A NEW SPECIES OF GLYPHEOID LOBSTER, *PSEUDOGLYPHEA FOERSTERI* (DECAPODA: ASTACIDEA: MECOCHIRIDAE) FROM THE LOWER JURASSIC (PLIENSBACHIAN) OF RAASAY, INNER HEBRIDES, UK

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ABSTRACT. Mecochirid lobsters assigned to the genus *Pseudoglyphea* Oppel, 1861 have previously been recorded from several localities in Europe. In this paper *Pseudoglyphea foersteri* sp. nov. is described from the Lower Jurassic of Raasay, Inner Hebrides, Scotland, providing the first evidence of a vagile benthic predator/scavenger in the Scalpa Sandstone Formation. Re-examination of the systematic placement of the genus supports allying the Mecochiridae with the Glypheidae within the Astacidea, not the Palinura as traditionally done.

KEY WORDS: Glypheidae, Lower Jurassic, Raasay.

FOSSIL lobsters tend to be uncommon and, as a result, discovery of the first well-preserved lobster from the Lower Jurassic Scalpa Sandstone Formation in Scotland is noteworthy. This organism not only represents a new species of mecochirid lobster but also documents the first vagile, benthic predator/scavenger in this marine unit, which is otherwise dominated by sessile filter and suspension feeders and pelagic predator/scavengers. This discovery also prompts re-examination of the systematic position of the genus *Pseudoglyphea* and the assignment of the Mecochiridae to the Astacidea.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

Lower Jurassic sedimentary rocks of the Hebrides Basin are well-exposed in the Inner Hebrides of Scotland, UK (Hesselbo *et al.* 1998). The Isle of Raasay lies to the east of the Isle of Skye (Text-fig. 1). On Raasay, Jurassic sedimentary rocks overlie Triassic non-marine sediments of the Penarth Group and comprise (from oldest to youngest) the Broadford Shale, Pabba Shale, Scalpa Sandstone, Portree Shale, Raasay Ironstone, and the Bearreraig Sandstone formations (Morton and Hudson 1995). The Scalpa Sandstone Formation is well exposed to the south of Rudha na Leac, where it is in fault contact with Triassic sandstones of the Stornoway Formation (Morton and Hudson 1995). In addition, the Scalpa Sandstone Formation also crops out on the foreshore 2 km to the north-west below Hallaig (Text-fig. 1) where it has a transitional lower boundary with the underlying Pabba Shale Formation (Morton and Hudson 1995). The Scalpa Sandstone Formation is dominated by silty sandstones/sandy siltstones and supports a fully marine fauna with *in situ Pholadomya*, and at particular levels a more diverse macrofauna including *Gryphaea*, brachiopods, crinoids, belemnites and ammonites (Morton and Hudson 1995). Typically the formation shows an overall coarsening-up trend from siltstone to massive fine-grained sandstone, with evidence for both tidal and storm activity with deposition on a shallow marine shelf (Morton and Hudson 1995). The age of the Scalpa Sandstone Formation is well constrained on the basis of ammonite biostratigraphy and ranges from the lower Pliensbachian to the basal Toarcian (Lower Jurassic). The unit is further subdivided into the Ibex, Davoei, Margaritus, and Spinatum ammonite zones (Text-fig. 2; Howarth 1956; Morton and Hudson 1995; Hesselbo and Jenkyns 1998; Hesselbo *et al.* 1998).
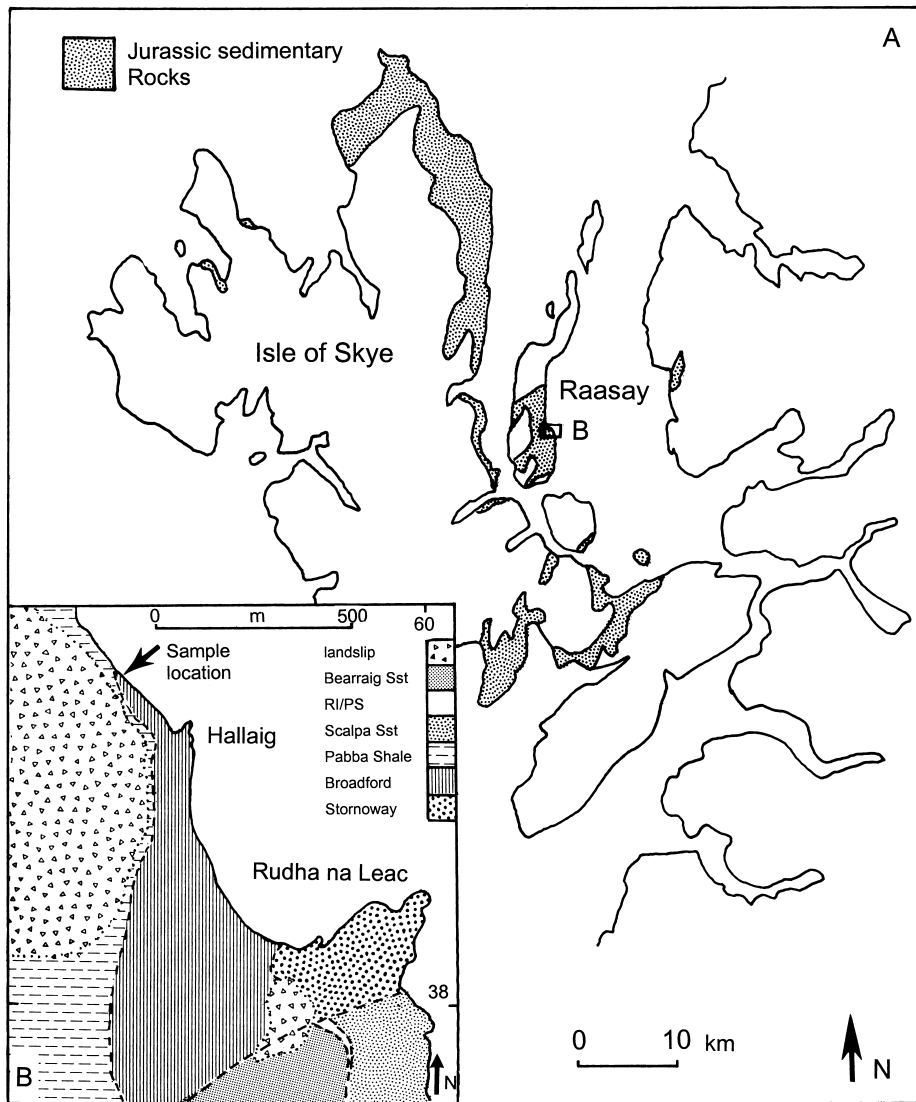
TEXT-FIG. 1. A, schematic geological map of Skye and Raasay, Inner Hebrides, Scotland, showing the distribution of Jurassic strata; area B is outlined. B, geological map of the Hallaig area, eastern Raasay, showing the sample location and mapped formations in this area (after Morton and Hudson 1995). RI, Raasay Ironstone Formation; PS, Portree Shale Formation.

