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A systematic survey of the genus *Notopocorystes* McCoy, 1849 (Crustacea, Decapoda, Raninidae)

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Abstract

A historical account of the raninid crab genus *Notopocorystes* McCoy, 1849, is followed by a review of the species within the three recognised subgenera, *Notopocorystes, Eucorystes* and *Cretacoranina.*

Key words: Crustacea, Decapoda, Raninidae, *Notopocorystes*, Cretaceous, review.

Introduction and historical review of the genus *Notopocorystes* McCoy, 1849

'With new forms rife
Now prospers far and wide Crustacean life.
Crabs, that of yore were "few and far between."
Are numerous now and widespread on the scene ;
And the crusted groups would seem to be
The most progressive in this Creta sea;
Holding the palm that in the watery ways
Was borne by lobsters in Jurassic days.'

Thus runs a stanza of the 'Cretaceous Period' in Knipe's monumental history of the Earth in verse, 'Nebula to Man' (1905). In the appended notes the crabs are identified as *Dromiopsis* and *Palaeocorystes* [=*Notopocorystes*]. The reference to *Dromiopsis,* without doubt, alludes to the abundance of carapaces of that genus met with in the Palaeogene Middle Danian which, in 1905, was still an integral part of the Upper Maastrichtian.

Notopocorystes, the oldest known genus of raninid crabs, is stratigraphically widely distributed and ranged from the early Albian to late Campanian or early Maastrichtian. The precise origins and early evolution of this genus of back-burrowing crabs are not yet known, but, as suggested by Glaessner (1960, p. 46), it is closer to *Necrocarcinus* than to its known descendants and it is probable that *Notopocorystes* was derived from the latter early in Cretaceous, or even late Jurassic, times. The latter assumption is not unreasonable inasmuch as the genus was evidently well advanced - as indicated by the presence of three clearly defined subgenera, *Cretacoranina, Eucorystes* and *Notopocorystes* - by the time of its first known appearance in the Lower Albian.

The first allusion to a species of fossil crab that was to become included in the genus *Notopocorystes* was made by Leach *in* Mantell in 1822 when he referred to 'a species of a genus of the family Corystidae'. It fell to Mantell (1844), however, to describe and figure the specimens involved as *Corystes stokesii* and *Corystes broderipii*, but not before referring the latter species to the Leucosiadae [Leucosiidae] in 1833.

Adding further to the confusion at about this period, McCoy (1849) gave a concise description of *Notopocorystes mantelli*, with reservations that it might belong to *stokesii* and placed the species in the Anomura. Bell (1863), recognising the synonymy, spoke critically of McCoy's choice of generic name,

Notopocorystes, saying it was derived from an 'erroneous notion of the structure of the posterior pair of walking legs', and thereupon introduced his own taxon, *Palaeocorystes*. Bell was also rather caustic concerning the paucity of Mantell's (1844) description and 'scarcely recognisable' figures.

In the same work, Bell (1863) described a Cenomanian species *Notopocorystes normani*, and erected a new genus, *Eucorystes*, for *Notopocorystes carteri* McCoy, 1854. Woodward's (1874) London Clay (Ypresian) species *Palaeocorystes glaber*, was included in *Raninoides* (Förster & Mundlos, 1982; Collins & Smith, 1993), but has since been transferred to *Laeviranina* (Tucker, *in prep*). In 1896 Woodward founded *Notopocorystes harveyi*, which remains the only member of the genus known from Canada.

Other species described among faunas abroad were soon forthcoming although three of them, the Maastrichtian *Notopocorystes muelleri* van Binkhorst, 1857 and the two Turonian species, *Notopocorystes laevis* Schlüter, 1868 and *Notopocorystes callianassarum* (Fritsch, 1887), were transferred to other genera within a comparatively short time. By the turn of the centuary, however, two more European species had been made known, as well as species from the Cenomanian/Santonian of Japan (Jimbô, 1894). Since then the geographical distribution has been further extended to include Jamaica (Withers, 1927), Syria (Withers, 1928), the United States (Rathbun, 1935; Stenzel, 1945; Bishop, 1983, 1992), Madagascar (Secretan, 1964), Australia (Glaessner, 1986) and west Greenland (Collins & Rasmussen, 1992).

Bell (1863) distinguished *Eucorystes* not so much by the 'strap' ornament, characteristic of the genus, as by the width of the front and size of the orbits. However, as pointed out by Wright & Collins (1972), the orbital width is not significantly greater than that of comparably sized specimens of other depressed species such as *N. broderipii* or *N. stokesii*, while the width of the front is a function of the whole orbitofrontal margin; neither feature justifies generic or subgeneric separation. Wright & Collins (1972), however, argued that *Eucorystes*, which makes its appearance in the Lower Albian *D. mammillatum* Superzone of Surrey, England, should be maintained as a subgenus for species without sharp tubercles on the upper surface and with the characteristic 'strap' ornament.

The first known appearance of *Notopocorystes broderipii* is also in the *D. mammillatum* Superzone (JSHC Coll.). It has virtually no tubercles on the gastric region, but there is a well-developed median ridge posterior to the cervical furrow. It is clearly transitional to the almost smooth Upper Cretaceous group for which Mertin's (1941) name *Cretacoranina* is available; indeed, *N. broderipii*, included by Mertin (1941) in *Cretacoranina*, at least foreshadows the characteristic depressed frontal area of some of the later forms included in the genus.

