

Middle to Late Jurassic bivalves of the genera *Neocrassina* and *Trigonopsis* from New Zealand

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Abstract Bivalves of the genera *Neocrassina* and *Trigonopsis* are described from the Middle–Late Jurassic of New Zealand. *Neocrassina* is represented by three new species. The new subfamily Trigonopinae is introduced to accommodate the genus *Trigonopsis*, which was previously classed as a subgenus of *Opis*. *Trigonopsis* is represented by one previously described species and one new species. Paleobiogeography is analysed in terms of the global distribution of *Neocrassina* and *Trigonopsis*. *Neocrassina* was present in most regions of the Boreal and Tethyan realms. In New Zealand, it is first recorded from rocks of Early Tertiary age (Aalenian–Bajocian). The distribution of *Trigonopsis* shows that this genus was common in European Tethyan regions, but sparsely distributed elsewhere. A comparison of New Zealand species, with forms from other regions, demonstrates that *Trigonopsis* most likely migrated to the Jurassic southern ocean, by way of the temporary seaway connecting the Tethys Sea with the Bay of Antarctica, during the Callovian marine transgression.

Keywords Antarctica; Astartidae; Astartinae; Australia; Boreal; Jurassic; Murihiku Supergroup; *Neocrassina*; new taxa; New Zealand; *Opis*; paleobiogeography; paleontology; Tethyan; Trigonopinae; *Trigonopsis*

INTRODUCTION

Gardner & Campbell (2002) provided a detailed analysis of astartid morphology, and demonstrated that protandric hermaphrodite sexual dimorphism was present in Middle Jurassic astartines. They also described new genera and new species from the Middle–Late Jurassic of New Zealand and New Caledonia. This study supplements Gardner & Campbell (2002) and deals with the genera *Neocrassina* and *Trigonopsis* from the Middle–Late Jurassic of New Zealand.

Fischer (1886) introduced *Neocrassina* to accommodate large, thick-shelled, posteroventrally projecting astartid

species. However, this work was largely overlooked and subsequent new species were consistently placed in *Astarte* (s.s.). Chavan (1945) provided a detailed analysis of taxonomic differences between *Astarte* (s.s.) and *Neocrassina*. This work was responsible for *Neocrassina* becoming accepted as a distinct genus. In this study, a number of species previously placed in *Astarte* have been transferred to the genus *Neocrassina*, and are listed in Appendix 1 together with their synonyms.

Defrance (1825) introduced the genus *Opis* to represent astartines with narrow subtrigonal shells, high erect beaks and umbones above the hinge plate, and with obsolete or absent anterior lateral teeth. Subsequently, *Trigonopsis* Munier-Chalmas, 1887 was introduced as a subgenus of *Opis* to accommodate shells with a subtrapezoidal outline and a shallow lunule. Chavan (1952) transferred *Opis* to his new subfamily Opinae, but maintained that *Trigonopsis* has obsolete or absent anterior lateral teeth. During the course of this work, a study of *Trigonopsis* species has shown that anterior lateral teeth are functional and well defined. Our observations have also shown that there is a large degree of intraspecific variation in length of the anterior hinge area and corresponding lateral teeth.

In describing New Zealand forms of *Neocrassina* and *Trigonopsis*, we have determined species primarily by hinge morphology, and have avoided the introduction or use of subgenera. Where possible, variation within a given species has been studied. Species have also been analysed to establish the presence or absence of sexual dimorphism. *Neocrassina* is represented by three new species, and *Trigonopsis* by one new and one previously described species.

New Zealand type specimen collection localities for *Neocrassina* and *Trigonopsis* are shown in Fig. 1–3. International and New Zealand stage correlation is that used by Gardner & Campbell (2002).

During the course of this work, comprehensive collections were examined at the Natural History Museum, London. Substantial collections were borrowed and examined from the Institute of Geological & Nuclear Sciences Limited and from the Geology Department of the University of Auckland.

Locality and specimen information (e.g., H46/f167 [608107]) consists of a New Zealand Map Series 260 reference, followed by a Fossil Record File number and an optional grid reference in parentheses. The New Zealand Fossil Record File is a national database administered by the Geological Society of New Zealand.

Specimens with the prefix “BM” (e.g., BM L48047 or BM LL32019) are held at the Natural History Museum, London, England. All other specimens are held in the following New Zealand institutions: Geology Department of the University of Auckland, prefix “L” (e.g., L4052); and the Institute of Geological & Nuclear Sciences Limited, prefix “TM” (e.g., TM8118).

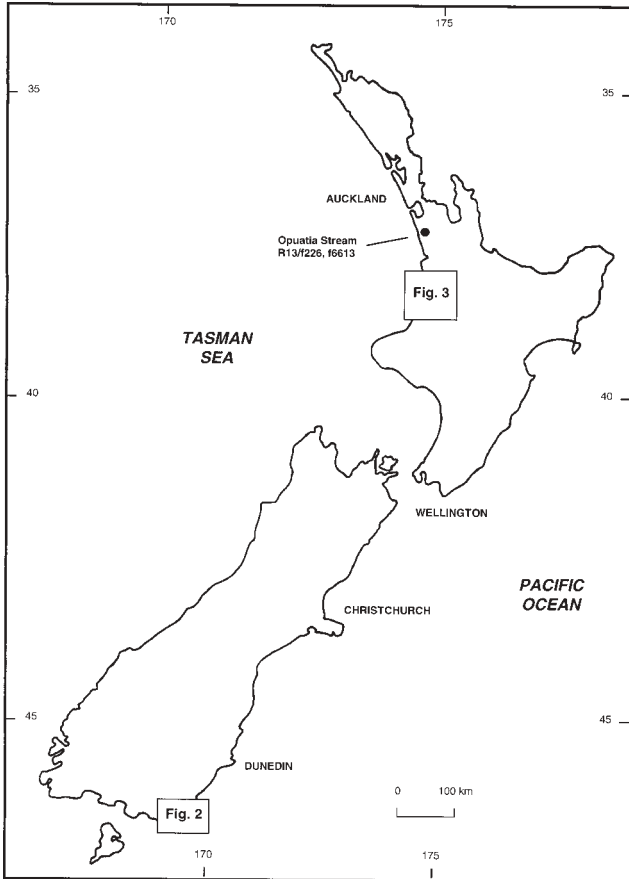


Fig. 1 Locality map of New Zealand showing the geographic distribution of known *Neocrassina* and *Trigonopsis* fossil sites.

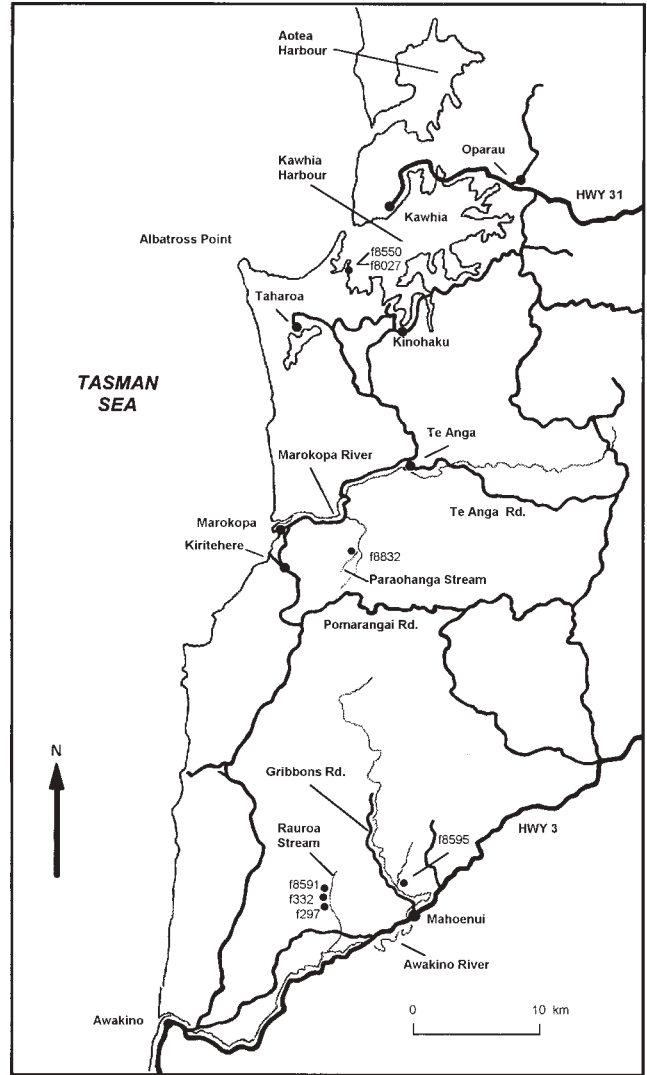


Fig. 3 The Kawhia–Awakino districts within the New Zealand Map Series 260 sheets R15, R16, and R17, showing the principal *Neocrassina* and *Trigonopsis* fossil sites.