The sample described here was collected during regional mapping by one of us (GC) from a dislodged block 3 m across included within a large landslide at Hallaig (National Grid Reference NG 5861 4030). The block is dominantly composed of bioturbated, micaceous, silty sandstones yielding an abundant bivalve, brachiopod, and ammonite fauna along with pyritised fossil wood. Although the decapod was found in a loose block, the lithology can be clearly correlated with the Scalpa Sandstone Formation. Ammonites recovered from the same block include *Aegoceras* cf. *brevilobatum* (Trueman) (Howarth, pers. comm. 2000); hence it is likely that this block was derived locally from the Davoei (ammonite) Zone (Pliensbachian). More precisely, the presence of *Aegoceras* cf. *brevilobatum* would suggest that this block

Stage	Ammonite Biozone	Lithostratigraphy
Pliensbachian	Spinatum	Scalpa Sandstone Fm
	Margaritus	
	Davoei	
	Ibex	
	Jamesoni	Pabba Shale Formation
Sinemurian	Raricostatum	
	Oxynotum	
	Obtusum	
	Turneri	
	Semicostatum	
	Bucklandi	Broadford Formation
Hettangian	Angulata	
	Liasicus	
	Planorbis	

TEXT-FIG. 2. Lithostratigraphy and ammonite biozones for the Lower Jurassic on Raasay. The sample described here is from the Pliensbachian, Davoei Biozone of the Scalpa Sandstone Formation (after Hesselbo *et al.* 1998).

is from the Lataecosta Subzone, which is the middle subzone of the Davoei Zone (Howarth 1956, and pers. comm. 2000).

SYSTEMATIC PALAEONTOLOGY

Order DECAPODA Latreille, 1802

Infraorder ASTACIDEA Latreille, 1802

Discussion. Forest and de Saint Laurent (1989) discussed the details of the anatomy of the only extant species of glypheid lobster, *Neoglyphea inopinata* Forest and de Saint Laurent, 1975, and presented convincing arguments supporting the reassignment of the Glypheidae to the Astacidea. Previously, the family had been allied with the Pemphicidae and the Mecochiridae within the infraorder Palinura (Glaessner 1969; Briggs *et al.* 1993; Garassino 1996). Because a living representative of the Glypheidae is available for study, the basis for re-assignment included many characters that are not preserved in the fossil record. There are no living Mecochiridae or Pemphicidae, and for that reason Forest and de Saint Laurent (1989) did not support transfer of these two families to the Astacidea.

