Neozanthopsis americana (Decapoda, Brachyura, Carpilioidea) from the Middle Eocene Cane River Formation of Louisiana, USA, and associated teleost otoliths

C.E. Schweitzer, R.M. Feldmann & G.L. Stringer

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Carrie E. Schweitzer, Department of Geology, Kent State University at Stark, 6000 Frank Ave. NW, North Canton, Ohio 44720, USA (cschweit@kent.edu); Rodney M. Feldmann, Department of Geology, Kent State University, Kent, Ohio 44242, USA (rfeldman@kent.edu); Gary L. Stringer, University of Louisiana at Monroe, Monroe, Louisiana 71209, USA (stringer@ulm.edu)

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A large collection of *Neozanthopsis americana* (Rathbun, 1928) from the Middle Eocene (Lutetian) Cane River Formation in Louisiana, USA, represents the first opportunity to describe the species in detail. Detailed analysis of associated teleost otoliths and other vertebrate remains documents a palaeoenvironmental setting characterised by a soft-sediment, inner-shelf setting with normal salinity under tropical or subtropical conditions. Anatomical and morphometric analysis of 21 of the better-preserved crabs demonstrates that gender discrimination cannot be made from dorsal carapace characteristics and that the sample represents post-juvenile individuals. Exocuticle and endocuticle are preserved on some specimens and document the presence of erect endocuticular pillars with exocuticle draped over them. Occurrence of some fractured and expanded specimens results from the presence of expandable clays within the matrix.

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Introduction

The Cane River Formation in north-central Louisiana is well known for its molluscan and vertebrate fossils (Stringer, 2002; references therein). However, until recently decapod crustaceans were noted from the unit (Andersen, 1993), but not described. Examination of an exposure in Natchitoches Parish, Louisiana (Fig. 1), in January 2013, by one of us (GLS) yielded a large number of well-preserved crabs. This discovery is significant because it permits emending the description of a characteristic Eocene form, *Neozanthopsis americana*, and elucidating the environmental conditions in which it lived. Because 50 fossil crabs were recovered, it has been possible to conduct morphometric and morphological analyses to broaden our understanding of the taxon. Numerous

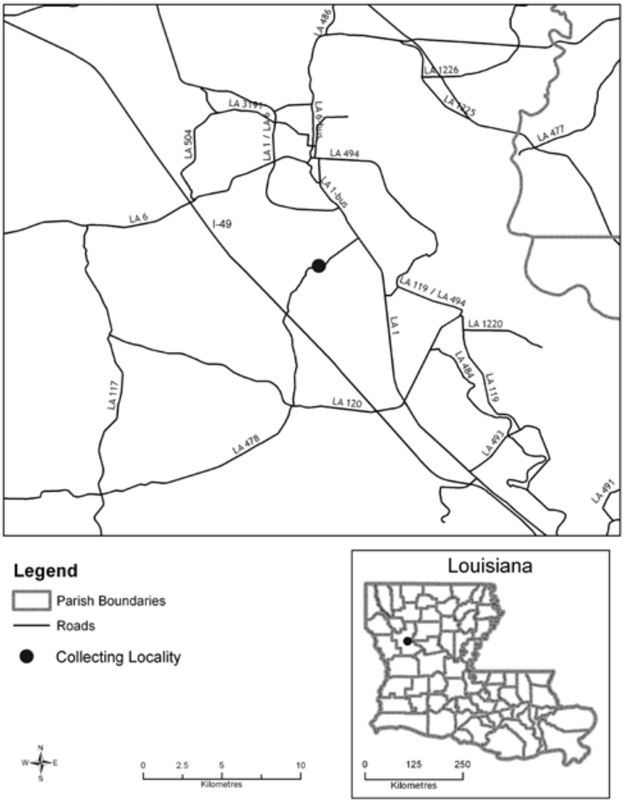

Fig. 1. Map showing the locality from which *Neozanthopsis americana* (Rathbun, 1928) was collected for the present study.

teleost otoliths preserved in intimate association with the decapods can be used to constrain depth, substrate and salinity conditions at the site of deposition.

Palaeoenvironmental setting

Bulk samples and surface collections were utilized to reconstruct the palaeoenvironment associated with the decapod specimens in the Middle Glauconitic Clay Member of the Cane River Formation at the locality. Both invertebrates and vertebrates were analysed. Approximately 30 kg of fresh and unweathered sediment was collected from the same horizon from which the decapods originated. A primary consideration was to examine teleost otoliths to assist in determining the palaeoecological conditions. While the sample size is large for typical micropalaeontological investigations (i.e., foraminifera), it is not so for otolith studies. Otolith studies typically employ much larger samples to increase the probability of recovering specimens, and some exceed 100 kg and even 1,000 kg (Nolf & Dockery, 1990; Nolf & Stringer, 2003).

The bulk sample was air-dried for several weeks to assist in the disaggregation and processing of the clay matrix. The sediment was wet screened using plain water with no additives because of their potential adverse effect on the aragonitic otoliths. During the wet screening all residue that was retained on a U.S. Standard Sieve #30 was kept for study. Following the wet sieving, the residue was labelled and air-dried. U.S. Standard sieves (#5 to #30) were employed to separate the residue into similar-sized material for easier microscopic examination. An Olympus binocular microscope (0.8 to 40 ×) was employed to extract the otoliths from the residue. A smaller representative sample was also screened for foraminiferal and ostracod analysis using an 80 mμ-mesh sieve. All otoliths, one-quarter intact or more, were picked from the residue under a variable (0.7 × to 3.0 ×) binocular microscope with 10 × and 20 × oculars. The otoliths were identified by comparing them to specimens from extant fish or fossil specimens from comparative collections.