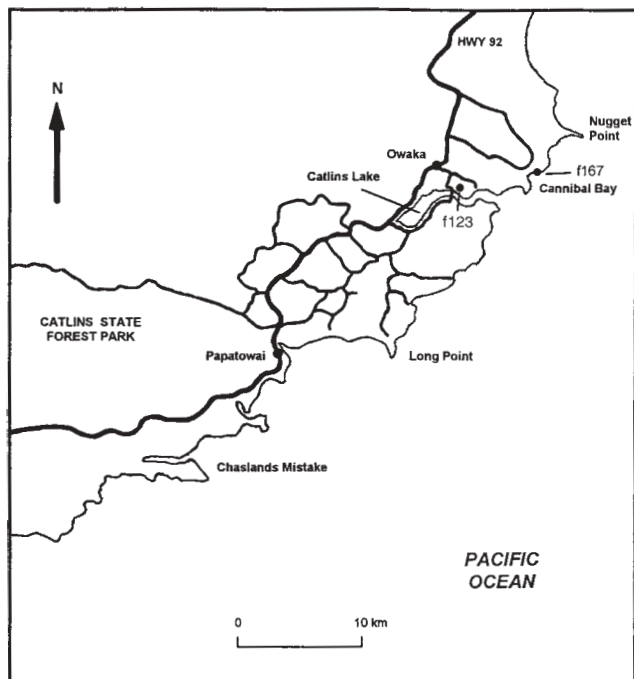


Fig. 2 The Catlins district of South Otago within the New Zealand Map Series 260 sheets G47 and H46, showing the principal *Neocrassina* fossil sites.

PALEOBIOGEOGRAPHY

Distribution and time range of Jurassic *Neocrassina* and *Trigonopsis* species

The paleogeographic distribution of astartids studied by Gardner & Campbell (2002) demonstrates that some astartid genera allow species to be grouped on a regional basis. These authors also showed that during the Middle Jurassic the majority of Tethyan marine faunas migrated to the continental shelf of southern Gondwanaland, during the Bajocian and Callovian marine transgressions, by way of the temporary seaway linking the Tethys Sea with the Bay of Antarctica.

The time range of New Zealand *Neocrassina* and *Trigonopsis* species is shown in Fig. 4 and 5.

Neocrassina

The genus *Neocrassina* most commonly occurs in fine-medium sandstones. This implies a preference for a middle shelf environment. *Neocrassina* became established in most regions of the Boreal and Tethyan realms (Fig. 6). It is first recorded in New Zealand from rocks of Early Tertiary age

Fig. 4 Time range of *Neocrassina* from the Middle Jurassic of South Otago, New Zealand (after Gardner & Campbell 2002).

NEW ZEALAND STAGES	RANGE CHART OF <i>NEOCRASSINA</i> IN MIDDLE JURASSIC FORMATIONS OF THE SOUTHLAND SYNCLINE, SOUTH OTAGO, NEW ZEALAND		
	SOUTH LIMB	RANGE	NORTH LIMB
LATE TEMAIKAN	False Islet Pounaweia Tuhawalki	<i>Neocrassina densicostata</i> 	False Islet Pounaweia
MIDDLE TEMAIKAN	Ratanui Hinahina Purakaunui Tucks Bay upper Purakauti		Sweetwater Tucks Bay upper Ironwood
EARLY TEMAIKAN	lower Purakauti McPhee Cove Conglomerate		lower Ironwood Boatlanding Bay upper Oamaru

Fig. 5 Time range of *Neocrassina* and *Trigonopis* species from the Middle–Late Jurassic of Kawhia Regional Syncline, New Zealand (after Gardner & Campbell 2002).

NEW ZEALAND STAGES	RANGE CHART OF <i>NEOCRASSINA</i> AND <i>TRIGONOPIS</i> IN MIDDLE TO LATE JURASSIC STAGES OF THE KAWHIA REGIONAL SYNCLINE, NEW ZEALAND			
	AWAKINO	MAROKOPA	KAWHIA	WAIKATO
LATE HETERIAN				
MIDDLE HETERIAN	<i>Trigonopis anatona</i>	<i>Trigonopis anatona</i>	<i>Trigonopis morgani</i> <i>Neocrassina faceta</i>	
EARLY HETERIAN				
LATE TEMAIKAN				<i>Neocrassina faceta</i>
MIDDLE TEMAIKAN				
EARLY TEMAIKAN	<i>Neocrassina fessicostata</i>			

(Aalenian–Bajocian), and is last recorded during the Middle Heterian (Early Kimmeridgian). A number of species have been recorded from Antarctica, with a similar Heterian time range to New Zealand forms. The Middle Jurassic sequence of New Caledonia has yielded some poorly preserved

specimens that resemble *Neocrassina*, but are generically indeterminable

New Zealand Middle–Late Jurassic forms of *Neocrassina* resemble species from East Africa, India, and also Japan. In contrast, species recorded from Antarctica are similar to

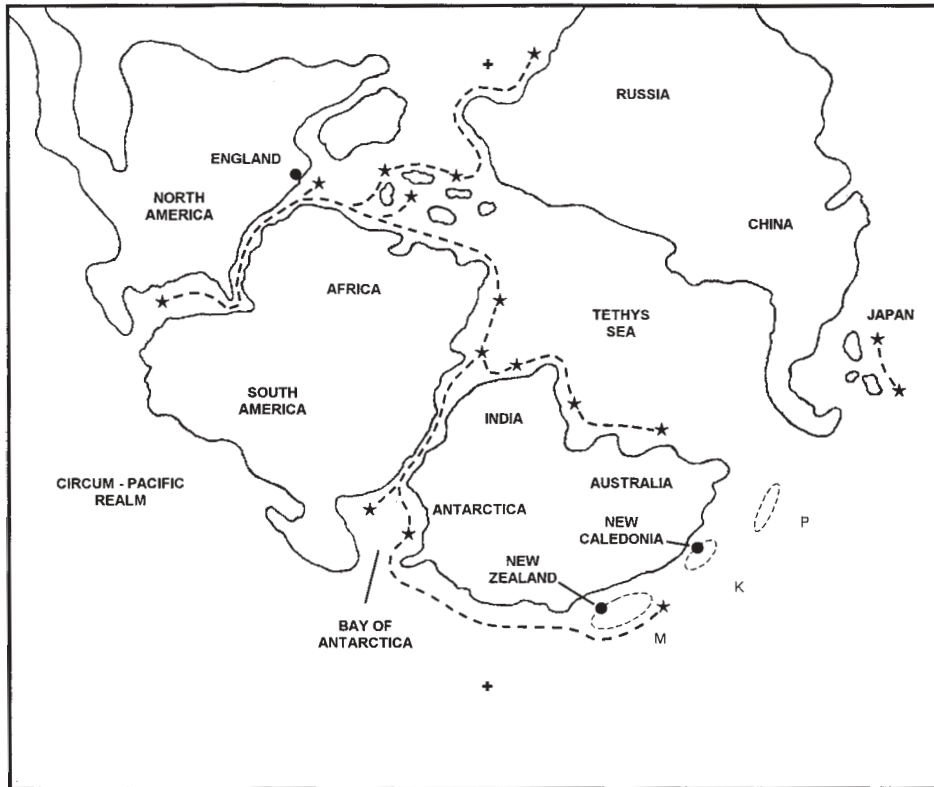


Fig. 6 Paleogeographic distribution of the genus *Neocrassina* during the Middle-Late Jurassic (180–135 Ma), based on known geographic locations of species indicated by “★”. The Jurassic North and South Poles are indicated by “+”. Elliptical dashed lines represent the Murihiku Terrane (M), Baie de St-Vincent Terrane (K), and Pahau Terrane (P) after Hallam (1983), Stevens (1987), Brassier & Geleta (1993), Grant-Mackie et al. (2000), and Gardner & Campbell (2002).