Although Withers (1928) was to draw attention to inaccuracies in the diagrams, it appears that Van Straelen (1923), who accepted the four genera, *Notopocorystes, Eucorystes, Eumorphocorystes* and *Palaeocorystes* was the first author to pay attention to the sternites; he also recognised the raninoid characters of the genus and removed it from among the corystids where it had remained since Leach's time. Lőrenthey & Beurlen (1929) maintained both *Notopocorystes stokesii* and *Palaeocorystes broderipii*; their arguments concerning evolutionary trends of their included species are to a large extent outdated by the earlier occurrence of *Cretacoranina* and *Eucorystes*. Roger in the Traité de Paléontologie (1953, pl. 8, figs. 12, 13) also recognised the three nominal genera within *Notopocorystes* and included *Palaeocorystes* – represented by *P. broderipii* – with the much modified diagnosis of 'Forte carêne medians'. Mertin (1941) introduced the system whereby the closely related *Notopocorystes, Eucorystes* and his newly described *Cretacoranina* should more sensibly be regarded as subgenera of *Notopocorystes*, rather than as distinct genera. This system was adopted by Wright & Collins (1972), who draw attention to the three distinct phyletic lines that are developed within *Notopocorystes* during the Albian and which persist throughout the present known range of the genus. Secretan (1964), Bishop (1986) and Bishop *et al.* (1992), however, preferred to recognise only *Notopocorystes*.

The W. B. D & Gideon Mantell Collections were taken to New Zealand by Mantell's elder son, Walter, and there remained until Dr. C. A. Fleming F. R. S.,

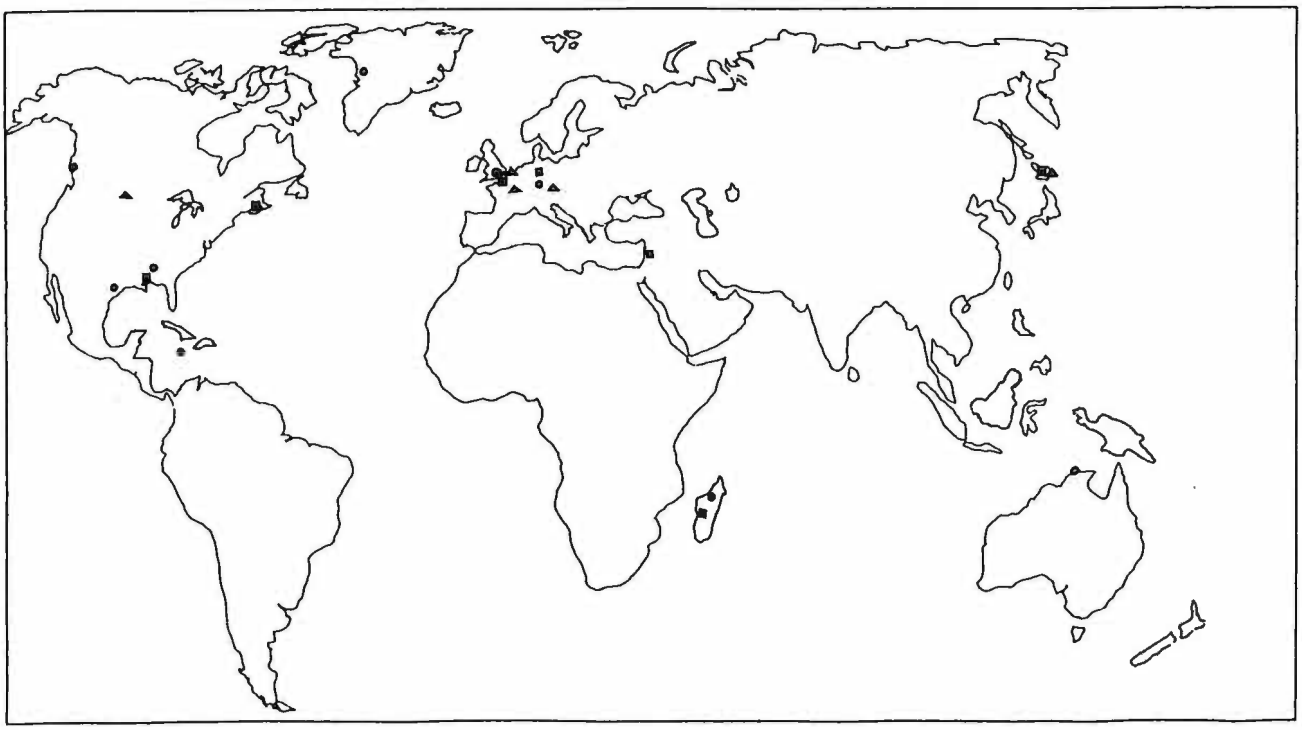


Fig. 1 Distribution of the genus *Notopocorystes*. The squares indicate the subgenus *Notopocorystes*; the dots, *Cretacoranina* and the triangles, *Eucorystes*.

late of the New Zealand Geological Survey, generously presented this important type series to the British Museum (Natural History) c. 1968. During the course of preparation of their monograph (1972), Wright & Collins observed that four of these specimens bore original labels relating to the 2nd edition of Mantell's Medals of Creation (1854), while two specimens, "might conceivably be the originals of plate 29, figures 15 and 16 in 'Fossils of the South Downs.' "

It was, perhaps, de Tribolet (1874) who omitted the terminal i of both *stokesii* and *broderipii*, thus committing an error compounded by numerous subsequent authors.

To date, 35 species (including 1 unnamed) have been included in *Notopocorystes* (Table 1), of these 1 has been placed in synonymy with another species, 1 is based on a chela and 7 have been relegated to different genera. Of the 21 undisputed species (ex subspecies) currently recognised, 12 (57%) belong to *Cretacoranina* and 5 (24%) to *Notopocorystes* and 4 (19%) *Eucorystes*.

Notopocorystes McCoy, 1849

Type species: By subsequent designation of Withers (1928, p. 456); *Notopocorystes mantelli* McCoy, 1849 = *Corystes stokesii* Mantell, 1844.