Skeletal vertebrate remains were very rare in the bulk sample residues, with only five specimens recovered (two shark teeth, two fish spines and a single fish vertebra). However, the remains of teleostean otoliths were much more common with approximately 150 specimens extracted from the residue. The otoliths were utilized to determine palaeoecological parameters of the locality. Otolith analysis revealed an assemblage of 17 teleost taxa representing 11 families. The teleostean assemblage is dominated by Ophidiidae (35.48 per cent), Bregmacerotidae (21.77 per cent), Congridae (13.71 per cent), Holocentridae (8.87 per cent), and Albulidae (4.84 per cent). These five families account for nearly 85 per cent of the total number of specimens.

The basic premise of the analysis is to utilize the identified fossil otoliths to obtain data on the preferred habitats of comparable modern fish. Examination of the otolith assemblage from the bulk sample reveals the absence of representatives that are indicative of deep waters only (> outer shelf or 200 m). All but one of the teleost taxa represented by otoliths from the locality are presently found in shore waters of the continental United States on or above the continental shelf (less than 200 m) according to Nelson *et al.* (2004). The pterothrissids are the only group reported from the site that is not listed; however, the presence of pterothrissids in Paleogene nearshore deposits of the United States has been well established by numerous studies including Nolf (1985, 1995), Nolf & Dockery (1993), Müller (1999) and Nolf & Stringer (2003). Therefore, as a general interpretation, the bony fish represented by otoliths indicate a marine environment no deeper than outer shelf and probably shallower.

Specific analysis of the otolith assemblage can provide additional insight into the palaeoenvironment at the locality during the Middle Eocene. When the Cane River Formation bony fish represented by otoliths are compared to the modern ichthyological fauna from the Gulf of Mexico and the Atlantic Ocean (Hoese & Moore, 1998; McEachran & Fechhelm, 1998, 2005; Nelson, 2006), the fossil otoliths turn out to represent fish that are mainly tropical and subtropical in nature. Furthermore, most of the fossil otoliths represent fish expected in normal marine salinity although a few of the forms could tolerate reduced salinities. Many of the taxa prefer soft or muddy substrates. There is an absence of representatives of Myctophidae (myctophids) or Macrouridae (macrourids). Nolf & Brzobohaty (1992) stated that otolith assemblages that were free or almost free of myctophids indicate a neritic environment with little oceanic influence.

The most abundant otoliths as well as the largest number of taxa in the Middle Glauconitic Clay Member are from Ophidiidae (35.48 per cent). Extant representatives of this family are commonly known as cusk eels and are mainly bathybenthic fish with a few neritic and pelagic forms (Nelson, 2006). However, during the Paleogene, the ophidiids were represented by a very rich neritic fauna living mainly on soft and muddy substrates. In the early Paleogene, the ophidiids were some of the most common and most speciose groups of teleosts and have long been noted in shallow-marine deposits around the world (Nolf, 1980, 1985; Schwarzhans, 1981; Radwańska, 1992; Stringer, 1986; Breard & Stringer, 1995). The extant species should be considered relicts of a formerly much larger group which were widely distributed in shelf environments (Schwarzhans, 1981; Nolf, 1985). Several of the ophidiids at the study site are believed to be closely related to the extant genus *Lepophidium*, which has a depth range from 0-400 m.

Otoliths of Bregmacerotidae are the second most abundant otoliths (21.77 per cent) and are represented by *Bregmaceros*, which is a codlet, a small midwater fish (Hoese & Moore, 1977). *Bregmaceros atlanticus* is the only species known from the Gulf of Mexico, and it is common and widespread on the middle shelf. It commonly occurs in water depths of 20 to 36 m in the northern Gulf of Mexico according to Dawson (1966). However, it should be noted that Dawson's sampling stations did not go deeper than 36 m. Although the worldwide depth distribution of the genus is 0-400 m, the species in the Gulf of Mexico is commonly found between 0-200 m.

Taxa within Congridae, or conger eels, are represented by three forms in the otolith assemblage and include *Rhynchoconger*, *Gnathophis* and *Paraconger*. Congrid otoliths are very common and abundant in many Paleogene sediments of neritic environments with soft, muddy bottoms (Stringer, 1986) and constitute 13.71 per cent of the total otoliths from the Cane River Formation sample. Extant congrids generally prefer tropical and temperate seas with the juveniles being found mainly in shallow, marine, coastal waters (Hoese & Moore, 1998). Extant congrids are reported as marine only with the adults occurring primarily in deeper waters (Nelson, 1994). Modern representatives of *Rhynchoconger flava* from the Gulf of Mexico are found from 20-175 m, while *Gnathophis* are encountered from 50-600+ m.

The third most abundant otoliths from the locality are those of Holocentridae, commonly known as squirrelfish and soldierfish. The family is represented by one taxon, *Myripristis*, which constitutes 8.87 per cent of the total otoliths. This percentage of myripristid otoliths in the assemblage is quite unusual. Although Nolf (1985) noted that otoliths of Holocentridae are commonly found in neritic Cenozoic sediments, they are rarely abundant in the Cenozoic of the Gulf Coast. Stringer & Breard (1997) reported on six Middle and Upper Eocene sites in Louisiana and Mississippi involving approximately 7,500 otoliths. The percentage of myripristids ranged from 0 to 2 per cent in these assemblages. Therefore, the almost 9 per cent of myripristids at the locality is unusual and noteworthy.