The question of whether the Mecochiridae and Pemphicidae should be considered representatives of the Astacidea and continue to be placed near the Glypheidae must be based solely upon preservable characteristics because neither group is represented in the modern fauna. It would be worthwhile to subject these groups to a cladistic analysis; however, the vagaries of preservation and the general scarcity of specimens makes the possibility of this type of analysis remote. As with many other fossil groups, too few characters are available for study and quite different morphological features are preserved on specimens representing different taxa. The specimen herein, referred to the Mecochiridae, permits placement within that family but provides no new information on the character of the family.

There are several characters of the cephalothorax of the Mecochiridae that indicate that the Mecochiridae should be placed within the Astacidea. Representatives of the Mecochiridae exhibit cylindrical carapace cross-sections, which is a reflection of the very narrow sternum and closely spaced pereiopods. This condition is invariably seen within genera in the Astacidea and is in opposition to the typical palinurid characteristic of having a broad, often posteriorly widening, sternum and pereiopods that are inserted far from the midline. A point of interest in this regard is that most fossil Astacidea are preserved in lateral view because upon death the stable position of repose is on the side. In contrast, the stable position of repose of typical palinurids is with the dorso-ventral axis perpendicular to the substrate. Thus, palinurid fossils generally reveal the dorsal or ventral surfaces, and not the lateral margin.

Mecochirids also possess a well-developed rostrum and well-defined groove pattern dominated by the cervical and postcervical grooves, typical astacoid features. In fact, the only character of the Mecochiridae that is not typical of the Astacidea is the development of pseudochelate closures on the pereiopods; but, as discussed below, this character occurs across infraordinal lines and is, therefore, probably not a useful character. Thus, the preponderance of evidence supports placement of the Mecochiridae in the Astacidea. Although the morphology of the Pemphicidae strongly suggests similar reassignment, formalization of that conclusion must await further study.

Superfamily GLYPHEOIDEA Winckler, 1883
Family MECOCHIRIDAE van Straelen, 1925

Genus PSEUDOGLYPHEA Oppel, 1861

Type species. Glyphea grandis von Meyer, 1837, by original designation.

Included species. Pseudoglyphea alpina (Förster, 1971); *P. amalthea* Oppel, 1861; *P. ancylochelis* (Woodward, 1863), as *Scapheus*; *P. etalloni* Oppel, 1862; *P. eximia* Oppel, 1861; *P. gigantea* Garassino and Teruzzi, 1993; *P. grandis* (von Meyer, 1837), as *Glyphea*; *P. jourdani* (Dumortier, 1867), as *Eryma*; *P. mulleri* (van Straelen, 1936), as *Platypleon*; *P. numismalis* [Oppel, 1853 (1854)], as *Glyphea*; *P. paronae* (Colosi, 1921), as *Heteroglyphea*; *P. spinosa* (Assmann, 1927), as *Pseudopemphix*; *P. straeleni* Théobald, 1953; and *P. terquemi* Oppel, 1861.

Pseudoglyphea hamifera Tate, *in* Tate and Blake (1876) was recognized as lacking both a documenting specimen and an illustration (Woods 1926, p. 42), and was considered a *nomen nudum* by Förster (1971, p. 401), who considered *Erymastacus bordenensis* Copeland, 1960, to be referrable to *Pseudoglyphea*; however, examination of that material led Feldmann and McPherson (1980, p. 3) to assign the species to *Eryma*. Reconsideration of that placement by one of us (RMF) yields no clear indication that the species should be reassigned to *Pseudoglyphea*; it should be retained in *Eryma*.

Diagnosis. Carapace subcylindrical, rostrum long; cephalic region with longitudinal ridges that may be reduced or absent in some forms; cervical groove well defined, deep; post-cervical and branchiocardiac grooves closely spaced and parallel over most of their length, approaching or extending to dorsal midline; hepatic groove well defined, deep, extends in smooth arc defining posterior, ventral, and anterior margins of 'adductor testis' muscle attachment; inferior groove absent or weakly defined; abdominal terga pitted or smooth, not strongly ornamented; exopods of uropods may lack diaresis; first pereiopods strong, with terminal dactylus, not chelate.