Diagnosis: After Wright & Collins (1972) : Carapace elongated, more or less flat to moderately inflated with small projecting bifid rostrum, straight orbitofrontal margin, large oval orbits with two fissures above and one below and sharp sides. A distinct longitudinal keel may or may not be present. The cervical furrow at first runs forward from the margin, then backwards, forming three forwardly concave arcs. An epibranchial lobe is delimited by a short furrow. The branchiocardiac furrows are weak to absent. The upper surface may bear sharp tubercles, or be bare, or have strap-like ornament or may have a transverse lobed line behind a depressed frontal area. The pterygostomian regions are strongly ridged.

Table 1. Species historically and presently included in *Notopocorystes*

australis Secretan, 1964	*Notopocorystes*	*Cretacoranina*	Sant-L. Camp
bechei (= *labeschii*) Deslongchamps, 1835	*Notopocorystes*	*Necrocarcinus*	
bituberculatus Secretan, 1964	*Notopocorystes*	*Notopocorystes*	Albian
broderipi (= *brorderipii*)	*Palaeocorystes*		
brorderipii Mantell, 1844	*Corystes*	*Cretacoranina*	Albian
	Palaeocorystes		
callianassarum Fritsch, 1887	*Callianassa*	*Hemioon*	
	Palaeocorystes		
	Eucorystes		
c. cartei McCoy, 1854	*Notopocorystes*	*Eucorystes*	U. Albian
c. lingulatus Wright & Collins, 1972	*Eucorystes*	*Eucorystes*	U. Albian
denisae Secretan, 1964	*Notopocorystes*	*Cretacoranina*	Campanian
dichrous Stenzel, 1954	*Notopocorystes*	*Cretacoranina*	Turonian
eichhorni Bishop, 1983	*Eucorystes*	*Eucorystes*	L. Campanian
exiguus Glaessner, 1980	*Cretacoranina*	*Cretacoranina*	L. Cenomanian
fritschi Glaessner, 1929	*Palaeocorystes?*	*Cretacoranina*	Campanian
glaber Woodward, 1874	*Palaeocorystes*	*Laeviranina*	
harveyi Woodward, 1896	*Palaeocorystes*	*Cretacoranina*	L. Sant/E. Camp
	Notopocorystes		
intermedius Nagao, 1931	*Notopocorystes*	*Eucorystes*	Cenom-Sant
isericus Fritsch, 1887	*Palaeocorystes*	*Necrocarcinus*	
japonicus Jimbô, 1894	*Eucorystes*	*Notopocorystes*	Cenom-Sant
laevis Schlüter, 1868	*Palaeocorystes*	*Hemioon*	
mantelli McCoy, 1849	*Palaeocorystes*	*Notopocorystes*	
muelleri van Binkhorst, 1857	*Notopocorystes*	*Pseudoraninella*	
normani Bell, 1863	*Palaeocorystes*	*Notopocorystes*	Cenomanian
ornatus Wright & Collins, 1972	*Cretacoranina*	*Cretacoranina*	Cenomanian
oxtendensis Wright & Collins, 1972	*Eucorystes*	*Eucorystes*	L. Albian
parvus Rathbun, 1935	*Notopocorystes*	*Raninella*	
paututensis Collins & Rasmussen, 1992	*Cretacoranina*	*Cretacoranina*	M. Alb/Sant
punctatus Rathbun, 1935	*Notopocorystes*	*Raninella*	
ripleyensis Rathbun, 1935	*?Notopocorystes*	*?Notopocorystes*	E. Campanian
stokesii (= *stokesii* s.l.)			
s. stokesii Mantell, 1844	*Corystes*	*Notopocorystes*	Albian
	Palaeocorystes		
s. praecox Wright & Collins, 1972	*Notopocorystes*	*Notopocorystes*	Albian
s. serotinus Wright & Collins, 1972	*Notopocorystes*	*Notopocorystes*	Albian
syriacus Withers, 1928	*Notopocorystes*	*Notopocorystes*	Cenomanian
schloenbachi Schlüter, 1879	*Raninella*	*Cretacoranina*	Cenom-Coniac
testacea Rathbun, 1926	*Raninella*	*Cretacoranina*	L. Camp/Maastr
trechmanni Withers, 1927	*Ranina*	*Cretacoranina*	?Campanian

Notopocorystes (*Notopocorystes*) McCoy, 1849

(Pl. 22, Figs. 1-6)

Diagnosis: After Wright & Collins (1972): *Notopocorystes* with distinct tubercles on the anterior part of the upper surface of the carapace and a smooth or dentate median keel or row of tubercles.

Range: Lower Albian - Campanian.

N. (*N.*) *stokesii s.l.*, the first member of the genus to be described, remains the earliest known species within this subgenus; it is the commonest Gault crab and perhaps the commonest fossil crab in England. Because of the great number of carapaces available, a

gradual morphological development - hardly discernible in other Gault crab species - is apparent. Bell did not distinguish between the markedly different Lower Gault and Cambridge Greensand forms, while Withers (1928, p. 457) merely referred to the greater transverse convexity and narrower orbitofrontal width of the latter. Examination of specimens from known Subzones has shown that successive populations can be grouped in three rather stable forms in Lower, and Middle to Upper Gault respectively (Collins *in* Hancock, 1965). Although the differences between them are greater than those sometimes used to distinguish fossil crabs, Wright & Collins (1972) preferred to treat them as chronological subspecies.

The earliest of these, *N.* (*N.*) *s. praecox* Wright & Collins, 1972, from the *Douvilleiceras mammillatum* Superzone, is moderately arched transversely; the orbitofrontal width is half that of the carapace or even more, averaging 58%; the median carina is nearly continuous and notched into tubercles; and the major dorsal tubercles are subdued, as are six small tubercles forming a crescent bordering each hepatic lobe. The subspecies is not known above its type horizon. The familiar, nominate form, *N.* (*N.*) *s. stokesii*, was well developed by as early as the *Lyelliceras lyelli* Subzone. From below upwards there are changes in the outline and ornament of the carapace such as, an increase then a decrease of the orbitofrontal width ranging from 75% - 66% of the carapace width (Collins, 1965), a reduction of the median carina to a row of discreet tubercles, while those forming the hepatic crescentic rows become reduced in number by loss or absorption, and variations in granulation of the test. The subspecies is not known to occur above the *Dipoloceras cristatum* Subzone.

