend from proximal end to posterolateral corners. Axial region granular. Endopod with paired, longitudinal, spinose axial ridges and finely spinose field; exopod apparently with diaeresis very near distal margin.

Eyestalks twice as long as rostrum, apparently arise near base of rostrum and extend beyond tip of rostrum, stout at base and flaring distally at base of corneal field so that width of corneal field exceeds length of eyestalk; corneal field not preserved.

First pereopod elongate, stout, spinose; length of carpus and propodus about 66 percent cephalothorax length. Carpus twice as long as high, slightly tapered proximally; outer and upper surfaces with poorly defined rows of moderately strong spines; inner surface with single, distally directed large spine near joint with propodus. Propodus twice as long as carpus and 3 times as long as high. Upper and outer surfaces with about 10 rows of spines; spines alternate from small to moderate size in alternating rows. Lower surface with row of coarse, distally directed spines becoming larger distally, distalmost three of which are much longer and form occlusal surface with dactylus as pseudochela. Dactylus about 66 percent length of propodus, slender, slightly curved, with three longitudinal keels on outer surface; occlusal surface smooth.

Measurements. — Measurements, in millimeters, taken on the holotype are given in fig. 4.

Etymology. — The trivial name honors Prof. Jacques Forest, whose pioneering work on *Neoglyphea inopinata* provided the basis for our present understanding of the Glypheidae.

Remarks. — Forest (1981) eloquently described the history of discovery, description, and interpretation of *Neoglyphea inopinata*, based upon a single specimen collected during the "Albatross" cruises, which were conducted near the end of the 19th century and the beginning of the 20th century. The remarkable similarity of this living species with the glypheids known only from the fossil record of the Mesozoic and early Cenozoic permitted study of anatomical details that would never be possible with fossils. Some of the key morphological features seen on *N. inopinata* can also be observed on *Glyphea foresti* n. sp.; for example,

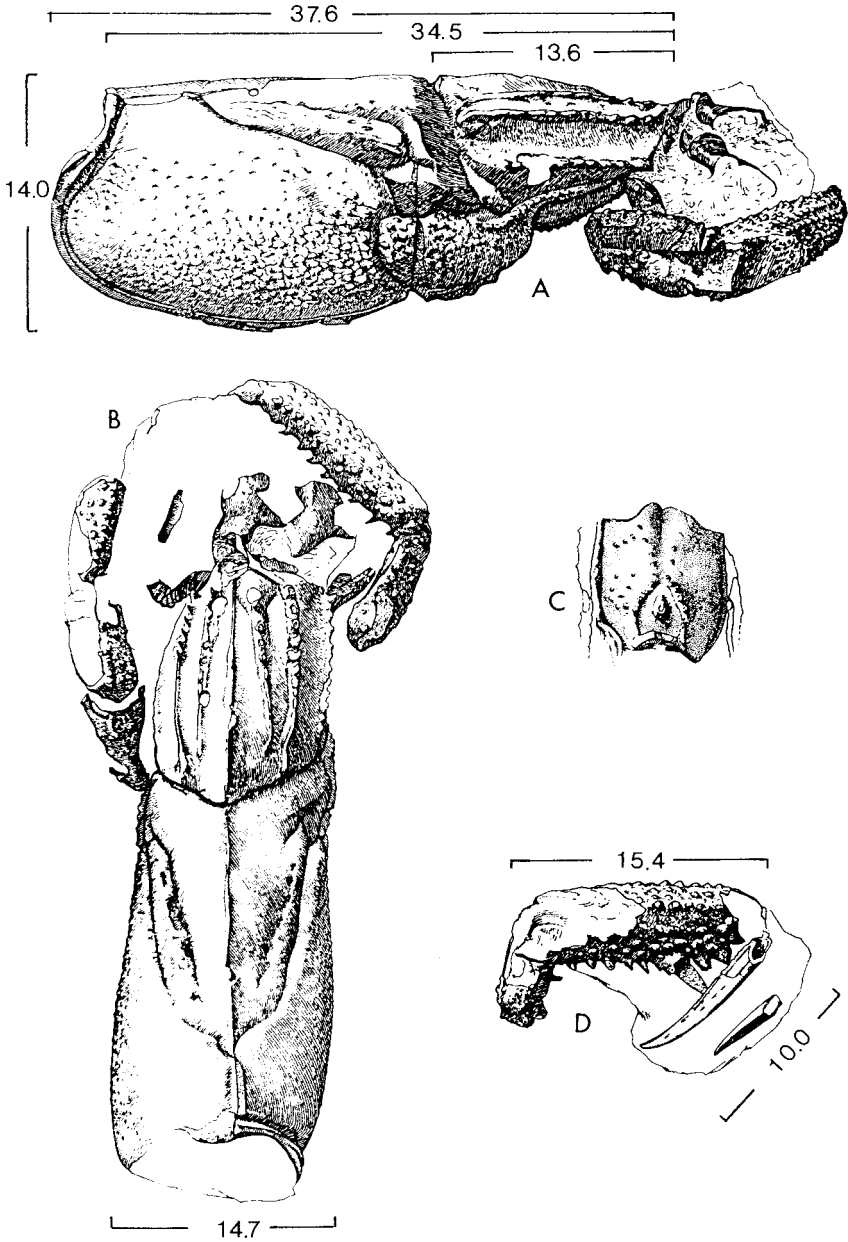


Fig. 4. *Glyphea foresti* n. sp. A, B, right lateral and dorsal views of holotype, MNHN R.63537, showing the orientation and values of measurements taken; C, ventral view of epistome of holotype MNHN R.63537; D, carpus (partial), propodus, and dactylus of right first pereiopod of holotype, MNHN R.63537, showing orientation and values of measurements taken.

both possess huge flaring eyes that extend well beyond the tip of the rostrum and both have incomplete postcervical grooves.