Discussion. Garassino (1996) provided a detailed history of the placement of *Pseudoglyphea*. He discussed whether *Pseudoglyphea* should be placed within the Glypheidae or the Mecochiridae if they are retained as separate families. Some authors consider these two families to be synonymous; however, we consider them as separate. Garassino (1996) followed Glaessner (1969) in placing *Pseudoglyphea* in the Mecochiridae; however, he suggested that strong arguments could be made to refer it to the Glypheidae. One major point turned on whether or not the terminations of the first three pairs of pereiopods have a terminal dactylus, as in the Mecochiridae, or are pseudochelate, as is typical of the Glypheidae. Work in progress by one of us (RMF) suggests that this character does not always follow strict taxonomic lines, as

defined by other criteria, and thus may not be definitive. The pattern of carapace grooves may be more useful in assigning *Pseudoglyphea* at the family level.

Among the Astacidea, presence or absence of an inferior groove is diagnostic at the family level. This groove, which extends from the ventral margin of the cephalothorax to the hepatic groove when completely developed, defines the posterior margin of an epibranchial region that extends along the anteroventral margin of the carapace. A well-developed inferior groove is present in species of *Glyphea* and other genera within the Glypheidae, as currently defined. A well-developed inferior groove is also typical of species within the Erymidae, another family within the Astacidea, with which some glypheoids might be confused. The Mecochiridae seem to be unique among the Glypheoidea in lacking a well-defined inferior groove, supporting retention of the family. Absence of the inferior groove is more typical of the Nephropidae and the other, more derived forms, of the infraorder Astacidea. Although the inferior groove has not been considered to be one of the key morphological features in classification of the Astacidea, its importance has been underestimated and, in fact, it can be used as a family-level character.

The inferior groove in species of *Pseudoglyphea* tends to be obscure or absent, indicating placement in the Mecochiridae. When present, it is generally a subtle groove near the ventral margin that does not extend to the hepatic groove; the inferior groove is well developed in only a few species.

Another character that seems to typify most specimens referable to *Pseudoglyphea* is the presence of relatively strong, spinose or nodose ornamentation on the dorsal and dorso-lateral parts of the carapace that becomes reduced or absent on the ventrolateral portion. This feature is not present on all species, however, and cannot always be used as a diagnostic feature.

Presence of a diaresis on the exopod of the uropod of representatives of *Pseudoglyphea* is contested. The feature has been used as a diagnostic character of the genus by van Straelen (1925, p. 196), Woods (1926, p. 42), Förster (1971, p. 399) and Garassino (1996, p. 349); however, Glaessner (1969, p. R467) noted that some species referable to *Pseudoglyphea* either lacked the feature or that the diaresis was obscured by preservational processes. Examination of illustrations of the species in which the telson and uropods are preserved reveals a well-developed diaresis on some (e.g. *P. gigantea* Garassino and Teruzzi, 1993). Other species, however, show no evidence of the diaresis; therefore, presence of a diaresis should not be taken as a consistent diagnostic feature.

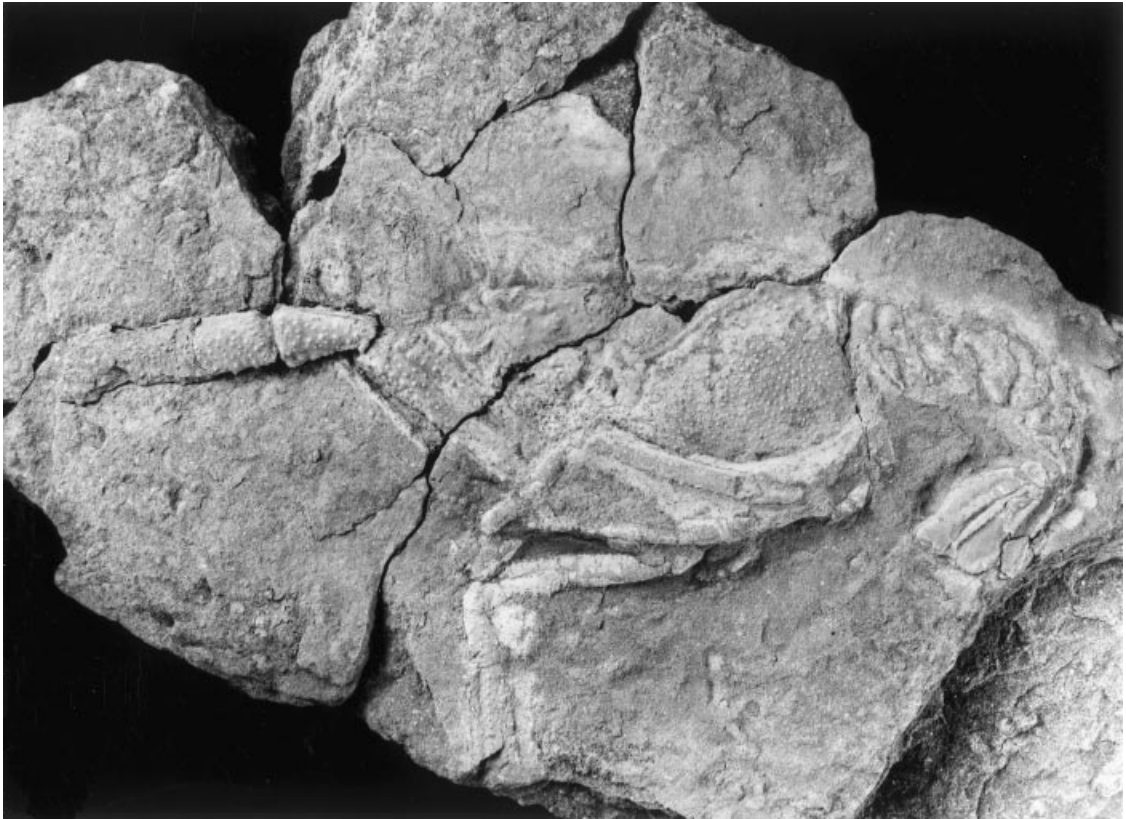*Pseudoglyphea foersteri* sp. nov.