A few aberrant forms in the *Anahoplites intermedius* Subzone with an extra tubercle on one side or the other of the mesogastric median one occur together with those with paired tubercles. This latter form, *N.* (*N.*) *s. serotinus* Wright & Collins, 1972, had stabilized thus far by the *Dimorphoplites niobe* Subzone; it was coeval with and underwent similar changes in carapace morphology to *N.* (*N.*) *s. stokesii* to the *D. cristatum* Subzone, where the two subspecies occur in about equal number. From the *Hysteroceras orbignyi* Subzone and beyond to the Cambridge Greensand; the carapace becomes considerably arched in both sections, the median ridge is almost or quite reduced to a row of separate tubercles, additional tubercles on the epibranchial lobes and a scabrous urogastric lobe; the orbitofrontal margin of carapaces from the *H. orbignyi* Subzone occupies about 66% of the carapace width, while on specimens from the Cambridge Greensand it has reduced to 62% (Collins, 1965). The subspecies occurs also in the distinctive facies of the Red Chalk (*H. orbignyi* Subzone) of Hunstanton, Norfolk and seems to be the direct ancestor of *N.* (*N.*) *normani* (Bell, 1863) known by a handful of specimens from the Cenomanian of the Isle of Wight, Dover, Kent and Hanover, Germany. In this species, which Carter (1898) opined was no more than a variant of *N.* (*N.*) *stokesii*, the orbitofrontal/width percentage is further reduced to about 49%.

None of these variations in carapace morphology is attributable either to ontogeny or sexual dimorphism.

A statement by Carter (1898) of specimens from the Upper Greensand of the Isle of Wight has not been verified. *N.* (*N.*) *stokesii* occurs also in the French Albian where it is known, with *N.* (*C.*) *broderipii*, from Boulonnais, etc., but no subspecific records have been kept.

The subgenus was also established in Madagascar by Albian times where it is known by *N.* (*N.*) *bituberculatus* Secretan, 1964, founded on a single carapace lacking much of its anterior part: it differs from *N.* (*N.*) *stokesii* in the distribution of the (remaining) gastric tubercles and a double row of median longitudinal tubercles commencing with a pair on the mesogastric lobe.

The Japanese Cenomanian - Santonian species, *N.* (*N.*) *japonicus* Jimbô, 1894 would appear to be a regressive form of *N.* (*N.*) *s. praecox*. Not only does it have a comparable orbitofrontal/carapace width of 56.5%, but it retains the crescentic tubercle-lined hepatic ridge and protogastric tubercles, although the median carina is developed only on the branchial region. It differs from *N.* (*N.*) *s. praecox* in having a transverse pair of tubercles on the cardiac region.

Notopocorystes (*Eucorystes*) Bell, 1863
(Pl. 23, Figs. 4-5)

Type species: By monotypy: *Notopocorystes carteri* McCoy, 1854.

Diagnosis: After Wright & Collins, 1972 : at least the anterior part of the carapace has a well marked system of furrows and lobes (straps), the latter consisting of more or less subdivided flat topped, steep sided areas.

Range: Lower Albian - Campanian.

Withers (1928) united *Eucorystes* with *Notopocorystes* on the grounds that the strap ornament of the former was unreal and was only the effect of differential weathering. Why Withers should have been misled into considering the entire population of Cambridge Greensand *carteri* should be effected thus, yet weathering leave no comparable marks on coeval crabs or the Gault *N.* (*C.*) *broderipii*, remains enigmatical.

Once they had been adequately prepared, it was seen that specimens from the *D. mammillatum* Superzone of Surrey, England, previously identified by Wright & Wright (1948, p. 85) as *Notopocorystes broderipii*, were quite distinct and were later described as *N.* (*Eucorystes*) *oxtedensis* Wright & Collins, 1972. This species is obviously the direct ancestor of the well known *N.* (*Eucorystes*) *carteri* McCoy from the Cambridge Greensand, differing from it in a number of minor characters; in outline its sides are rounded, not straight and the angulation of the anterolateral margin is less pronounced; the orbitofrontal margin is relatively narrower, the transverse section somewhat more strongly arched, the mesogastric lobe rounded triangular in shape; the areolation of the front part of the carapace, though considerable, is not so extreme, both because the strap ornament is less fragmented and because the edges of the straps are less steep.

A plaster cast of a carapace (original kindly lent to JSHC some 20 years ago by Dr. P. Destombes from the *Lyelliceras lyelli* Subzone, Courcelles, Aube, France) has a similar outline to British specimens of *N.* (*E.*) *oxtedensis*, but the anterior characters are more sharply defined. Additionally, the branchiocardiac furrow separates a narrow, elongate mesobranchial node from a larger one either side of the cardiac region. Regarded as little more than differences in preservation at the time, these differences would now no doubt be considered sufficiently distinct for at least subspecific recognition, should the original French specimens be located.

The subspecies *N.* (*E.*) *carteri lingulatus* Wright & Collins, 1972, differs from the nominate form by the addition of three longitudinal straps on the branchial region; its matrix suggests that the only known specimen came from an uppermost Albian horizon immediately above the Cambridge Greensand nodules and it was regarded by Wright & Collins (1972) to be a late development of the typical form of the species which is known from France and also from Switzerland (Van Straelen, 1936).