N. compressa (J. de C. Sowerby, 1840), from the Oxfordian to Early Kimmeridgian of India. The large degree of intraspecific variation in *Neocrassina*, observed during this study, makes it difficult to group species on a regional basis. The weight of evidence suggests that *Neocrassina* migrated to the continental shelf of southern Gondwanaland during the Bajocian marine transgression, by way of the temporary seaway connecting the Tethys Sea with the Bay of Antarctica.

Neocrassina (Coelastarte) (Böhm, 1893) has not been recorded from Jurassic rocks of Antarctica, New Zealand, or New Caledonia. Morphological shell characters in *Coelastarte* differ considerably from those in *Neocrassina* (s.s.) species. In the systematic section below, these differences are discussed, and *Coelastarte* is raised to generic level.

Neocrassina is represented by numerous nominal species, many of which have been incorrectly placed in the genus *Astarte*. Species thought to be valid members of the genus, and not likely to be conspecific with other forms, include: *Neocrassina ellsworthensis* (Quilty, 1977), Heterian (Late Callovian to Early Kimmeridgian) of Antarctica; *N. andium* (Gottsche, 1925), Bajocian of Argentina; *N. unilateralis* (J. de C. Sowerby, 1840), Callovian of east Africa, and Callovian–Oxfordian of India; *N. recki* (Dietrich, 1933), Late Kimmeridgian of east Africa; *N. sowerbyana* (Holdhaus, 1913), Late Oxfordian–Tithonian of India, and the Late Oxfordian and Late Kimmeridgian of Tanzania, east Africa; *N. compressa* (J. de C. Sowerby, 1840), Oxfordian to Early Kimmeridgian of India; *N. cliftoni* (Moore, 1870) and *N. tibraddenii* (Skwarko, 1974) from the Bajocian of Western Australia; *N. obliqua* (Deshayes, 1830) and *N. elegans* (J. Sowerby, 1818) from the Bajocian of northwestern Europe; and *N. ovata* (Smith, 1817), Oxfordian to Early Kimmeridgian of England.

Trigonopsis

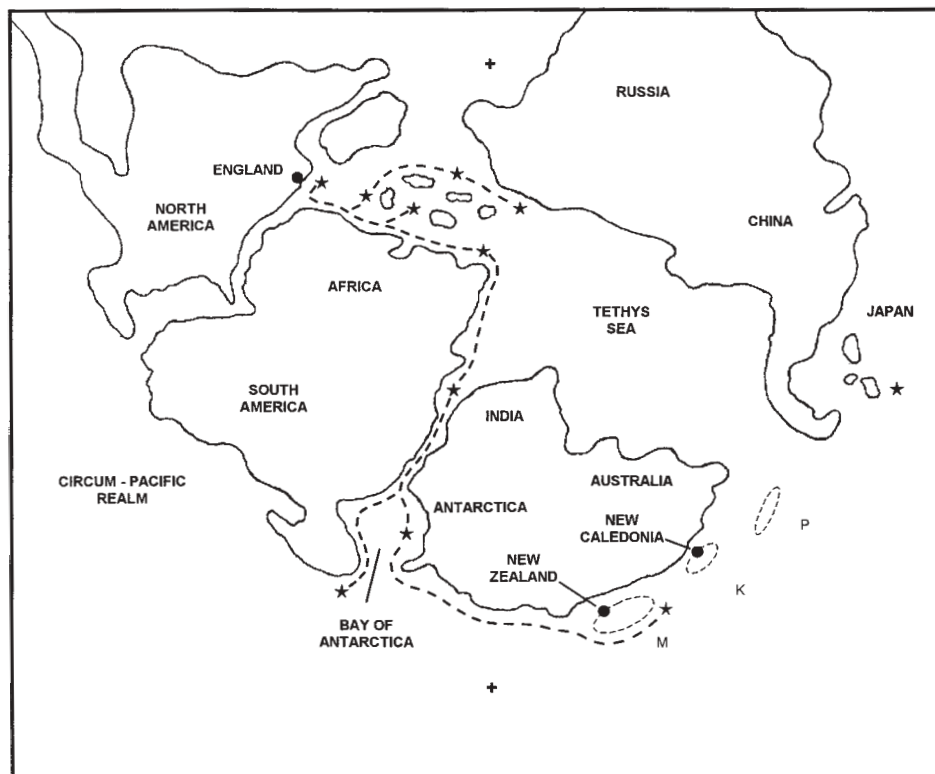
Throughout the Middle-Late Jurassic, the genus *Trigonopsis* was well established in Boreal and Tethyan regions of Europe but only sparsely represented in more southerly regions of the Tethyan realm. For example, the genus has not been recorded from Africa, India, or Australia. Specimens lodged with the Natural History Museum in London show the genus present in the Bathonian of Palestine and the Middle Jurassic of Madagascar. Nevertheless, *Trigonopsis* has a wide Middle-Late Jurassic distribution (Fig. 7).

Trigonopsis torinosuensis (Kimura, 1956) has been described from the Late Jurassic of Japan. Although examined specimens lack morphological detail, and hinge characters are poorly preserved, the outline together with moderately strong ornamentation, shallow lunule, very high umbones, and a well-defined anterior hinge area are characters typical of *Trigonopsis*.

This group of bivalves is also represented by *Trigonopsis stevensi* (Quilty, 1977), from the Heterian (Late Callovian to Early Kimmeridgian) of Ellsworth Land, Antarctica. Two species are recognised from New Zealand, with a Middle Heterian (Early Kimmeridgian) time range. The disappearance of *Trigonopsis* from the New Zealand region, during Middle Heterian times, approximately coincides with the disappearance of the genus *Neocrassina* (subfamily Astartinae).

Species from Antarctica and New Zealand have strong affinities with European forms. This is exemplified by the relationship between *Trigonopsis similis* (J. Sowerby, 1819), from the Bajocian–Bathonian of England and *T. anatona* n. sp. from the Middle Heterian (Early Kimmeridgian) of New Zealand. *Trigonopsis corallina* (Damon, 1860), from

Fig. 7 Paleogeographic distribution of the genus *Trigonopsis* during the Middle–Late Jurassic (180–135 Ma), based on known geographic locations of species indicated by “★”. The Jurassic North and South Poles are indicated by “+”. Elliptical dashed lines represent the Murihiku Terrane (M), Baie de St-Vincent Terrane (K), and Pahau Terrane (P).



the Oxfordian of England, has similar characteristics to *T. morgani* (Trechmann, 1923) from the New Zealand Middle Heterian (Early Kimmeridgian). However, species from Antarctica and New Zealand have morphological characters that differ to a certain degree from forms from Japan. For example, species recorded from Japan have narrower umbones, and the lunule is considerably wider. These factors suggest that *Trigonopsis* migrated to the continental shelf of southern Gondwanaland, possibly during the Callovian marine transgression, by way of the temporary seaway linking the Tethys Sea with the Bay of Antarctica.

SYSTEMATIC PALEONTOLOGY

DEFINITIONS: Taxonomic terms used in this report are those defined by Cox (1969). Generic diagnostics and species descriptions are based on morphological definition in Gardner & Campbell (2002). Abbreviations used are defined as follows: L = length; LA = anterior length; H = height; I = inflation for two valves; S3 = apical angle of cardinal tooth 3b socket; RV = right valve; LV = left valve; DV = disarticulated valves.