Text-figures 3–4

Derivation of name. The trivial name honours the late Dr Reinhard Förster whose contributions to the study of Mesozoic decapods modernized the field. He was a good friend.

Holotype. The holotype and sole specimen, BM(NH), is deposited in the Invertebrate Palaeontology collections of The Natural History Museum, London, acquisition number IC 117.

Locality and horizon. The specimen was collected from the Lower Jurassic Scalpa Sandstone Formation from the Isle of Raasay, in the Inner Hebrides of Scotland. The age of the formation is well constrained on the basis of ammonite biostratigraphy to the Pliensbachian–lower Toarcian; the sole sample of *Pseudoglyphea foersteri* is from the Pliensbachian Davoei (ammonite) Zone (Howarth 1956; Morton and Hudson 1995).

Diagnosis. Large *Pseudoglyphea* with three well-delineated transverse grooves of which postcervical groove is parallel to branchiocardiac groove and is least well developed. Ornamentation pustulose to granulose on cephalothorax and smooth to pustulose on abdominal somites (Text-fig. 3).

Description. Dorsal surface not well preserved, generally straight with prominent re-entrant where branchiocardiac groove crosses midline; posterior margin straight near dorsum and inferred to be smoothly convex elsewhere, joining ventral margin in smoothly decreasing curve. Posterior and posteroventral margins with prominent, narrow, smooth lateral rim and furrow. Frontal margin with deep, biconvex orbit bordered by prominent, smooth orbital rim. Rostrum not preserved.

TEXT-FIG. 3. *Pseudoglyphea foersteri* sp. nov.; male?, holotype in Lower Jurassic Scalpa Sandstone Formation, left lateral view; ×0·6.

Cervical groove generally straight, approaches dorsal midline at an angle of about 65 degrees, broad, deep, not well preserved dorsally, curving smoothly into short, more weakly developed antennal groove. Postcervical groove weak, originates anteriorly as shallow, narrow groove curving ventrally and posteriorly, turning posterodorsally to closely parallel branchiocardiac groove, and terminating before reaching dorsal midline. Hepatic groove prominent, narrow, deeply incised, arising at cervical groove, curving postero-ventrally and extending around smooth, domed 'adductor testis' muscle attachment to merge with straight, deeply incised, narrow branchiocardiac groove which intercepts dorsal midline in deep re-entrant at angle of about 40 degrees.

Carapace surface with sparse, coarse nodes on cephalic region and dorsal part of branchiostegite, becoming densely pustulose ventrally (Text-fig. 4).

Abdomen with apparently smooth terga which merge smoothly into pustulose, transversely sulcate pleura that terminate in sharp, posteroventrally directed tips. Endopod and exopod of uropods with prominent posterior ridge. Telson well calcified to tip, poorly exposed.

Pereiopods generally long, slender, adorned by rows of nodes and distally curved spines. First pereiopod largest and stoutest; merus cylindrical, longer than high; carpus slightly longer than high, becoming higher distally; propodus cylindrical, at least three times as long as high. Second and ?third pereiopods moderately strong; fourth and fifth pereiopods most slender. Terminations of pereiopods not preserved.