Nolf & Brzobohaty (1992) indicated that *Myripristis* was found from 0-100 m, based on modern bathymetric data. Nelson (1994, 2006) also stated that squirrelfish and soldierfish occur between the shoreline and 100 m. Nelson further noted that they are nocturnal, usually hiding in crevices or beneath ledges of reefs in the daytime. Hoese & Moore (1998) stated that squirrelfish are a tropical family represented by several species found, so far, only on the offshore reefs in the Gulf of Mexico. In their classic work on the fish of the Bahamas and adjacent tropical waters, Bohlke & Chaplin (1968) stated that squirrelfish and soldierfish are reef fish that occur in tropical waters around the world. The abundance of myripristid otoliths and ecological data on modern myripristids strongly suggests the presence of an offshore reef environment, possibly a patch reef at or near the locality (Bohlke & Chaplin, 1968; Greenberg, 1977; Hoese & Moore, 1998; Nelson, 1994, 2006).

Albulidae (bonefish), which was represented by *Pterothrissus*, comprised almost 5 per cent of the total otoliths. The two modern species of *Pterothrissus* are found in marine waters ranging from 50-500 m in depth. However, as noted above, pterothrissids in Paleogene nearshore deposits of the United States have been well established by numerous studies. Nolf (1985) noted that *Pterothrissus* was found in neritic Cenozoic deposits and that some species were confined to shallow-water deposits.

Although found in smaller numbers, several other taxa in the Middle Glauconitic Clay Member provide relevant palaeoenvironmental data. Haemulids (grunts) are represented by one taxon, *Haemulidarum*? *obliquus*, comprising 4 per cent of the total otoliths. Recent species of the genus *Haemulon* are typically found from 0-50 m. A representative of Sciaenidae, *Sciaenidarum*? *eporrectus*, also constitutes 4 per cent of the otolith assemblage. The sciaenids, which include the drums and croakers, are quite common in shallow-marine waters, estuarine, and coastal areas (Schwarzhans, 1993; Hoese & Moore, 1998). Myers (1960) noted the strict confinement of the Sciaenidae to continental coasts while Nelson (2006) noted that sciaenids occur mainly in shallow water near continental regions. Most sciaenids prefer shallow waters with muddy bottoms and feed on benthic organisms. Studies by Darnell *et al*. (1983) in the modern Gulf of Mexico indicated that areas of highest density for sciaenids were generally located in waters shallower than 40 m, but sciaenids were not abundant at the locality.

In summary, the teleost otoliths indicate a shallow-marine palaeoenvironment with normal marine salinities. Palaeowater depths were most likely in the 20-50 m range (inner to middle shelf). The substratum was most likely soft, and climatic conditions were probably tropical to subtropical. The unusual abundance of myripristids indicates the likely presence of an offshore reef environment, possibly a patch reef, at or near the locality. Invertebrate and vertebrate groups present at the site also support this interpretation of the palaeoenvironment. The invertebrate macrofauna appears to have a fairly low diversity (around 30 species) and is dominated by marine taxa including bivalves (*Corbula*, *Cubitostrea* and *Venericardia*), gastropods (*Pseudoliva*, *Athleta* and *Architectonica*), cephalopods (*Belosaepia*) and cnidarians (two colonial corals, *Madracis* and *Madrepora*, as well as the solitary coral, *Flabellum*). Foraminifera are fairly common, especially the macroscopic *Discocyclina advena.* The foraminiferal assemblage has mainly inner to middle shelf species; deeper shelf taxa are rare. Ostracods are also fairly common as well and also appear to be mainly inner- to middle-shelf. Although vertebrate skeletal remains were quite rare in the bulk sample residue, limited surface collections did reveal additional chondrichthyan and actinopterygian skeletal material. Chondrichthyan taxa represented at the site included *Carcharias* (sand tiger shark), *Galeocerdo* (two species of tiger shark), *Abdounia* (catshark), *Hemipristis* (snaggletooth shark), *Isurus* (mako shark), *Cretalamna* (mackerel shark), *Myliobatis* (eagle ray) and *Pristis* (sawfish). Skeletal remains of actinopterygians include teeth of *Sphyraena* (barracuda) and spines of *Cylindracanthus*. All of the vertebrate skeletal remains represent modern taxa that would be found in the proposed palaeoenvironment (Breard & Stringer, 1999; Stringer & Miller, 2001). This supports the previous interpretation of the palaeoenvironment for the crab family Zanthopsidae of an open marine, mid- to outer-shelf environment, often associated with glauconite and/or larger benthic foraminifera (Schweitzer *et al*., 2005).

Systematic palaeontology

Superfamily Carpilioidea Ortmann, 1893
Family Zanthopsidae Vía, 1959

Included genera – *Fredericia* Collins & Jakobsen, 2003; *Harpactocarcinus* A. Milne-Edwards, 1862; *Harpactoxanthopsis* Vía, 1959; *Lovaracarcinus* De Angeli & Beschin, 2010; *Martinetta* Blow & Manning, 1997; *Neozanthopsis* Schweitzer, 2003 and *Zanthopsis* M'Coy, 1849.