Class BIVALVIA Linnaeus, 1758
 Subclass HETERODONTA Neumayr, 1884
 Order VENEROIDA Adams & Adams, 1858
 Superfamily CRASSATELLACEA Ferussac, 1822
 Family ASTARTIDAE d’Orbigny, 1844
 Subfamily ASTARTINAE d’Orbigny, 1844

DIAGNOSIS (emended): Subtrigonal, vertically subovate to subelliptical, subcircular to sublunate, or subtrapezoidal to posteroventrally subcircular shells. Height commonly less than or

equal to length. Umbones low relative to beaks. Cardinal and lateral dentition functional and well defined except for lateral teeth *A1* and *A11* that may be absent or obsolete. Cardinal tooth 3b subtrigonal in form, and lateral tooth *A1V* forming a lamella between cardinal tooth 3a socket and anterodorsal margin. Lateral tooth *A111* positioned along ventral edge of right valve anterior hinge area; lateral tooth *AV* situated along ventral slope of right valve anterodorsal margin; lateral tooth *P111* placed along right valve posterodorsal margin; lateral tooth *A1V* positioned along, and equal in width to, left valve anterior hinge area; lateral tooth *P11* placed along ventral edge of left valve posterior hinge area; lateral tooth *P1V* lies along ventral slope of left valve posterodorsal margin. Hinge formula:

<i>A111</i>	(<i>AV</i>)	3a	3b	(5b)		<i>P111</i>
<i>A1V</i>		2	4b	(6b)	<i>P11</i>	(<i>P1V</i>)

COMPARISONS: The subfamily Astartinae is best compared with Trigonopinae n. subfam. (see below), and also with the subfamily Eriphyliinae Chavan, 1952. Shells in Trigonopinae differ by having umbones that are positioned considerably higher above the cardinal area. The posterior area is more strongly inclined towards the posterodorsal margin, and the height:length ratio is usually 1; with the exception of some rare variants, species in Astartinae have a height:length ratio of 1. Additionally, shells in Trigonopinae have cardinal teeth that are more strongly projecting, and cardinal tooth 3b is pyramidal in form.

Shell characters that differentiate shells in Eriphyliinae from Astartinae include a crassatelliform to lenticular outline, and the presence of lateral teeth *A1* and *A11* in addition to *A111* and *A1V*. Lateral tooth *A1V* differs by reaching almost to the beak before forming a lamella, and its socket forms a narrow groove between cardinal tooth 3a and the anterodorsal margin.

Genus *Neocrassina* Fischer, 1886nom. subst. *pro Crassinella* Bayle, 1878, *non* Guppy, 1874.Synonyms: *Puschia* Rouillier & Vossynski, 1847;*Pruvostiella* Agrawal, 1956.TYPE SPECIES (by subsequent designation Dall, 1903): *Astarte obliqua* Deshayes, 1830 (= *Cypricardia obliqua* Lamarck, 1819), Middle Jurassic, western France.

DIAGNOSIS (emended): Shell large for subfamily, strongly inequilateral, posteroventrally elongate; subtrapezoidal to posteroventrally subcircular in outline. Beaks low and prominent above cardinal area, 0.15–0.3 of shell length from anterior margin; position of umbones ranging from below to slightly above beaks. Interior of lower margins ranging from smooth to bearing weak crenulations. Commarginal costae evenly spaced and about constant width during early stages of growth, with subtrigonal cross-section. During later stages costae irregular, of variable width and strength, or fading leaving remainder of shell smooth, or with irregular surface folds of variable relief. Interspaces and commarginal ornamentation of constant width across flank, decreasing in width across anterior and posterior areas, and extending across lunule and escutcheon in form of costellae. Lunule short, escutcheon elongate, both well defined; escutcheon crest rounded in cross-section. Dorsal margin bordering cardinal area subtrigonal in outline. Cardinal area ventral edge moderately slanting anteriorly. Anterior hinge area short, broad on right valve; cardinal tooth 3a straight; cardinal tooth 2 subequal to cardinal tooth 3b; cardinal 4b elongate; lateral teeth *AIII* and *AIV* short. Hinge formula:

<i>AIII</i>	3a	3b	<i>PIII</i>
<i>AIV</i>	2	4b	<i>PII</i>

COMPARISONS: The genus *Neocrassina* differs from other Astartinae by encompassing shells that are larger and thicker, with a posteroventrally subcircular to subtrapezoidal outline. The beak is more anteriorly placed, with a considerably shorter anterodorsal margin and lunule, together with a much longer posterodorsal margin and escutcheon than in other members. The hinge plate has a wider and notably longer nymph, a longer posterior hinge area, and a shorter anterior hinge area that is considerably broader on the right valve. The posterior lateral teeth are thicker, and anterior lateral teeth thicker and notably shorter. The absence of cardinal teeth 5b and 6b, and lateral teeth *AV* and *PIV*, further distinguish *Neocrassina* from *Notoastarte*, *Nicaniella*, and *Astarte*.

Coelastarte Böhm, 1893, which was previously classed as a subgenus of *Neocrassina*, is raised here to generic level. *Coelastarte* species differ from those in *Neocrassina* by having compressed and considerably less projecting cardinal teeth, so that the entire hinge has an almost flat aspect. Cardinal tooth 3b is elongate and relatively narrow, lateral teeth *PII* and *PIII* terminate much closer to the cardinal area, the lunule is far more depressed with much stronger concavity, and the posterodorsal margin is almost straight with a shallow escutcheon. *Coelastarte* species differ further by having a slightly sinuous ventral margin, lacking strong posteroventral elongation, and also by having a weakly projecting dorsal margin.

REMARKS: *Neocrassina* may be considered to be an extreme form of astartid in terms of size, outline, and dorsal area characters. During the present study, protandric hermaphrodite sexual dimorphism was not recognised in *Neocrassina*,

perhaps largely due to unavailability of an adequate growth series. Adult shells in some species have either internally crenulated or smooth lower margins, so it is possible that *Neocrassina* was sexually dimorphic (see discussion in Gardner & Cambell 2002).

Agrawal (1956) introduced *Pruvostiella* as a subgenus of *Astarte* to accommodate large Astartinae from India. Singh & Kanjilal (1982) placed it under *Neocrassina*, considering that characters such as the flat depressed umbones, and the presence of coarse angular costae in early stages of growth, justified its revised subgeneric placing. These characters are highly variable, and fall well within the diagnosis for the genus *Neocrassina*. Many authors consider *Pruvostiella* to be a synonym of *Neocrassina* (Chavan 1969; Zakharov 1970; Duff 1978; Jaitly 1992). Furthermore, descriptions and illustrations of the type species *Neocrassina (Pruvostiella) freneixae* Agrawal (1956) suggest that this species is likely to be a synonym of *Neocrassina unilateralis* (J. de C. Sowerby).

Neocrassina densicostata n. sp.

Fig. 8

ETYMOLOGY: From the Latin *densus*, dense, and *costatus*, ribbed, referring to the numerous commarginal costae on this species.

TYPE MATERIAL: Holotype TM8118 (Fig. 8: 1), fine-grained medium to dark grey sandstone bed, Pounaweia Formation, Late Temaikan (Early–Middle Callovian), Murihiku Supergroup. Locality H46/f167 [608107], Cannibal Bay, South Otago, New Zealand. Collected by R. N. Gardner, January 1995.

Paratype: BM LL32019 (Fig. 8: 2), dark bluish grey silty mudstone bed, Pounaweia Formation, Late Temaikan (Early–Middle Callovian), Murihiku Supergroup. Locality H46/f123 [536102], Hinahina Quarry, South Otago. Collected by R. N. Gardner, August 1995.