Measurements. Because the sole specimen has been compressed laterally and the margins are not entirely exposed, the measurements must be considered best estimates and are given to the nearest millimeter. Carapace length from base of orbit to posterior margin, 81 mm; carapace height, 41 mm; distance, along dorsal midline, from branchiocardiac groove to posterior margin, 17 mm.
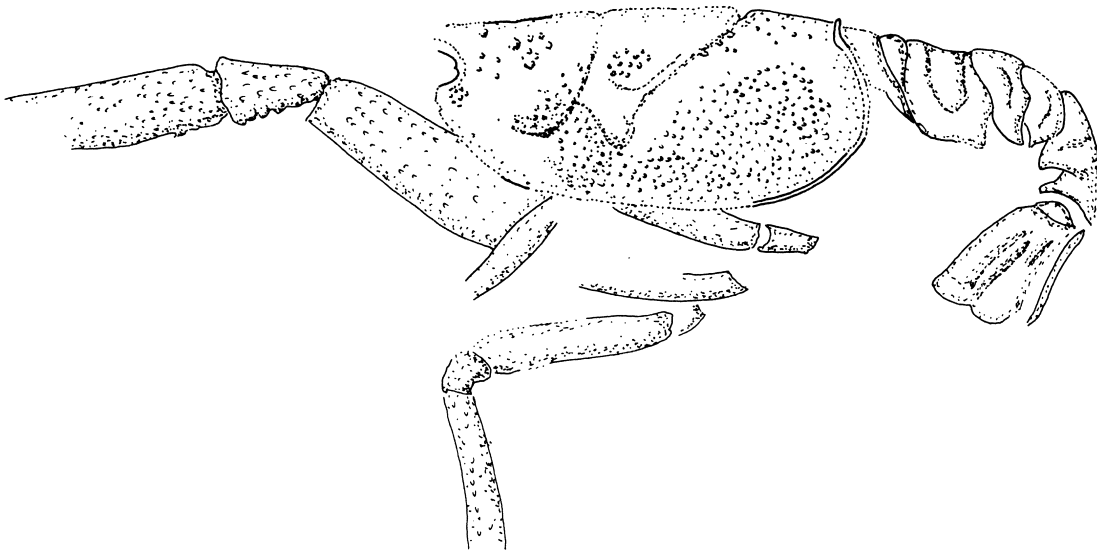
TEXT-FIG. 4. Line drawing of *Pseudoglyphea foersteri* sp. nov., showing position of groove pattern and general carapace outline, abdomen, and preserved appendages, dashed where inferred; pereiopods were not drawn where they lie over the carapace and obscure the carapace outline; ×0·65.

Discussion. Pseudoglyphea foersteri exhibits all the characters necessary to permit certain placement within *Pseudoglyphea*, as discussed above. The species is, however, distinct from all other known species in possessing a coarsely nodose dorsal cephalic region in which the nodes are not arrayed on discrete ridges, reduced coarseness of ornamentation between the cervical and postcervical grooves, a cervical groove that does not extend ventrally quite to the level of the hepatic groove, absence of an inferior groove, a postcervical groove that is weak and does not extend to the dorsal midline, and a very strong branchiocardiac groove that crosses the midline in a distinct depression.

The species that *Pseudoglyphea foersteri* most closely resembles is *P. etalloni*, known from several localities in Lower Jurassic rocks of France (Oppel 1862; van Straelen 1925) and England (Woods 1926). The details of ornamentation are very similar in the two species; however, the nodes on the cephalic region of *P. etalloni* are arranged in recognizable rows rather than at random, and the region between the cervical and postcervical grooves is more strongly nodose. The cervical groove on *P. etalloni* exhibits features that distinguish it from *P. foersteri* because the groove appears to bifurcate near the dorsum with the anteriormost element crossing the midline at right angles; the posteriormost element approaches the midline at a low angle, nearly merging with the branchiocardiac groove. Both of these features differ from those of *P. foersteri*. Holthuis (1974, p. 734) illustrated all the groove configurations known on nephropid lobsters and, using that terminology, the posteriormost of these two elements might be the urogastric groove, if the anteriormost element is considered the dorsal extension of the postcervical groove. Although this feature is also exhibited in other glypheoids, it is particularly well developed on *P. etalloni* (see, for example, Woods 1926, pl. 11, fig. 5A–B). The region of the dorsum between the branchiocardiac and cervical grooves is incomplete on the sole specimen of *Pseudoglyphea foersteri* and, therefore, the presence of the urogastric groove cannot be determined.