Diagnosis – See Schweitzer (2003, pp. 1116, 1117).

Genus *Neozanthopsis* Schweitzer, 2003

Type species – *Harpactocarcinus americanus* Rathbun, 1928, by original designation.

Included species – *Neozanthopsis achalzica* (Bittner, 1882); *N. americana* (Rathbun, 1928); *N. bruckmanni* (von Meyer, 1862), *N. carolinensis* (Rathbun, 1935); *N. rathbunae* (Stenzel, 1934); *N. sonthofenensis* (von Meyer, 1862) and *N. tridentata* (von Meyer, 1862).

Diagnosis – Carapace ovate to hexagonal, wider than long, length about 81 per cent maximum carapace width; front with four short, blunt spines, including inner-orbital spines, about 25-30 per cent maximum carapace width; fronto-orbital width about 52 per cent maximum carapace width; anterolateral margin entire or with 3-5 blunt spines, last spine extending onto carapace as oblique ridge; carapace regions developed as broad swellings; both male and female sterna ovate, with swellings on sternite 4 near articulation of coxae, those of female tall, large, serving as pleonal locking mechanisms; all female pleonites free; male pleonites 3-5 fused, somite 3 with swellings on each end; chelae large, heterochelous, with large swellings on outer surface.

Neozanthopsis americana (Rathbun, 1928)
Pls. 1, 2.

Diagnosis – Carapace ovate in large specimens and hexagonal in smaller ones, wider than long, length about 81 per cent of maximum carapace width; front with four short, blunt spines, including inner-orbital spines, about 26 per cent of maximum carapace width; fronto-orbital width about 52 per cent of maximum carapace width; anterolateral margin with 5 spines, last spine extending onto carapace as oblique ridge; carapace regions developed as broad swellings; axial regions broadly inflated; both male and female sterna ovate, with swellings on sternite 4 near articulation of coxae, those of female tall, large, serving as pleonal locking mechanisms; all female pleonites free; male pleonites 3-5 fused, somite 3 with swellings on each end; chelae large, heterochelous, with large swellings on outer surface.

Emendation to original description – Carapace ovate in large specimens, hexagonal in smaller specimens, wider than long, widest at position of penultimate anterolateral spine; length about 82 per cent of maximum carapace width strongly vaulted longitudinally, moderately vaulted transversely.

Front with four blunt, well-separated spines including inner-orbital spines, occupying about 26 per cent of maximum carapace width; orbits circular, directed forwards, broadly rimmed, fronto-orbital width about 52 per cent of maximum carapace width. Anterolateral margins arched, with about 5 small spines excluding outer-orbital spine, first spine separated from outer-orbital spine by straight segment, last spine longest, entire margin crispate. Posterolateral margin sinuous, with anterior swelling from oblique branchial ridge, posterior swelling from mesobranchial swelling. Posterior margin narrow.

Regions defined as broad carapace swellings; protogastric region weakly inflated; hepatic region with transverse inflation distally and longitudinal inflation axially positioned posterior to proximal end of transverse inflation. Axial regions weakly differentiated; mesogastric region very weakly inflated; metagastric region longer than wide, about same size and inflation as longitudinal hepatic swelling; urogastric and cardiac regions confluent, very long. Branchial regions with arcuate ridge extending obliquely posteriorly towards axis from last anterolateral spine; metabranchial region with oblique-longitudinal ridge subparallel to axis; two branchial ridges appear to intersect.

Female sternum ovate, sternites 1-3 fused, triangular. Sternite 3 short, poorly known because it is broken, with lateral articulations with third maxillipeds. Sternite 4 axially concave, with large, high knob at base of coxa, apparently functioning as pleonal holding mechanism, apparently a fused episternal projection of sternite 3; sternal sutures 4/5 and 5/6 incomplete; gonopores ovate, large, positioned centrally on sternite 6 and bounded anteriorly by suture 5/6; sutures 6/7 and 7/8 appear to be complete. All pleonal somites free, pleon overall ovate.

Male sternum ovate; sternite 3 wider than long, longest axially, deep groove between sternites 3 and 4, forming Y-shaped groove pattern with axial groove extending anteriorly from pleonal cavity. Sternite 4 long, swelling at base of coxa which is apparently a fused episternal projection of sternite 3; sternites and overall sternum appear narrower than those of female. Pleon with somites 3-5 fused, somite 3 with swellings on each end.

Measurements – Measurements (in mm) taken on the dorsal carapace of *Neozanthopsis americana* are presented in Table 1.

Material examined – Fifty-five specimens were examined, NLU2F-1 to NLU2F-55 (collections of the University of Louisiana Museum of Natural History, Geosciences Division, University of Louisiana at Monroe, Monroe, Louisiana, USA).

Occurrence – Specimens reported here were collected from the intersection of Highway 478 and Bayou Country Road, near Scott, Natchitoches Parish, Louisiana, by one of us (GLS), from the Middle Glauconitic Clay Member of the Cane River Formation (Claiborne Group; Lutetian, Middle Eocene; see Andersen, 1993).

Discussion – *Neozanthopsis americana* differs from congeners in having up to five anterolateral spines and very broadly inflated carapace regions. *Neozanthopsis rathbunae* has multiple anterolateral spines, but the carapace ornamentation consists of a narrow axial swelling and more discrete swellings on the branchial and hepatic regions. *Neozanthopsis carolinensis* has discrete, large swellings on the hepatic and branchial regions. Thus, we

Table 1. Measurements (in mm) taken on the dorsal carapace and gender of specimens of *Neozanthopsis americana*. F = female, M = male, U = undetermined sex.