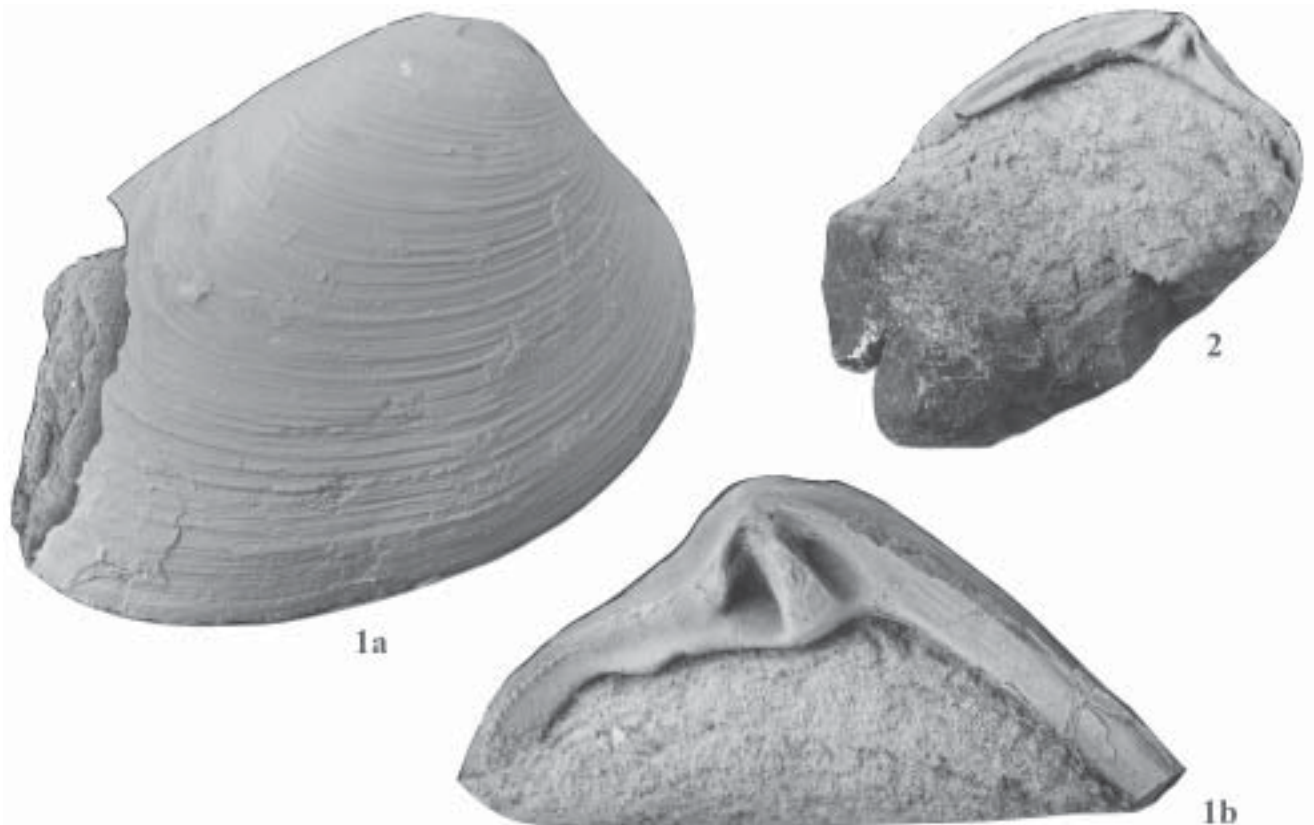
DIMENSIONS (in millimetres):

		L	H	I	LA/L	I/L
TM8118	(RV)	c. 53.0	45.5	23.0	0.26	0.43
BM LL32019	(LV)	24.4	18.3	10.4	0.30	0.43

DIAGNOSIS: Medium size shell, anterodorsal margin slightly to moderately concave, umbones broad, flank almost flat antero-posteriorly. Lunule elongate, depression concave in width and length, bordered by weakly defined ridge; escutcheon 3/5 width of lunule. Adductor scars not seen. Nymph elongate, relatively broad, surface with coarse evenly spaced laminae parallel to posterodorsal margin. Cardinal area wide dorsoventrally below beak with elongate, narrow cardinal tooth 3b. Anterior hinge area and lateral teeth *AIII* and *AIV* moderately elongate. Apical angle S3: 28°.

DESCRIPTION: Medium size for genus (largest specimen recorded c. 53 mm long), subtrapezoidal to posteroventrally subovate in outline. Anterodorsal margin slightly to moderately concave, posterodorsal margin very gently convex. Beaks rounded, prominent; umbones broad. Shells moderately inflated (I/L = 0.43). Anterior, ventral and posterior margins with internal fine crenulation.

Ornamentation consisting of evenly spaced, moderately strong commarginal costae in early stages of growth (c. 20 costae); intercalated secondary costellae absent. During later growth stages, ornamentation growing progressively more erratic, forming irregularly spaced subtrigonal or rounded primary costae of variable width and strength. Interspaces flat or subtrigonal to rounded, variable in depth and width, varying from 1 to 3 times width of

**Fig. 8**

1a, b. *Neocrassina densicostata* n. sp., holotype TM8118, Pounaweia Formation, Late Temaikan (Early–Middle Callovian), Cannibal Bay, South Otago, New Zealand, exterior and interior of right valve, subtrapezoidal form showing erratic growth of dense commarginal costae, $\times 1.56$. **2.** *Neocrassina densicostata*, paratype BM LL32019, Pounaweia Formation, Late Temaikan, Hinahina Quarry, South Otago, interior of left valve, $\times 2.0$.

costae, and frequently bearing up to 3 intercalated secondary costellae. Complex fusion occurs between costae and costellae irregularly over shell surface. Growth lines moderately strong, numerous over shell surface.

Lunule broadly cordate, elongate, with moderately deep concave depression, bordered by very weakly projecting rounded crest. Escutcheon lanceolate, elongate, with shallow wedge-shaped depression, bordered by weakly projecting rounded crest, and with moderately well defined arch along crest near umbonal area; escutcheon $3/5$ width of lunule.

Adductor and pedal retractor scars not seen. Ligament suture relatively wide and long, opisthodic, slightly incurved.

Hinge plate thick, with cardinal area wide dorsoventrally below beak; anterior hinge area long for genus, broad on right valve. Nymph long, relatively wide, surface covered by coarse evenly spaced laminae parallel to posterodorsal margin.

Dentition with lateral teeth *AIII* and *AIV* relatively long and thick, and lateral tooth *AIII* weakly convex ventrally above adductor scar; lateral teeth *PII* and *PIII* thick and long, both terminating well posterior of cardinal area; cardinal tooth 3b strong and elongate; cardinal tooth 2 moderately strong, only slightly elongate, with cardinal tooth 4b narrow and elongate, both cardinals separated by moderately narrow cardinal 3b socket ($S3 = 28^\circ$).

COMPARISONS: The type species *Neocrassina obliqua* (Deshayes, 1830), from the Bajocian of France (Fig. 9: 4–6), is distinguished from *Neocrassina densicostata* by having a considerably more strongly anteroventrally slanting anterodorsal margin, narrower umbones on equivalent

morphotypes, a more evenly rounded external shell surface between the anterodorsal and posterodorsal margins, and a shorter and less depressed lunule. The anterior hinge area is considerably shorter, resulting in shorter lateral teeth *AIII* and *AIV*.

Characters that separate *Neocrassina densicostata* from *Neocrassina cliftoni* (Moore, 1870), and *Neocrassina tibraddeni* (Skwarko, 1974), both from the Bajocian of Western Australia (Fig. 9: 7–9), include its larger size, wider umbones on equivalent morphotypes, less depressed lunule, and much weaker commarginal costae over the entire shell surface. In addition, shells have considerably weaker curvature across the flank, a more elongate nymph, and a shorter anterior hinge area on both valves, resulting in shorter lateral teeth *AIII* and *AIV*.

Neocrassina andium (Gottsche, 1925), from the Bajocian of Argentina, is similar in outline to *N. densicostata*, but differs by having narrower umbones on equivalent morphotypes, a more steeply sloping anterodorsal margin, more anteriorly placed beaks, and stronger commarginal costae over the entire shell surface.