With regard solely to groove patterns, there is a recognizable difference in the degree of development of the postcervical groove among species within the genus. This groove is reduced in *Pseudoglyphea foersteri*, as it is in *P. grandis* and *P. alpinus*; however, in *P. grandis* the hepatic groove is curved in such a way that the axis of the 'adductor testis' insertion-region is directed posteroventrally rather than ventrally (Woods 1926, p. 44), and in *P. alpinus* the branchiocardiac groove is also reduced (Förster 1971, p. 403).

The position that would be occupied by the diaresis on the uropod is well preserved on *Pseudoglyphea foersteri*, and there is no evidence whatsoever of the structure. Several species of *Pseudoglyphea*, including *P. etalloni*, appear to have fractures across the tail fan and few clearly exhibit a diaresis.

DISCUSSION

The previously known fauna of the Scalpa Sandstone Formation includes a diverse assemblage of organisms characteristic of normal marine salinities. However, from the standpoint of trophic levels represented, there are notable absences. The fauna contains infaunal as well as sessile epifaunal bivalves, brachiopods, and crinoids, all of which are suspension feeders. The belemnites and ammonites that are known are pelagic predator/scavengers. The niche occupied by vagile, benthic predator/scavengers was not represented until the discovery of *Pseudoglyphea foersteri*. Decapod crustaceans in general have successfully occupied this niche at least since the Permian, culminating in the remarkably diverse modern assemblage of crabs, lobsters, and mud shrimps.

Within this broad array of crustaceans there are various morphological modifications that permit a more precise interpretation of their adaptation. Lobsters in general tend to be cryptic, occupying shallow and simple or deep and complex burrow systems or simply hiding under rocky or coralline ledges. With regard to defensive mechanisms, rapid, backward motion propelled by a strong muscular tail, large claws, and formidable spines are hallmarks of lobster morphology. The claws not only serve as defensive weapons but are also used in food gathering. The role of lobsters as predators would certainly be facilitated by the presence of large, strong claws. The absence of claws in *Pseudoglyphea foersteri*, and for that matter all the Mecochiridae, suggests that they were probably more adapted to scavenging than they were to preying on live food. The long first pereiopods, with the dactylus extended outward from the distal end of the propodus, might have served well as an elongate tactile organ for sensing and locating food on the seafloor.

In addition to discussing the systematic position of the Glypheidae, Forest and de Saint Laurent (1989) noted that male *Neoglyphea inopinata* were characterized by abdominal terga bearing spines on the posteroventral corners and that females exhibited smoothly rounded terga. That same relationship was recognized by Etallon (1859) in *Glyphea regleyana* from the Oxfordian of France. If the same criterion is applied to *Pseudoglyphea foersteri*, the sole specimen is a male. In the absence of additional specimens confirming that dimorphism exists, however, the suggestion must be considered tentative.

REFERENCES

ASSMANN, P. 1927. Die Decapodenkrebsae des deutschen Muschelkalks. *Jahrbuch der Preussischen Geologischen Landesanstalt und Bergakademie in Berlin*, **48**, 332–356.

BRIGGS, D. E. G., WEEDON, M. J. and WHYTE, M. A. 1993. Arthropoda (Crustacea excluding Ostracoda). 321–342. *In* BENTON, M. J. (ed.). *The Fossil Record 2*. Chapman and Hall, London, 845 pp.

COLOSI, G. 1921. Un nuovo Crostaceo fossile 'Heteroglyphea Paronae'. *Atti della Reale Accademia delle Scienze di Torino*, **56**, 79–82.

COPELAND, M. J. 1960. *Erymastacus bordenensis,* a new Mesozoic decapod from the Canadian arctic. *Geological Survey of Canada, Bulletin*, **60**, 55–57.

DUMORTIER, E. 1864–1874. *Études paléontologiques sur les dépôts jurassiques du bassin du Rhône*. F. Savy, Paris, 4 volumes.

ETALLON, A. 1859. Description des crustacés fossiles de la Haute-Saôet du Haut-Jura. *Bulletin de la Société Géologique de France, Series 2*, **16**, 169–205, pls 3–6.

FELDMANN, R. M. and MCPHERSON, C. B. 1980. Fossil decapod crustaceans of Canada. *Geological Survey of Canada, Paper*, **79–16**, 20 pp.

FOREST, J. and SAINT LAURENT, M. DE 1975. Présence dans la faune actuelle d'un représentant du groupe mésozoïque des Glyphéides: *Neoglyphea inopinata* gen. nov., sp. nov. (Crustacea Decapoda, Glypheidae). *Compte Rendu Hebdomedaires Séances de l'Academie des Sciences, Paris,* (*D*), **281**, 155–158.

—— —— 1989. Nouvelle contribution à la connaissance de *Neoglyphea inopinata* Forest & de Saint Laurent, à propos de la description de la femelle adulte. *Résultats des Campagnes MUSORSTOM*, **5**, 75–92.