Specimen	Sex	Width	Length	Fronto-orbital width	Frontal width	Somite 4 width	Sternite 5 width	Orbit depth
NLU2F-1	F	68.9	56.3	33.1	12.9	13.9		
NLU2F-2	F	46.0	37.3					
NLU2F-3	F	41.3	35.3	23.4	9.7		17.6	
NLU2F-4	F	48.5	38.7	27.6		16.3		3.4
NLU2F-5	F	46.6	37.3	23.2	15.8	15.4		
NLU2F-6	F	33.3	28.3	17.7	9.4	9.7		
NLU2F-7	F	39.6	31.7	22.2		13.1		
NLU2F-8	F	39.6	37.4	18.9	9.7	11.4		2.7
NLU2F-9	F	53.6	45.1	24.2		13.8		
NLU2F-10	U	44.4	38.0	24.2	12.5			3.0
NLU2F-12	M	62.0				10.0	15.2	3.0
NLU2F-13	M	56.4	43.0	32.4	19.8	8.3		
NLU2F-14	M	44.6	35.6	21.2	11.7			3.0
NLU2F-15	M	43.3	36.2	22.7	11.8	5.4	18.2	
NLU2F-16	M	42.8	36.0	21.4	11.8			
NLU2F-17	M	53.0	41.8	25.9	13.7	8.7		4.4
NLU2F-18	M	47.2	38.1	24.4	12.0			4.3
NLU2F-20	F	36.6	31.5	20.5			15.6	2.6
NLU2F-23	U	38.4	30.8	21.4	10.8			
NLU2F-24	U	57.0	41.5	25.3	11.5			4.4
NLU2F-25	U	52.8	43.3	26.8	13.2			
NLU2F-26	U	46.6	36.6	25.0	12.0			
NLU2F-27	F	53.1	43.5	26.0	13.2	16.8	20.0	4.2

have placed the new specimens within *N. americana* based upon their more subdued dorsal carapace ornamentation.

The relatively large number of specimens made it possible to test whether there were differences in various aspects of the size and shape of the carapace between males and females. Several measurements, including maximum carapace width, the ratio of fronto-orbital width to maximum width, the length to width ratio of the carapace, the ratio of the width of the sternum compared to the total width of the carapace, and the maximum depth of the orbits as compared to the total length of the carapace, were compared between males and females, using a t-test for unpaired independent samples (SPSS v. 21, Levene's test showed equal variances could be assumed in all cases) (Table 2). Sternal width was tested using the Independent Samples Mann-Whitney U Test as the Levene's test indicated that the variances between groups were unequal in this case. None of the measured distances or ratios was significantly different between males and females at the 0.05 level of significance. This was somewhat surprising, especially for the sternal width, as the female sternum appears to be broader than that of the male. However, it may not be broader in terms of the entire width of the carapace. In addition, for that particular test, n = 3, a low number.

These results indicate that in this group of crabs, carapace characters alone cannot be used to determine sex of the crab. However, the standard characters of the shape of

Table 2. Statistical results for various tested variables of *Neozanthopsis americana*.

Tested Variable	**Number of measurements**	**t value**	**Degrees of freedom**	**Significance (two-tailed) at the 0.05 level**
Carapace width	Female, n = 11			
	Male, n = 7	t = -0.865	df = 16	0.400
Fronto-orbital width/ width ratio	Female, n = 10			
	Male, n =6	t = 0.244	df = 14	0.810
Length/width ratio	Female, n = 11			
	Male, n =6	t = 1.549	df = 15	0.142
Orbit Depth/length ratio	Female, n = 4			
	Male, n = 3	t = -1.712	df = 5	0.148
Sternite 5 width/total width	Female, n = 3 Male, n = 2	Mann-Whitney U = 1.00 Wilcoxon W = 4.00		Exact sig. (2 sided) = 0.400

the pleon can be used. It is broadly ovate with all somites free in females and narrow with concave sides, with somites 3-5 fused in males. These patterns are typical in heterotreme crabs (i.e., Guinot, 1979; Schweitzer, 2003; Karasawa & Schweitzer, 2006). In addition, the male of *Neozanthopsis americana* has swellings on pleonal somites 3, and the female has long, stout knobs on sternite 4 which act as locking mechanisms for the pleon. This made it possible to recognise two specimens that with additional preparation could be confirmed as females by exposing gonopores on the sixth sternite. Thus, these additional characters may prove useful in future for determining gender when most of the pleon or sternum is missing.

A survivorship curve for the specimens of *Neozanthopsis americana* was constructed, using size (carapace width) as a proxy for age (Pl. 3, fig. 1). Its shape is unlike that of typical Type I (large mammals, high survivorship until old age), Type II (small mammals, relatively constant attrition), and the strongly concave Type III curve for invertebrates with massive early life losses. The crab curve shows higher survivability at smaller size, and then constant attrition to larger size, where attrition flattens out, a rather sigmoid curve. A similarly shaped curve was derived for fossil brachiopods, for example (Huang *et al.*, 2013), although they attributed their curve to early and mid-life losses.