Neocrassina elegans (J. Sowerby, 1818), from the Bajocian of northwestern Europe (Fig. 9: 1–3), differs from *N. densicostata* by having a more depressed lunule, narrower umbones on equivalent morphotypes, a more evenly rounded external shell surface between the anterodorsal and posterodorsal margins, considerably stronger commarginal costae over the entire shell surface, and a shorter nymph. The anterior hinge area together with anterior lateral teeth *AIII*

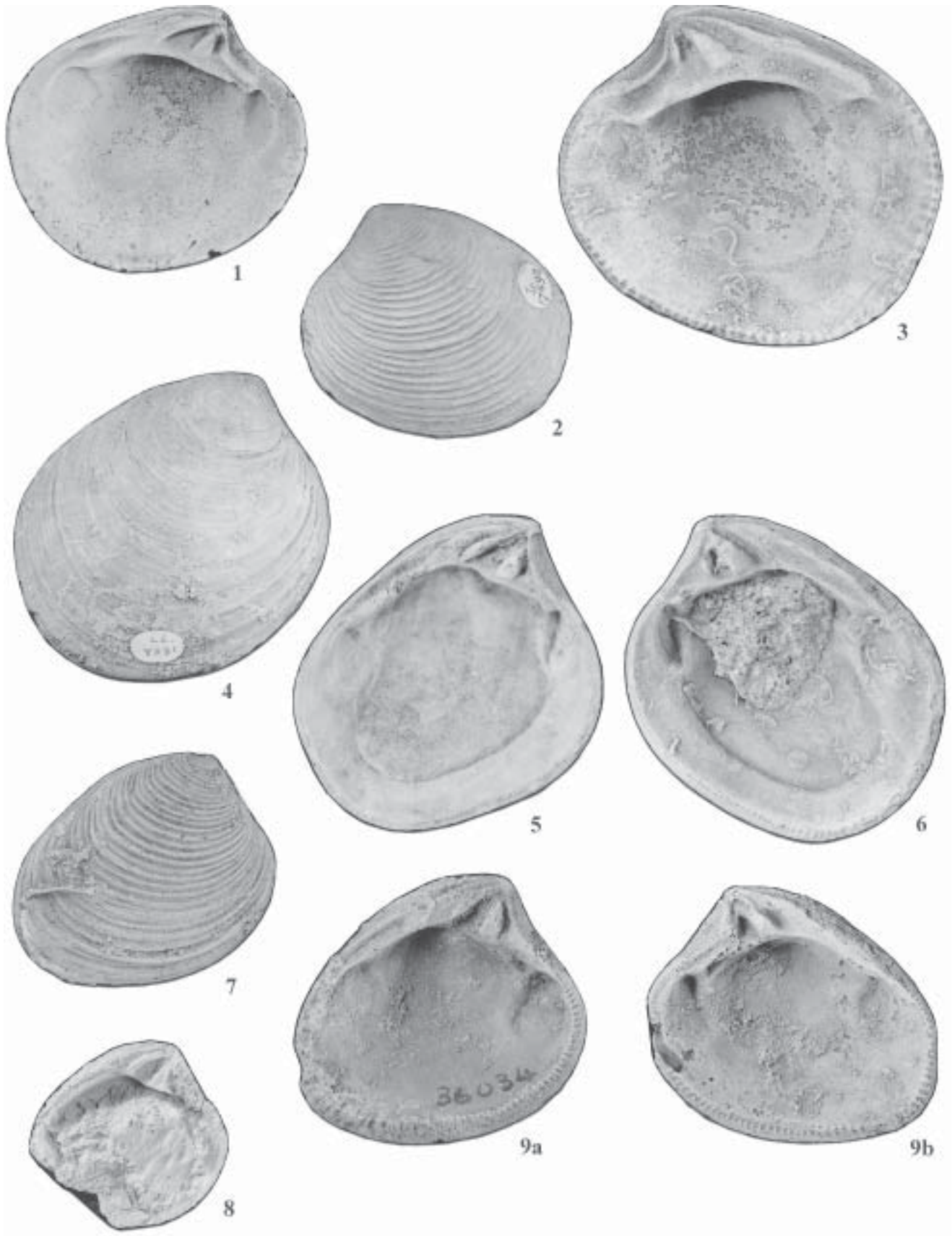


Fig. 9

1–3 *Neocrassina elegans* (J. Sowerby, 1818): 1, BM 81162, Bajocian, Laquaine (Calvados), France, interior of left valve, transitional between the posteroventrally subcircular and posteroventrally subquadrate form, $\times 1.5$; 2, BM L17692, Inferior Oolite, Bajocian, Rodborough Hill near Stroud, England, exterior of left valve, posteroventrally subovate form, $\times 1.0$; 3, BM 81094, Ferruginous Oolite, Bajocian, Les Moutiers en Cinglais (Calvados), France, interior of right valve, posteroventrally subquadrate form, $\times 1.5$.

and *AIV* are shorter, and the right valve anterior hinge area is much wider. Posterior lateral teeth *PII* and *PIII* are much shorter and terminate closer to the cardinal area.

REMARKS: *Neocrassina densicostata* has a long time range, spanning the Early–Late Temaikan (Aalenian to Middle Callovian). Specimens collected from Early Temaikan rocks, lodged with the Institute of Geological & Nuclear Sciences, are identical to their Late Temaikan counterparts. This species is similar to *Notoastarte variabilis* (Gardner & Campbell, 2002), from the Middle–Late Temaikan of New Zealand, in that it is morphologically variable at any given time but demonstrates very little change over time.

DISTRIBUTION: Early–Late Temaikan (Aalenian to Middle Callovian). *Neocrassina densicostata* is sporadically distributed in Temaikan rocks within the Southland Syncline of South Otago. On the northern limb of the syncline it is first recorded at Boatlanding Bay, from Early Temaikan rocks of Boatlanding Bay Formation. It has also been recorded from the Late Temaikan, in the lower part of Pounaweia Formation at Cannibal Bay. It is last recorded in South Otago from Late Temaikan rocks at Hinahina Quarry, on the southern limb of the syncline. At this locality it is sparsely distributed in beds within the middle part of Pounaweia Formation.

Neocrassina fessicostata n. sp.

Fig. 10, 11

ETYMOLOGY: From the Latin *fessus*, weak, and *costatus*, ribbed, referring to the subdued and often weak commarginal ornamentation of this species.

TYPE MATERIAL: Holotype L4044 (Fig. 10: 2), paratypes L4046 and L4047 (Fig. 10: 1, 3), fine–medium grained sandstone bed, Early Temaikan (Aalenian–Bajocian), Murihiku Supergroup. Locality R17/f332 [64939035], Rauroa Stream, Awakino valley, New Zealand. Holotype L4044 collected by N. Hudson and G. Westermann, December 1990.

Paratypes L4045 and L4049 (Fig. 11: 1, 2), age and locality as for holotype but R17/f297 [64949033]. Collected by N. Hudson and W. St George.

Paratype L4048 (Fig. 11: 3), possibly Early Temaikan (Aalenian–Bajocian), Murihiku Supergroup. Locality R17/f8591 [651893], 1.1 km upstream from ford on Taumatamaire Road, Rauroa Stream, Awakino valley. Collected by A. B. Challinor.

DIMENSIONS (in millimetres):

		L	H	I	LA/L	I/L
L4044	(DV)	52.4	44.8	25.2	0.24	0.48
L4045	(DV)	52.0	41.0	–	0.23	–
L4046	(LV)	52.4	45.3	24.0	0.23	0.45
L4047	(DV)	46.8	42.8	c. 24.0	0.32	0.51
L4048	(DV)	48.8	43.0	–	0.36	–
L4049	(DV)	c. 44.7	34.2	18.4	–	0.41

DIAGNOSIS: Medium size shell, anterodorsal margin moderately concave, umbones broad, flank almost flat anteroposteriorly. Lunule short, broad, depression concave in width and length, bordered by weakly defined ridge; escutcheon 3/5 width of lunule. Adductor scars moderately large, anterior narrowly subovate. Nymph moderately elongate, relatively broad, surface with coarse evenly spaced laminae parallel to posterodorsal margin. Cardinal area moderately wide dorsoventrally below beak with stout cardinal tooth 3b. Anterior hinge area and lateral teeth *AIII* and *AIV* short. Apical angle S3: 31–32.2°.

DESCRIPTION: Medium size for genus (largest specimen recorded 52.4 mm long), posteroventrally subovate to subtrapezoidal in outline; shell form similar to *Neocrassina densicostata*. Beaks rounded, prominent; umbones broad on all morphotypes. Inflation variable (I/L = 0.41–0.51).

Ornament consisting of evenly spaced moderately strong commarginal costae in early stages of growth (c. 9 costae); intercalated secondary costellae absent. During later growth stages, ornamentation rapidly weakens, forming a complex mix of weakly defined primary commarginal costae of variable width; interspace width variable, usually wider than costae. Costae infrequently foliated over anterior or posterior area, forming 2–3 secondary costellae. Interspaces angular or flat, frequently bearing up to 3 secondary costellae that may fuse at any point on shell surface to form a costa. Growth lines weak, numerous over shell surface.