In all regards, the specimens described herein conform to the definition of *Glyphea*. Although there is potential difficulty in distinguishing members of this genus from those of *Trachysoma* Bell, there are several points of difference that can be recognized as discussed above. *Glyphea foresti*, along with other species of the genus, is characterized by having a curving cervical groove that approaches the dorsal midline at a steep angle of less than 90 degrees, postcervical and branchiocardiac grooves that do not parallel one another, and development of an epibranchial region that extends as a projection beneath the posterior portion of the cephalic region.

Although no monographic treatment of the genus has been attempted recently, Woods (1925) presented a detailed summary of Cretaceous species known to that date, and Feldmann & McPherson (1980) summarized the criteria for distinguishing groups of species within the genus. Within *Glyphea*, they recognized wide variation in terms of the development of cephalic carinae, development of the postcervical groove, and ornamentation. The range of variation within the genus is great enough to suggest that revision of the systematics might be warranted. Species including *Glyphea arborinsularis*, *G. cretacea*, *G. oculata*, *G. prestwichi*, and *G. robusta* possess three pairs of cephalic carinae but none has carinae that are smooth posteriorly and becoming more spinose anteriorly. Similarly, several species, including *Glyphea alexandri*, *G. arborinsularis*, *G. australensis*, *G. calloviensis*, *G. christeyi*, *G. cretacea*, *G. georgianus*, *G. oculata*, *G. reticulata*, *G. robusta*, and *G. rostrata*, are characterized by the lack of an accessory groove connecting the midpoints of the postcervical and branchiocardiac grooves; however, none of these has a postcervical groove that is developed as a discontinuous series of slit-like depressions as in the case of *G. foresti* n. sp. Finally, several species, including *Glyphea arborinsularis*, *G. australensis*, *G. christeyi*, *G. foresti*, *G. oculata*, *G. prestwichi*, *G. robusta*, and *G. rostrata*, lack ornamentation between the cephalic carinae, although of these species only *G. christeyi* has an absolutely smooth surface between the cervical and branchiocardiac regions. *Glyphea christeyi*, however, has smooth supraorbital and orbital ridges and a pattern of ornamentation that becomes finer posteriorly and dorsally, quite unlike those characters on *G. foresti*. Thus, the combination of these characters renders *Glyphea foresti* unique.

SEXUAL DIMORPHISM

Expression of preservable secondary sexual characteristics including features of the cephalothorax and abdomen of lobsters is not particularly common. Herrick

(1911) noted that the females of the American lobster, *Homarus americanus* H. Milne Edwards, 1837, tended to be smaller, and to have smaller claws and broader abdomina than males; however, recognition of gender in fossil *Homarus* would be virtually impossible, based solely upon these criteria. Perhaps the best evidence for secondary sexual characteristics in lobsters lies within the Glypheidae. Forest & de Saint Laurent (1989) called attention to the work of Etallon (1858) in which sexual dimorphism was demonstrated in *Glyphea regleyana*. Males possessed longer and more slender first pereopods and sharply-pointed terminations on the abdominal pleura as opposed to rounded terminations in females. Similar dimorphic features were recognized in *Neoglyphea inopinata* (cf. Forest & de Saint Laurent, 1989). In that taxon, the first pereopods of males were longer and proportionately more slender than those of the females, and the terminations of pleura on abdominal somites 2-4 were pointed in males whereas pleura on all somites of the females were rounded. If these criteria are applied to the one specimen of *Glyphea foresti* possessing a well-developed abdomen (fig. 3E), that individual is a female. As such, this is only the second record of a fossil species of glypheid, and one of very few fossil macrurans, in which sexual dimorphism appears to be demonstrable in characters of the dorsal carapace and pereopods.

SOUTHERN HEMISPHERE GLYPHEIDS

The geographic distribution of *Glyphea* spp. appears to be bipolar. In the northern hemisphere, authentic species of the genus are found in subpolar and temperate paleolatitudes in Europe and North America. In the southern hemisphere, species are known from as far south as the Antarctic peninsula and as far north and Northern Territories, Australia. These localities would have been at subpolar to temperate paleolatitudes. None is known from tropical or subtropical paleolatitudes.

It appears that *Glyphea foresti* and the eight other representatives of this genus from the Southern Hemisphere: *Glyphea arborinsularis* and *G. oculata* from the Aptian and Albian, respectively, of Queensland, Australia; *G. alexandri* and *G. georgiensis* from the Lower Cretaceous of Antarctica; *G. australensis* from the Campanian and Maastrichtian of Antarctica; the sole Paleocene species, *G. stilwelli* from New Zealand; and the two Eocene species, *G. reticulata* from the Eocene of Antarctica and *G. christeyi* from the Eocene of New Zealand; may be related. All are characterized by relatively weak development of the postcervical groove and the absence of an accessory groove connecting the midpoints of the postcervical and branchiocardiac grooves. The two Eocene occurrences from Antarctica and New Zealand are the geologically youngest occurrences of *Glyphea* known. The observation that these are the youngest occurrences of the genus, in

addition to the apparent morphological affinities of the Southern Hemisphere forms to the tropical, western Pacific *Neoglyphea inopinata* may indicate a long period of relative isolation of these species from the Northern Hemisphere counterparts.

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