Problems with constructing such a survivorship curve for fossil invertebrates include the fact that none of the larval forms are included – they rarely, if ever, fossilise. Thus, survivorship of larval stages is unknown. A second problem is that very small individuals seem not to fossilise either – the smallest individual in the present study has a carapace width of 33.3 mm. What we may be seeing is a collection of and therefore a survivorship curve of the larger, post-juvenile surviving population, after the attrition of the smaller and larval individuals. It is notable that in the population of crabs in this study, the carapace width distribution of the entire population approaches normal (Pl. 3, fig. 2), skewed to the relatively smaller sizes, especially so in males (Pl. 4, fig. 2).

Taphonomy – The fossil decapods are preserved in a marly siltstone with floating grains of glauconite. The sediment is moderately consolidated, or weakly cemented by calcite which, when subjected to dilute hydrochloric acid, effervesces violently and yields a reddish-yellow residue resulting from finely divided iron oxide. The iron oxide may have been derived from weathering of the glauconite grains. There is apparently some expandable clay incorporated within the matrix as indicated by the fracturing and slight displacement of fragments of the cuticle in several specimens (Pl. 2, fig. 4).

The specimens are preserved with a range of qualities of preservation of the cuticle. None preserve the entire surface of the exocuticle; however, where preserved it may be almost pristine. The exocuticle is covered by uniformly sized and spaced nodes which, when eroded, appear to have endocuticle within the core. This would suggest the presence of erect pillars formed within the endocuticle that have exocuticle draped over them. The exocuticle is less than one-quarter the thickness of the endocuticle and no laminations are evident under normal microscopic examination.

Examination of the endocuticle confirms the presence of erect pillars, the spacing of which coincides with the spacing of the nodes on the exocuticle. Interspersed between the pillars are much smaller nodes on the surface of the endocuticle. These features are not reflected on the surface of the exocuticle. Laminations are clearly visible in well-preserved parts of the endocuticle.

Morphology of the surface of the mould of the interior of the cuticle, the surface of the endocuticle, and the surface of the exocuticle is quite different. The mouldic surface tends to reflect the development of regions of the carapace quite faithfully, but it is otherwise smooth.

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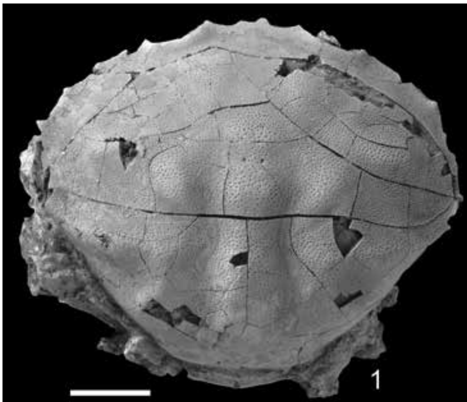
Plate 1

Neozanthopsis americana (Rathbun, 1928)
Figs. 1, 2. NLU2F-27, dorsal and ventral view of female showing pleonal locking mechanism on sternite 4 (arrows).
Figs. 3, 4. NLU2F-17, dorsal view of near-complete carapace, and ventral view showing large right first pereiopod.
Figs. 5, 6. NLU2F-24, dorsal view and oblique frontal view showing detail of front and orbits.

All specimens whitened with ammonium chloride. Scale bars equal 10 mm.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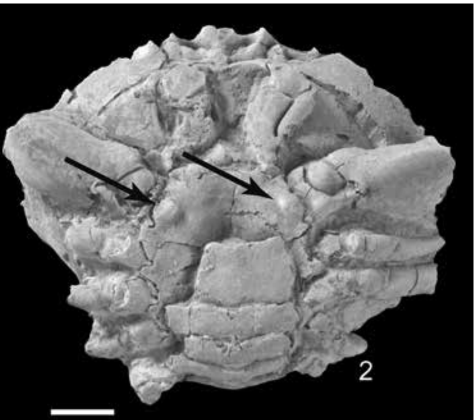
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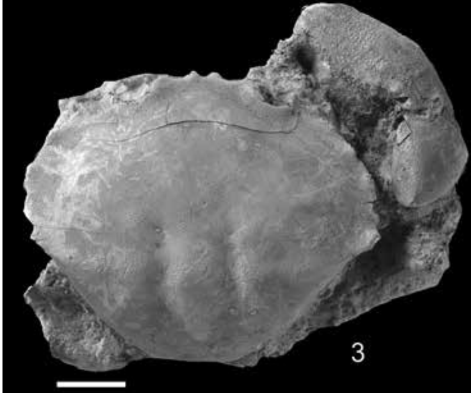
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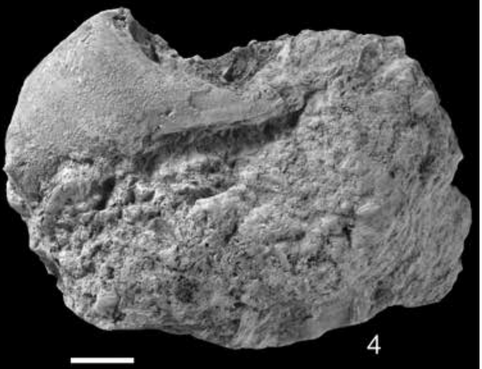
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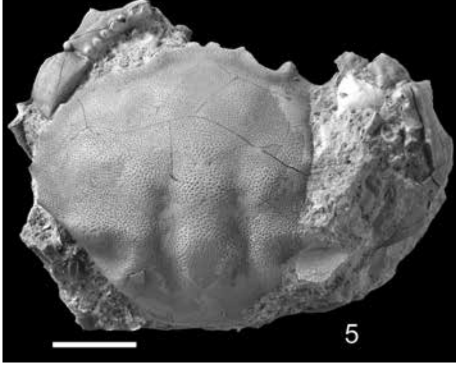
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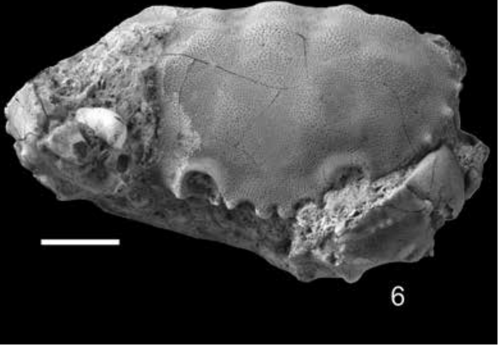
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Plate 2