Until a large collection of Japanese specimens of *Notopocorystes* became available for comparison with the originally described material (Collins, Kanie & Karasawa, 1993), some confusion had existed over the identities of *N.* (*N.*) *japonicus* and *N.* (*E.*) *intermedius* Nagao, 1931, even to the species sometimes being considered synonymous (e.g. Glaessner, 1929a; Bishop, 1983). Absence of a median ridge and presence of typical strap ornament on the gastric region, however, readily distinguishes Nagao's species. As a consequence Glaessner's (1929b) and Bishop's (1983) remarks concerning the similarity of *Notopocorystes japonicus* to *N.* (*E.*) *carteri* and *N.* (*E.*) *eichhorni*, respectively, should more properly be applied to *N.* (*E.*) *intermedius*. The transverse curvature of *N.* (*E.*) *intermedius* is flatter than that of *N.* (*E.*) *oxtedensis*, the anterolateral spines are sharper and slenderer and the gastric furrows are narrower.

The geological and geographical ranges of the subgenus were extended to the Campanian of the Western Interior of the U.S.A. with the description of *N.* (*E.*) *eichhorni* Bishop, 1983. A singular character or this species lays in the anterior part of the metabranchial lobes being rather tumid. Otherwise it differs from *N.* (*N.*) *oxtedensis* in having a relatively wider front and more sharply defined straps reaching behind the cervical furrow; from *N.* (*E.*) *carteri* in having more rounded lateral margins and stronger hepatic spines and *N.* (*E.*) *intermedius* may be distinguished by its

weak, less complex straps. Internal moulds of *N.* (*E.*) *eichhorni* retain, among other 'ornament', the primitive features of the hepatic crescentic ridge and protogastric tubercles seen on *N.* (*N.*) *s. praecox*.

Notopocorystes (*Cretacoranina*) Mertin, 1941

(Pl. 23, Figs. 1-3)

Type species: By original designation *Raninella schloenbachi* Schlüter, 1879 (p. 612, pl. 18, fig. 2).

Diagnosis: After Wright & Collins (1972): the upper surface of the carapace is finely granulate or smooth with virtually no tubercles, and with or without a distinct depressed frontal area; the cervical furrow is entire or reduced to the median parts only, as is the branchiocardiac.

Range: Middle Albian - Maastrichtian.

Rather more than twice as many species of *N.* (*Cretacoranina*) are presently recognised than of *N.* (*Notopocorystes*) or *N.* (*Eucorystes*). However, from the lowest known form, the Lower Albian *N.* (*C.*) *broderipii*, no others are known until the Cenomanian, when four species: *N.* (*C.*) *exiguus* Glaessner, 1980, *N.* (*C.*) *ornatus* Wright & Collins, 1972, *N.* (*C.*) *schloenbachi*, and *N.* (*C.*) *syriacus* Withers, 1928, make their appearance. These species are known from Australia, England, Germany and Syria, respectively, and indicate the widespread dispersal of the subgenus which was to encompass Greenland, Jamaica, Madagascar and North America by the time of the last known species in the Maastrichtian.

The median ridge, prominent in the earliest known (*D. mammillatum* Superzone) form of *N.* (*C.*) *broderipii*, becomes subdued or well rounded in that species by the *Mojsisovicsia subdelaruei* Subzone of the Middle Albian. Elements of the hepatic crescentic ornament present on *N.* (*N.*) *stokesii* - found particularly on internal casts - of *N.* (*E.*) *broderipii* strongly suggest that *N.* (*Cretacoranina*) is closer to *N.* (*Notopocorystes*) than to *N.* (*Eucorystes*).

An almost entire carapace of *N* (*C.*) *harveyi* (Woodward, 1896) illustrated by Ludvigen & Beard (1994, fig. 94) differs markedly from the hitherto only known figure, that of Woodward (1896), in having only two pairs of lateral spines instead of the four figured. There is also discrepancy regarding the orbitofrontal margin: short, bluntly-rounded points of the rostrum are widely separated by a V-shaped sinus, the sides curve back to a wide notch in the upper orbital margin followed by a sharp spine; a little advanced, the margin continues straight to a weaker notch close to a fine, sharply pointed incurved outer orbital spine.

Wright & Collins (1972) considered that evolutionary change in *N.* (*Cretacoranina*) evolved around the number of anterolateral spines, the reduction of the cervical furrow and prominence of the median ridge. Whereas three pairs of spines occur in *N.* (*C.*) *broderipii*. *N.* (*C.*) *australis* Secretan, 1964 and *N.* (*C.*) *denisae* Secretan, 1964, all the other species with the exception of *N.* (*C.*) *harveyi* and *N.* (*C.*) *ornatus* Wright & Collins, 1972 have four pairs; however, whereas the cervical furrow is entire in *N.* (*C.*) *broderipii*, it is reduced in *N.* (*C.*) *australis* and *N.* (*C.*) *denisae*. An entire cervical furrow also occurs in *N.* (*C.*) *exiguus* Glaessner, 1980, *N.* (*C.*) *harveyi*, *N.* (*C.*) *ornatus*, *N.* (*C.*) *paututensis* Collins & Rasmussen, 1992 and *N.* (*C.*) *syriacus* Withers, 1928, but, with the exception of *N.* (*C.*) *broderipii*, all have a comparatively narrow front; the Australian (Bathurst Island) species *N.* (*C.*) *exiguus* differs further by its sculpture. The narrow front persists in *N.* (*C.*) *fritschi* Glaessner, 1929b otherwise this species is markedly vaulted and has a reduced cervical furrow. On the other hand, the wide fronted Turonian *N.* (*C.*) *dichrous* Stenzel, 1945 has a reduced cervical furrow, yet retains a weak median ridge. *N.* (*C.*) *exiguus*, seen largely as an internal cast, is rather more deeply sculptured than normally encountered in this subgenus, though these features were probably softened by the shell thickness. The most diverse of the species mentioned above is undoubtedly *N.* (*C.*) *ornatus* with its two pairs of small anterolateral spines and a surface ornament consisting of numerous rather large granules arranged in discreet rows on the epibranchial, mesobranchial and urogastric lobes, and nearly distinct rows on the anterior parts of the metabranchial lobe.