Lunule broadly cordate, length and width subequal, with moderately deep concave depression, bordered by weakly projecting rounded crest. Escutcheon lanceolate, elongate, with moderately deep wedge-shaped depression, bordered by rounded slightly projecting crest, and with moderately defined arch along crest near umbonal area; escutcheon 3/5 width of lunule.

Anterior adductor scar subovate, moderately large, strongly defined, becoming very deep dorsally and posteriorly, well impressed in ventral slope of hinge plate. Anterior pedal retractor scar small but very well defined, positioned posterodorsal of adductor scar, just below ventral edge of hinge plate. Posterior adductor scar weak, shallow, subovate. Posterior pedal retractor scar not seen. Pallial line integripalliate. Ligament suture relatively long and narrow, opisthodontic, slightly incurved.

Hinge plate thick, with cardinal area moderately wide dorsoventrally below beak; anterior hinge area relatively short, and broad on right valve. Nymph long, wide, surface covered by coarse evenly spaced laminae parallel to posterodorsal margin.

Dentition with lateral teeth *AIII* and *AIV* short and thick, and lateral tooth *AIII* moderately convex ventrally above adductor scar; lateral teeth *PII* and *PIII* thick, relatively long, both terminating well posterior of cardinal area; cardinal tooth 3a usually subvertical and well defined; cardinal tooth 3b strong, prominent, slightly elongate, with cardinal tooth 2 subequal and cardinal tooth 4b narrow, elongate; cardinal teeth 2 and 4b separated by moderately wide cardinal 3b socket (S3: min. = 31°; max. = 32.2°; av. = 31.6°).

4–6 *Neocrassina obliqua* (Deshayes, 1830): 4, BM LL8031, Inferior Oolite, Bajocian, Burton Bradstock, Dorset, England, exterior of right valve, posteroventrally subovate form, $\times 1.0$; 5, BM LL10869, Inferior Oolite, Bajocian, locality unknown, interior of left valve, subtrapezoidal form, $\times 1.0$; 6, BM L4714, Inferior Oolite, Bajocian, Halfway House, England, interior of right valve, posteroventrally subrectangular form, $\times 1.0$.

7, *Neocrassina cliftoni* (Moore, 1870), specimen 1 (36033) = BM LL28267, Newmarracarra Limestone, Bajocian, Moonyoonooka Homestead, Western Australia, exterior of right valve, posteroventrally subovate form, $\times 1.0$.

8, 9 *Neocrassina tibraddeni* (Skwarko, 1974): 8, BM 65194, Middle Jurassic, Western Australia, interior of left valve, posteroventrally subovate form, $\times 1.0$; 9a, b, specimen 1 (36034) = BM LL28268, Newmarracarra Limestone, Bajocian, Moonyoonooka Homestead, Western Australia, disarticulated valves, subtrapezoidal form, $\times 1.5$.

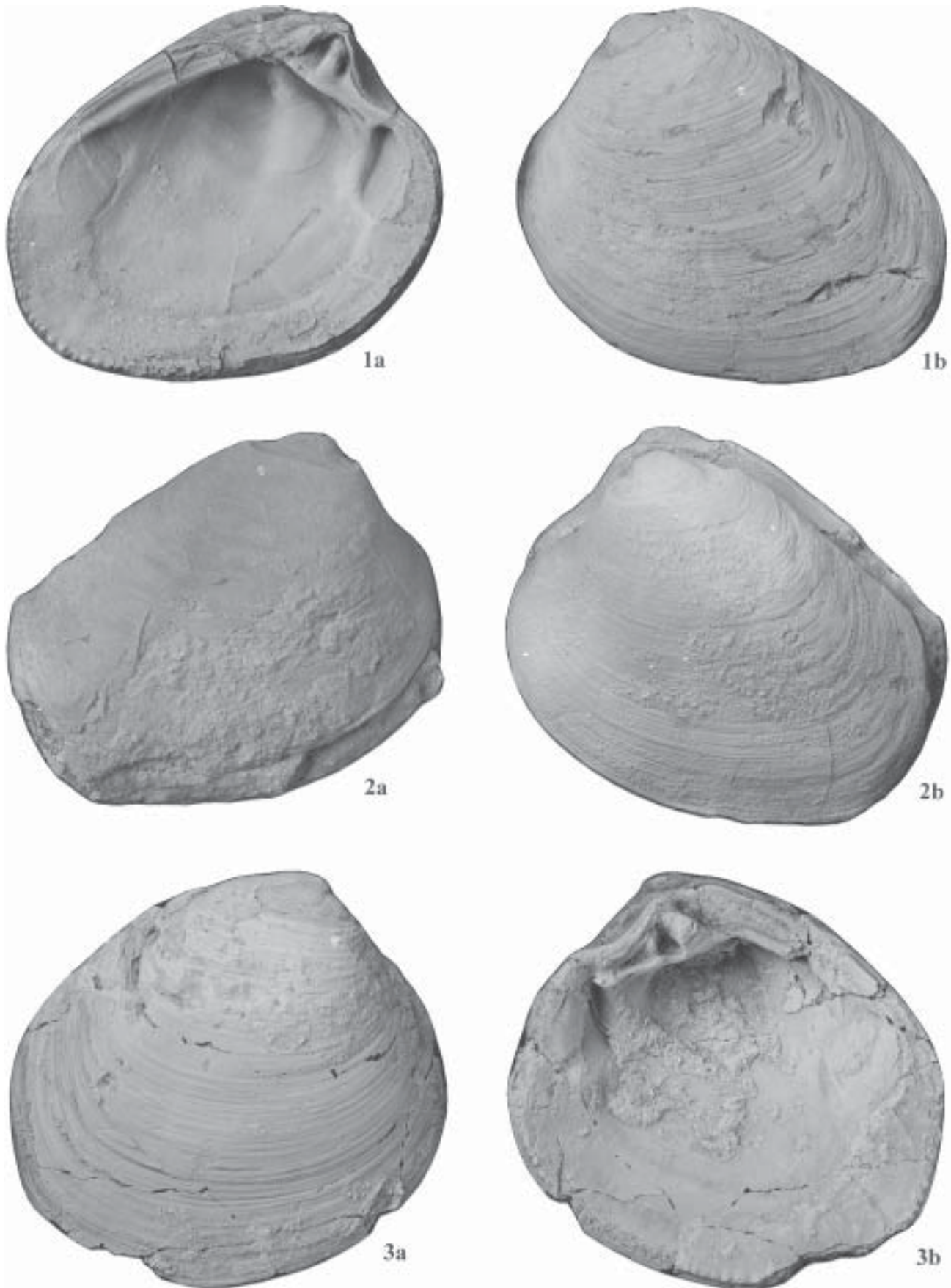


Fig. 10

1–3 *Neocrassina fessicostata* n. sp., Early Teraikan (Bajocian–Bathonian), Rauroa Stream, Awakino valley, New Zealand: **1a, b**, paratype L4046, interior and exterior of left valve, subtrapezoidal form, $\times 1.5$; **2a, b**, holotype L4044, exterior of articulated valves, subtrapezoidal form showing very weak commarginal costae, $\times 1.5$; **3a, b**, paratype L4047, exterior and interior of right valve, posteroventrally broad subovate form, $\times 1.7$.

VARIATION: Specimens of *Neocrassina fessicostata* are often slightly crushed due to compaction, causing ornamentation to have a deceptively coarse appearance. On undeformed specimens, such as the holotype L4044 and paratype L4046, ornamentation is consistently weak and poorly defined. There is little variation in interspace and costal width. Most specimens examined have a subtrapezoidal outline, with a small amount of variation in the curvature of the margins. This implies that the outline of shells is relatively constant. However, paratype L4047 has a broad posteroventrally subovate outline. The curvature of the margins is similar to that of shells with a subtrapezoidal outline, but the posterodorsal margin is shorter, and the ventral margin shorter and slightly more oblique. There is some variation in the length and strength of cardinal tooth 3a, and in its subvertical position.

COMPARISONS: *Neocrassina fessicostata* is distinguished from *N. densicostata* mainly by the characters of the dorsal area. It differs by having more anteriorly placed beaks, slightly wider umbones on equivalent morphotypes, and a wider nymph. The anterior hinge area is shorter, and narrower on the right valve, resulting in shorter lateral teeth *AIII* and *AIV*. *Neocrassina fessicostata* differs further in that the cardinal area is thinner and narrower below the beaks, with a weaker and less elongate cardinal tooth 3b, and by having a cardinal tooth 3b socket with a greater apical angle.