Neozanthopsis americana (Rathbun, 1928)
Fig. 1. NLU2F-3, ventral view showing prominent gonopore at arrow.
Fig. 2. NLU2F-7, ventral view showing female pleon and pleonal locking mechanism.
Fig. 3. NLU2F-12, ventral view showing male pleon and part of sternum.
Fig. 4. NLU2F-1, dorsal view of carapace showing fractured and expanded carapace fragments.

All specimens whitened with ammonium chloride. Scale bars equal 10 mm.

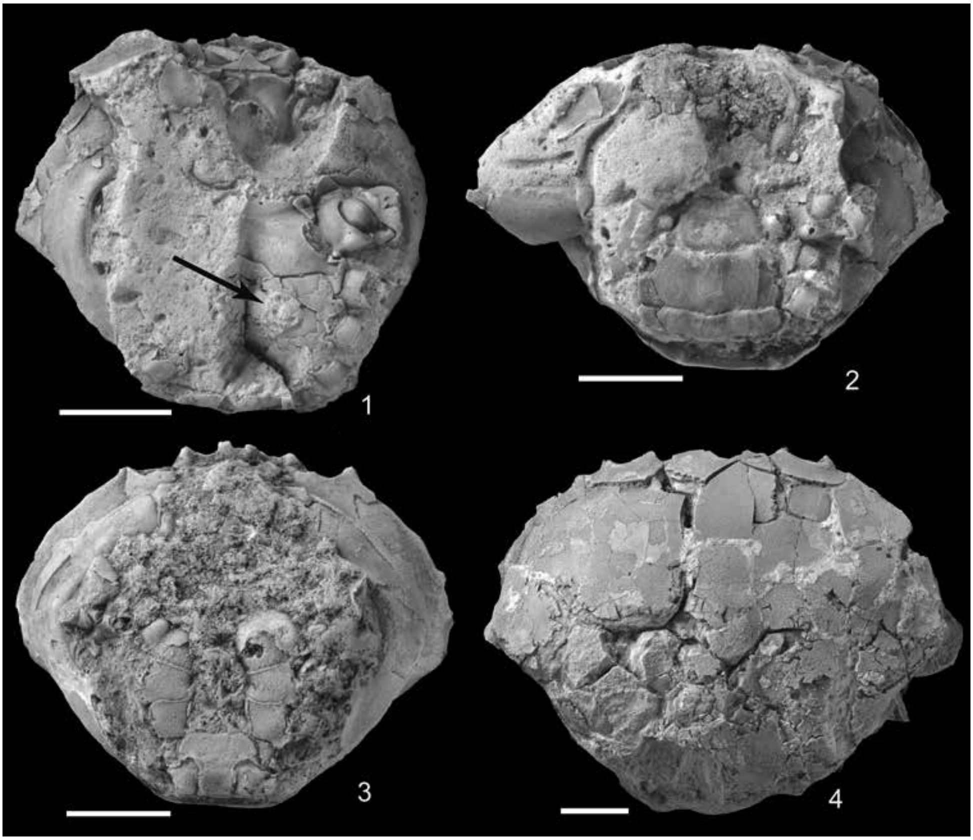

1
2
3
4

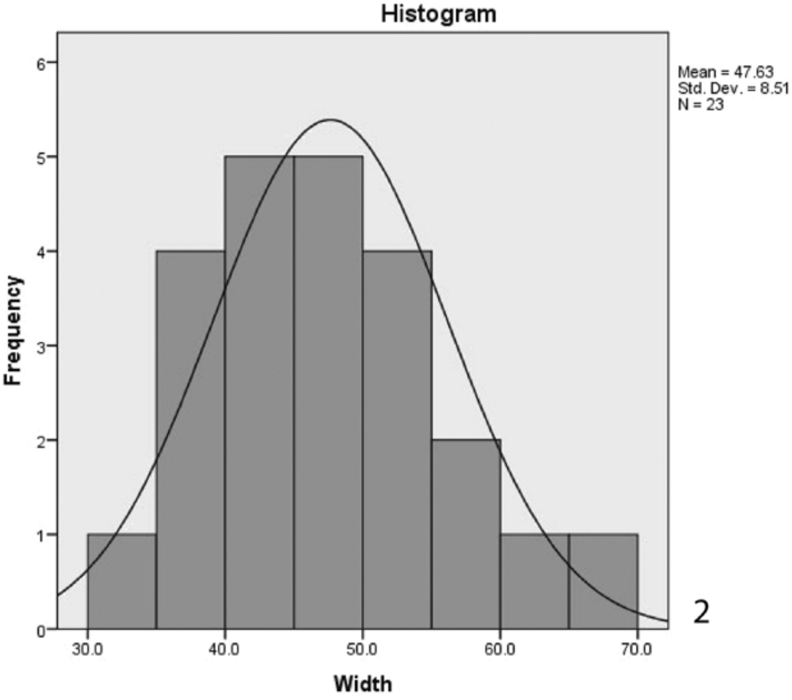
Plate 3

Fig. 1. Survivorship curve generated in Excel for measured specimens of *Neozanthopsis americana*, including males, females and those of undetermined sex. Size based upon carapace width (in mm), excluding last anterolateral spine.