Stenzel (1945) named *N.* (*C.*) *dichrous* from the distinct difference in colouration anterior to a lobate

postfrontal 'line' (by no means proud enough to be called a ridge) clearly defined on carapaces from the type, although less obvious from other localities. This feature also occurs on other species, e.g. *N.* (*C.*) *broderipii, N.* (*C.*) *syriacus, N.* (*C.*) *trechmanni*, *N.* (*C.*) *australis* and *N.* (*C.*) *denisae* but on other species it may be discontinuous or obscured by other surface features. In drawing attention to the similarity of the 'line' of *N.* (*C.*) *dichrous* to that of the Jamaican ? Campanian *N.* (*C.*) *trechmanni* and *N.* (*C.*) *broderipii*, Stenzel (1945) considered that *N.* (*C.*) *dichrous* was closer to the latter species. On the other hand, the North American late Campanian/early Maastrichtian N. (*C.*) *testacea* (Rathbun, 1926) has much in common with *N.* (*C.*) *trechmanni*.

Such combinations are by no means exhausted and it would seen, therefore, that for the most part, the primary characters of *N.* (*C.*) *broderipii* were rapidly modified to become specific characters within limited analogous species-groups, frequently distanced from one another by time and geographical distribution rather than phylogenetic ones.

Withers (1928) declared himself curious as to why *N.* (*Cretacoranina*) *broderipii* should occur commonly in the Gault, but not in the Cambridge Greensand where its, 'place is taken by the common crab *Eucorystes carteri*', and firmly concluded that *N.* (*E.*) *carteri* is the Cambridge Greensand derivative of the Gault *N.* (*C.*) *broderipii*. This opinion, however, can now be refuted by the presently known, more or less, simultaneous appearance of the two subgenera.

General observations

Evolutionary changes in carapace outline of the three subgenera have occupied the attention of a number of authors (e.g. Van Straelen, 1923, Lőrenthey & Beurlen, 1929, Secretan, 1964, Collins, 1965). In their discussion of the relative carapace outlines of the Gault *N.* (*N.*) *stokesii* and *Palaeocorystes broderipii*, Lőrenthey & Beurlen (1929) concluded that they were at the same evolutionary stage, because in both subgenera the carapaces are ovate and the anterolateral and posterolateral margins are clearly divided. Those authors also concluded that the ancestral form may have had a somewhat pronounced median ridge as in *N.* (*C.*) *broderipii* which regressed in this subgenus. The presence of the well-developed median ridge in the L. Albian *N.* (*C.*) *broderipii*, discussed above, would appear to substantiate this opinion. Lőrenthey & Beurlen (1929) further opined that it was almost certain that *Palaeocorystes* (*Cretacoranina*) and *Notopocorystes* descended from a common primitive stock; Wright & Collins (1972) included *Eucorystes* and considered that there are three phyletic lines within *Notopocorystes sensu lato*.

The median ridge common (during some stages, at least) to the subgenera is evidently not a primary character of *Eucorystes*, for it is not developed in the earliest known form, *N.* (*E.*) *oxtedensis*, and does not appear in that subgenus until the last known member, *N.* (*E.*) *eichhorni* in the Campanian.

The tuberculated median ridge and tubercular surface ornament attained by *N.* (*N.*) *s. serotinus* in the late Albian becomes degenerate to a large extent in the Cenomanian *N.* (*N.*) *normani* and this is considered regressive by Lőrenthey & Beurlen (1929). Extreme tubercular development was obtained by the Malagasy *N.* (*N.*) *bituberculatus* - a contemporary of *N.* (*N.*) *stokesii* - although, even here, the double row of median tubercles is restricted to the branchial region. Primitive characters of *N.* (*N.*) *s. praecox* consisting of a more or less smooth median ridge and weak surface ornament, are retained by the last known member, *N.* (*N.*) *japonicus* which survived into the Santonian.

Reference to the partial similarity of the sculpture of *N.* (*Eucorystes*) and the Maastrichtian *Eumorphocorystes sculptus* van Binkhorst, 1857 have been made by Bell (1863), Wright & Collins (1972). Lőrenthey & Beurlen (1929) remarked that this 'evolutionary pattern referred to in *Eumorphocorystes*, had its own developments', and that this evolutionary line *of Eucorystes* became extinct with *Eumorphocorystes sculptus*.

As remarked above, several references to the partial similarity of the sculpture of *N.* (*Eucorystes*) and *Eumorphocorystes sculptus* have been made, such as in Bell (1863) and Wright & Collins (1972), but no conclusion of its purpose had been reached. Savizzi

(1985, with additional references) has undertaken considerable research into the functional morphology of transverse cuticular terraces with regard burrowing habits of crabs; carapaces with irregular terraces ('straps'), however, do not appear to have received attention. Nevertheless, they could conceivably have served a similar function - even to the extent of being looked upon as 'experimental' steps towards the regularly transverse terraces perfected by *Lophoranina* Fabiani, 1910 and *Ranina* Lamarck, 1801. Although Bell (1863) drew attention to the inadequacy of McCoy's name, *Notopocorystes*, with regard to the 5th pair of limbs, he did not discuss further and it appears that Withers (1923) was the first author to relate the ornate leaf-like dactylus of the 5th limb (of *N.* (*C.*) *broderipii*) with its somewhat acute, slightly curved extremity, were features which he pointed out are, "closely parallel in the genus *Ranina*, in which the limb appears to have been used for swimming and digging."