FÖRSTER, R. 1971. Die Mecochiridae, eine spezialisierte Familie der mesozoischen Glypheoidea (Crustacea, Decapoda). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **137**, 396–421.

GARASSINO, A. 1996. The family Erymidae van Straelen, 1924 and the superfamily Glypheoidea Zittel, 1885 in the Sinemurian of Osteno in Lombardi (Crustacea, Decapoda). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale de Milano*, **135**, 1994 (2), 333–373.

—— and TERUZZI, G. 1993. A new decapod crustacean assemblage from the Upper Triassic of Lombardy (N. Italy). *Paleontologia Lombarda, Nuova Serie*, **1**, 1–27, pls 1–5.

GLAESSNER, M. F. 1969. Decapoda. R399–R533. *In* MOORE, R. C. (ed.). *Treatise on invertebrate paleontology, Part R. Arthropoda 4 (2).* Geological Society of America, Boulder, and University of Kansas Press, Lawrence, 651 pp.

HESSELBO, S. P. and JENKYNS, H. C. 1998. British Lower Jurassic sequence stratigraphy. 561–581. *In* DE GRACIANSKY, P. C., HARDENBOL, J., JACQUIN, T. and VAIL, P. R. (eds). *Mesozoic and Cenozoic sequence stratigraphy of western European basins.* SEPM (Society for Sedimentary Geology), Special Publication, **60**, 786 pp.

—— OATES, M. J. and JENKYNS, H. C. 1998. The Lower Lias Group of the Hebrides Basin. *Scottish Journal of Geology*, **34**, 23–60.

HOLTHUIS, L. B. 1974. The lobsters of the superfamily Nephropidea of the Atlantic Ocean (Crustacea: Decapoda). *Bulletin of Marine Science*, **24**, 723–884.

HOWARTH, M. K. 1956. The Scalpa Sandstone of the Isle of Raasay, Inner Hebrides. *Proceedings of the Yorkshire Geological Society*, **30**, 353–370.

LATREILLE, P. A. 1802–1803. *Histoire naturelle, général et particulière, des crustacés et des insectes: Volume 3.* F. Dufart, Paris, 468 pp.

MEYER, H. VON 1835–1838. Briefliche Mitteilungen. 328. *In: Leonhardt und Bronn's Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie.* C. F. Winter, Stuttgart.

MORTON, N. and HUDSON, J. D. 1995. Field guide to the Jurassic of the Isles of Raasay and Skye, Inner Hebrides, NW Scotland. 209–280. *In* TAYLOR, P. D. (ed.). *Field guide to the British Jurassic.* Geological Society, London, 286 pp.

OPPEL, A. 1853 [1854]. Der mittlere Lias Schwabens. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg*, **10**, 39–136.

—— 1861. Die Arten der Gattungen *Glyphea* und *Pseudoglyphea*. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg*, **17**, 108–111.

—— 1862. Ueber jurassische Crustaceen. *Palaeontologische Mittheilungen aus dem Museum des Koeniglichen Bayerischen Staates*, **1**, 1–120, pls 1–38.

STRAELEN, V. VAN 1925. Contribution à l'étude des crustacés décapodes de la période Jurassique. *Memoires de l'Académie Royale de Belgique, Classe des Sciences*, *Part 4, Series 2*, **7**, 1–462.

—— 1936. Sur des Crustacés Décapodes Triasiques du Nevada. *Bulletin du Musée Royale d'Histoire Naturelle de Belgique*, **12** (29), 1–7.

TATE, R. and BLAKE, J. F. 1876. *The Yorkshire Lias*. John Van Voorst, London, 475 pp.

THÉOBALD, N. 1953. Une nouvelle espèce de crustacé décapod fossile de l'Aalénien du Bas-Rhin. *Compte Rendu des Sciences, Société Géologique de France*, **10**, 150–152.

WINCKLER, T.-C. 1883. Étude carcinologique sur les genres ''*Pemphix*'', ''*Glyphea*'' et ''*Araeosternus*''. *Archive du Musée Teyler, Série 2*, **1**, 1–52, pl. 1.

WOODS, H. 1925–1931. A monograph of the fossil macrurous Crustacea of England. *Palaeontographical Society, Monograph* [parts 357, 359, 362, 365, 369, 377, 380], 122 pp., 27 pls.

WOODWARD, H. 1863. On a new macrurous crustacean ''*Schapheus ancylochelis*'' from the Lias of Lyme Regis. *Quarterly Journal of the Geological Society of London*, **19**, 318–321.

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