Fig. 2. Histogram generated in SPSS 21 of all specimens represented in Figure 1, arrayed into 5 mm bins by carapace width. Normal curve displayed for reference.


Survivorship
Number of Individuals
0
5
10
15
20
25
0
20
40
60
80
Carapace width in millimeters as a proxy for age
Survivorship

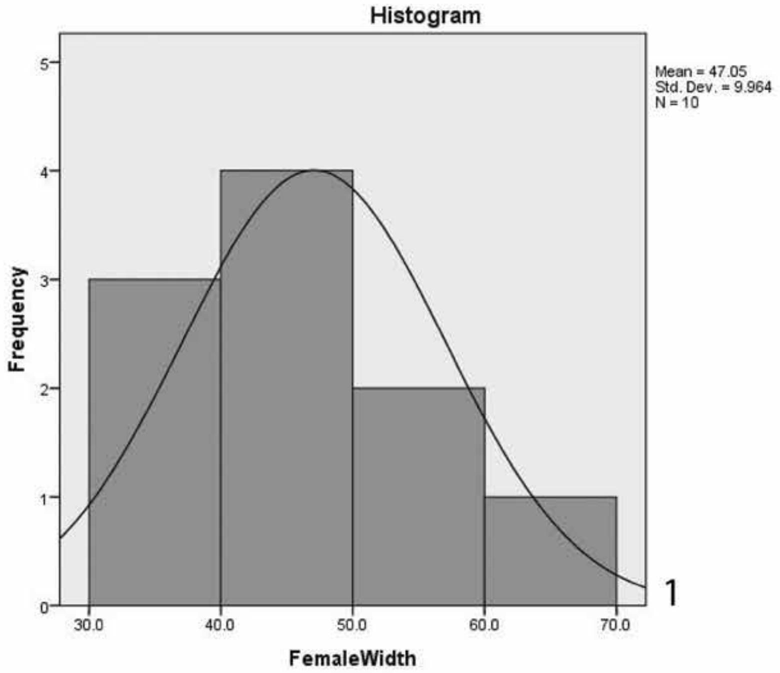
1


Histogram
Frequency
0
1
2
3
4
5
6
30.0
40.0
50.0
60.0
70.0
Width
Mean = 47.63
Std. Dev. = 8.51
N = 23

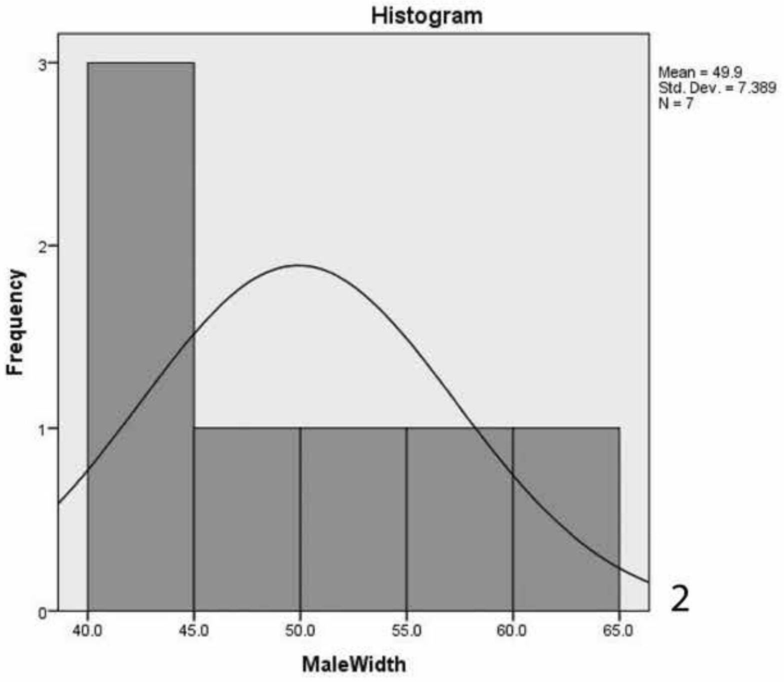
2

Plate 4

Fig. 1. Histogram generated in SPSS 21 of all female specimens represented in Plate 1, arrayed into 10 mm bins by carapace width. Normal curve displayed for reference.
Fig. 2. Histogram generated in SPSS 21 of all male specimens represented in Plate 1, arrayed into 5 mm bins by carapace width. Normal curve displayed for reference.


Histogram
Mean = 47.05
Std. Dev. = 9.964
N = 10
Frequency
0
1
2
3
4
5
30.0
40.0
50.0
60.0
70.0
FemaleWidth

1


Histogram
Mean = 49.9
Std. Dev. = 7.389
N = 7
Frequency
0
1
2
3
40.0
45.0
50.0
55.0
60.0
65.0
MaleWidth

2