According to Glaessner (1969) the posterior sternites in the (back) burrowing raninids are narrowed progressively, while the anterior portion (4th sternites) becomes shield-like. The inference, supported by Glaessner (1969, fig. 229), is that adaptation of the sternites in this manner is relative to burrowing efficiency. Sternites are known - and some of them imperfectly - in only a few *Notopocorystes* species.

In *N.* (*C.*) *broderipii* the isosceles-triangular 1st-2nd sternites are depressed from the broader, trapezoid 3rd element which is divided by an oblique cleft from the 4th elements on which a groove isolates crescentic episternites; the parallel-sided 5th-6th elements are successively a little narrower. In having 'primitive' parallel-sided 5th-6th sternal elements *N.* (*C.*) *broderipii* has much in common with those of *N.* (*N.*) *stokesii* and both species would appear to have had a poor burrowing efficiency compared with the markedly tapered 5th-8th elements of *N.* (*C.*) *schloenbachi* as figured by Glaessner (1969, fig. 229). The 5th-6th elements of *N.* (*N.*) *bituberculatus*, figured by Secretan (1964, fig. 88) differ considerably from those of *N.* (*N.*) *stokesii* in the lateral extension of the episternites. A specimen of *N.* (*E.*) *eichhorni* figured by Bishop (1983, fig. 6g) shows the 4th-5th sternites to be close to those of *N.* (*C.*) *broderipii*.

The comparative abundance of Gault *Notopocorystes* allows investigation into modes of preservation and possible aspects of taphonomy to be made. Both corpses and moulted exoskeletons may be preserved in a "closed" position, or in 'Salter's position' - i. e. - with the carapace inclined at an angle to the underside - and are not always easy to distinguish. With regard to *Notopocorystes*, the latter position is known in only one or two specimens of *N.* (*E.*) *carteri*. Instances of sternites disorientated from the dorsal midline of the carapace are rare.

Corpses and moults are subject to the action of scavengers/dessication and subsequent disintegration if cast on the beach, or disintegration by scavengers (particularly worms)/current action on the sea floor. Specimens from the *Dimorphoplites niobe*, *Hysteroceras orbignyi* and *Hysteroceras varicosum* Subzones have yielded the best examples of bioturbation among Gault species.

There are many instances among corpses of specimens burrowed by, apparently, two different kinds of worms or arthropods. The one, slender, for the most part a sub-cuticle burrower, especially about the gastric region; the other, larger, burrowed deep into the body cavity as well. Obvious moults are also burrowed - if not for food, then, possibly for shelter. Faecal pellets, occurring occasionally on the underside, are more often found clustered close to limb-joints. 'Prefossil fractures', as well as what Bishop (1986) termed 'disassociated' units among North American fossil crab assemblages are not infrequent in the Gault and some nodular crab-concretions could possibly be attributed to coprolites or regurgita.

A much greater degree of taphonomy, however, was described by Bishop *et al.*, (1992) among a large suite of *N.* (*C.*) *dichrous* of Cenomanian age from Texas. Chondrites was observed. as well as the worms/arthropods and abundant, faecal pellets. Many of the specimens were preserved in what could only be considered as a death-position; fragments of the endophragmal system are preserved and instances of partly decomposed cuticle invaginated into body cavities were noted.

In drawing attention to carapaces of *Linuparus* with

extensive damage to the gastric region on the dorsal surface of the carapace, Bishop (1986) concluded such damage was caused by the breakdown of the cuticle as a result of gastric enzyme action after death. One or two (*Dimorphoplites niobe* Subzone) carapaces of *N.* (*N.*) *stokesii* have damage extending through the cuticle into the cast beneath - certainly not from mechanical means - which can, without doubt, be similarly attributed to gastric corruption.

Occasional specimens of *N.* (*N.*) *stokesii* are found infested by a bopyriform parasite; typical swellings on the branchial region may occur on either the left or right side and, very rarely, both sides. *N.* (*C.*) *broderipii* on the other hand appears to have been less prone to attack and there are no reports concerning other members of the genus.

Crabs have rarely been used as zonal indicators; Price (1880), noted the abundance of *Palaeocorystes* and *Notopocorystes* in the Lower Albian *D. niobe* Subzone which he and other authors consequently referred to as the 'crab bed'. *Eumorphocorystes naselensis* Rathbun, 1926 was selected as a zonal indicator by Jeletzky (1954) to identify an Oligocene sequence extending over Vancouver Island and *N.* (*C.*) *dichrous* Stenzel, 1944 has the distinction of heading a decapod assemblage of Cenomanian age in Texas (Bishop *et al.*, 1992).

Ecological and palaeobiological conclusions

Almost throughout its history, *Notopocorystes* - an acknowledged back-burrowing genus - has been associated with one, or all, of three other genera, *Necrocarcinus, Xanthosia* and *Homolopsis* or other homolids, all bottom-dwellers. It occurs with *Homolopsis* in the *D. mammillatum* Superzone and with all three genera throughout the Gault into the Lower Cenomanian of southern England. Abroad *Notopocorystes* is found in company with *Necrocarcinus* and *Xanthosia* in the Upper Albian/Lower Cenomanian Paw Paw Formation and the Lower Turonian Denton Formation of Texas. In the Lower Campanian Merchantville Formation of the Northern Atlantic Coastal Plain the genus is accompanied by *Necrocarcinus, Xanthosia* and the homolid, *Hoplitocarcinus* Beurlen, 1928 (=*Metahomola* Collins & Rasmussen, 1992). It is present, with the homolid *Zygastrocarcinus*, in the Campanian Pierre Shale of Montana, but is yet to be found in the Pierre Shale of South Dakota, where conditions were favourable to *Necrocarcinus, Xanthosia* and homolids (Bishop, 1986). Only *Hoplitocarcinus* is coeval in the Turonian Yezo Group of Japan.

It is apparent that all these genera were readily adaptable to a considerable variation in bottom conditions. An exception may be noted, however, in the absence of *N.* (*Eucorystes*) through the Middle and Upper Gault; another is evident from the notably smaller specimens of both *N.* (*N.*) *stokesii* and *N.* (*C.*) *broderipii*, neither species, seemingly, was entirely compatible with the heavily ferruginous clays of the *D. niobe* Subzone, although such conditions did not otherwise effect their phyletic morphology. (A similar antipathy towards Gault conditions may be seen in *Diaulax oweni* (Bell, 1850), a reasonably common species in the Upper Aptian Shenley Limestone lenticles, reappearing in the Cambridge Greensand. Its place in the Gault being taken by *Diaulax feliceps* Wright & Collins, 1972.) Where *Notopocorystes* occurs in the early Maastrichtian of Mississippi and Tennessee, it is not yet known from the Maastrichtian type-section at Limburg where *Homolopsis* and *Xanthosia* are found with other raninid genera (Collins *et al.*, 1995).

In their discussion of evolutionary traits Lőrenthey & Beurlen (1929) stated that within *Notopocorystes, Palaeocorystes* [=*Cretacoranina*] is the most primitive form, but this is questionable in the light of probable development of *N.* (*Notopocorystes*) from *Necrocarcinus*, or necrocarcinid stock.. Those authors further stated that the Upper Cretaceous species, then known, of *Raninella* showed the same evolutionary tendency as *Eucorystes* and could therefore be traced back to *Cretacoranina*. The subsequent description of *Raninella parva* (Rathbun, 1935) and *Raninella punctata* (Rathbun, 1935) - both formerly placed in *Notopocorystes* - from the late Albian of Texas, however, rather than substantiating this reasoning, suggests a considerably earlier divergence from a common ancestral stock, as yet unknown. Lőrenthey & Beurlen (1929)

were also of the opinion that *Pseudoraninella* points more towards *Notopocorystes* and the short-lived, locally restricted genus *Eumorphocorystes* probably derived from *Eucorystes*.

Taking into consideration the number of species presently recognised in the three subgenera, it is evident that *N.* (*Notopocorystes*) and *N.* (*Eucorystes*) were the least successful. No *Notopocorystes* species is known to occur above the Maastrichtian; whereas the three companion genera, discussed above successfully survived the KT boundary event into the Middle Danian. It would seem therefore that prevailing conditions were evidently unfavourable for *Notopocorystes* and the genus was unable to keep up the pace.

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Plate 22

Notopocorystes (*Notopocorystes*) *stokesii praecox* Wright & Collins, 1972

Figs. 1a–c. Top, front and left side of Holotype, × 2, Lower Albian, *D. mammillatum* Superzone, Squerry's pit, Westerham, Kent, Casey Coll, G.S.M. ZM 1558.

Notopocorystes (*Notopocorystes*) *stokesii stokesii* (Mantell, 1844)

Figs. 2a, b. Top and front of early form, × 2, Lower Gault, *H. spathi* Subzone, Dunton Green, Sevenoaks, Kent, C. W. & E. V. Wright Coll, BM In60977.

Fig. 5. Genolectotype, × 2, Lower Gault, Sussex (probably Ringmer), W. B. D. & Gideon Mantell Coll. ex New Zealand Geological Survey, BM In61146.

Fig. 6. Paralectotype, underside showing sternites, × 2, Lower Gault, Sussex (probably Ringmer), W. B. D. & Gideon Mantell Coll., Ex New Zealand Geological Survey, In 61151.

Notopocorystes (*Notopocorystes*) *stokesii serotinus* Wright & Collins, 1972

Figs. 3a–c. Top, side and underside of female, × 2, Cambridge Greensand *M. alteonense* to *M. perinflatum* Subzones, Cambridge, GSM 108230.

Figs. 4, 7. Front and underside of male, showing abdomen, part of sternites and 3rd maxillipeds, × 2, the original of Bell, 1863, pl. 3, fig. 5, Cambridge Greensand, *M. altonense* to *M. periflatum* Subzones, Cambridge, SM B22902.

BM, Natural History Museum, London; GSM, Geological Survey Museum; SM, Sedgwick Museum, Cambridge.



1a



2a



3a



1b



2b



4



1c



5



3b



6



7



3c

Plate 23

Notopocorystes (*Cretacoranina*) *broderipii* (Mantell, 1844)

Fig. 1. Carapace and most of limbs; including short 5th pereiopods with leaf-shaped dactylus, × 2, from the Gault of Folkstone, Referred to by Withers, 1928, p. 459, BM In27329.

Figs. 2a-c. Top, front and left side, × 2, Lower Gault Dunton Green, Sevenoaks, Kent, C. W. & E. V. Wright ex Miss S. Stainforth Coll., BM In60979.

Fig. 3. Chelipeds and pereiopods, × 1, Note the dactylus is nearer the front of the carapace contrary to the normal situation in which the dactylus is on the side farther from the front. This may be due to post mortem distortion, but since the the position is the same with both chelae, it may be a natural feature in this species, J. Carter Coll., SM B30654, Gault, Folkestone.

Notopocorystes (*Eucorystes*) *oxtedensis* Wright & Collins, 1972

Fig. 4. Holotype, a partly decorticated carapace, × 2, Albian Folkestone Beds, *C. floridum* nodules, Coney Hill (Priory) sandpit, Oxted, Surrey, C. W. & E. V. Wright Coll., BM In60984.

Notopocorystes (*Eucorystes*) *carteri carteri* McCoy, 1854

Figs. 5a-c. Top, front and right side, × 2, Cambridge Greensand, Upper Albian, *M altonense* to *M. perinflatum* Subzones, Cambridge, SM B23091.

BM, Natural History Museum, London; GSM, Geological Survey Museum; SM, Sedgwick Museum, Cambridge.



1



2a



2c



2b



5c



5b



3



4



5a