Neocrassina unilateralis (J. de C. Sowerby, 1840) from the Callovian of east Africa and the Callovian–Oxfordian of India (Fig. 13: 4–6), is superficially similar to *N. fessicostata*, but differs by having a consistently less posteroventral projection, a less depressed lunule, a narrower nymph, a shorter ligament suture, and a longer anterior hinge area resulting in longer lateral teeth *AIII* and *AIV*.

REMARKS: The position of cardinal tooth 3a was examined on three right valves, and the position and orientation of its socket on several left valves. All valves examined possess a normal *Neocrassina* hinge without transposition. Cardinal tooth 3a is nearly always subvertically positioned, with only its dorsal half merging with the anterodorsal margin. The ventral half continues to project almost vertically in a ventral direction, and is clearly formed by lateral tooth *AIII* positioned along the ventral edge of the anterior hinge area. On paratype L4046, lamella *IV* clearly extends around the socket for cardinal tooth 3a, and forms cardinal tooth 4b.

DISTRIBUTION: Early Temaikan (Aalenian–Bajocian). *Neocrassina fessicostata* is fairly common in the Rauroa Stream section of Awakino valley, New Zealand.

Neocrassina faceta n. sp.

Fig. 12

ETYMOLOGY: From the Latin *facetus* meaning well made or elegant.

TYPE MATERIAL: Holotype L4050 (Fig. 12: 3), gritty greenish grey sandstone bed, Late Temaikan (Early–Middle Callovian), Murihiku Supergroup. Locality R13/f226 [72222270], Opuatia Cliff, Waikato, New Zealand. Collected by N. Hudson and G. Westermann, December 1990.

Paratype L4051 (Fig. 12: 2), age and locality as for holotype but R13/f6613 [721227]. Collected by B. L. Purser, 1952.

Paratypes TM8119 and L4052 (Fig. 12: 1, 4), Captain King's Shellbed, Middle Heterian (Early Kimmeridgian), Murihiku

Supergroup. Locality R15/f8550 [660411], Ohineruru Bay, Totara Peninsula, Kawhia Harbour, New Zealand.

DIMENSIONS (in millimetres):

		L	H	I	LA/L	I/L
L4050	(DV)	37.3	32.0	17.2	0.22	0.46
L4051	(RV)	c. 33.0	c. 28.2	12.0	0.33	0.36
L4052	(DV)	52.8	43.2	28.6	0.18	0.54
TM8119	(DV)	70.0	57.3	30.4	0.23	0.43

DIAGNOSIS: Shell large, anterodorsal margin gently concave, umbones broad, flank almost flat anteroposteriorly. Lunule length and width subequal, depression concave in width and length, bordered by weakly defined ridge; escutcheon 3/5 width of lunule. Adductor scars moderately large, anterior broadly subovate. Nymph slender, surface with weak evenly spaced laminae parallel to posterodorsal margin. Cardinal area narrow dorsoventrally below beak, with relatively elongate, narrow, cardinal tooth 3b. Anterior hinge area and lateral teeth *AIII* and *AIV* relatively long. Apical angle S3: 41.2–42°.

DESCRIPTION: Large for genus (largest specimen recorded 70.0 mm long), posteroventrally subovate to subtrapezoidal in outline. Anterodorsal margin gently concave, posterodorsal margin gently convex. Beaks rounded, prominent; umbones broad on all morphotypes. Inflation variable (I/L = 0.36–0.54). Anterior, ventral, and posterior margins with fine internal crenulations, or smooth with internal commarginal groove.

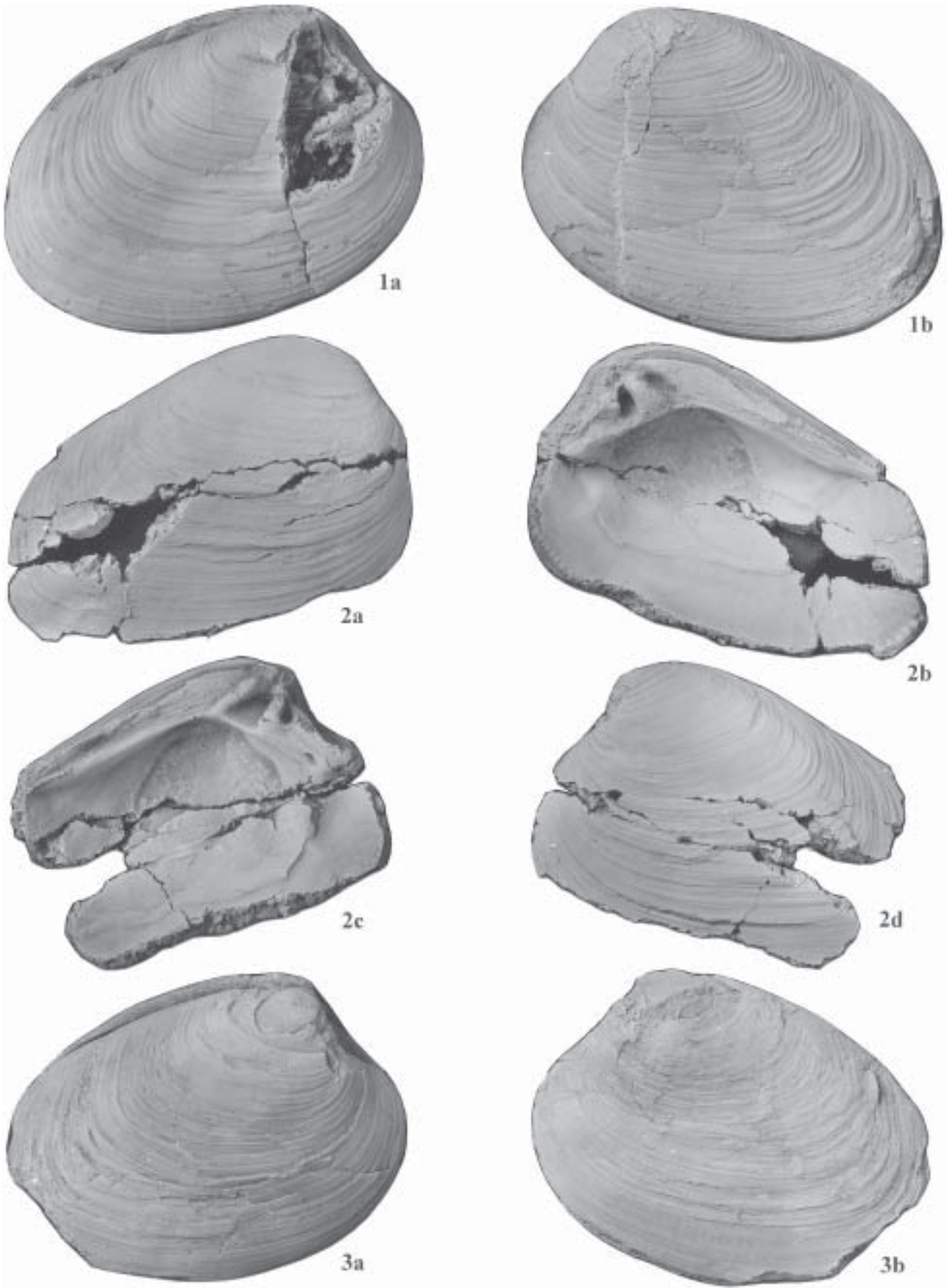
Ornament consisting of evenly spaced moderately strong commarginal costae during early stages of growth; intercalated secondary costellae absent. During later stages, ornamentation usually consisting of evenly spaced weak commarginal costae that grow weaker ventrally, with subequal interspaces. Alternative ornamentation during later growth stages consisting of unevenly spaced, subtrigonal or rounded primary commarginal costae of variable width and strength. On these forms, interspaces flat or subtrigonal to rounded, variable in depth and width, 1–3 times width of costae, and frequently bearing up to 3 intercalated secondary costellae. On all forms complex fusion occurring between primary costae and secondary costellae at varying points on shell surface. Growth lines moderately strong, numerous over shell surface.

Lunule cordate, length and width subequal, with moderately deep concave depression, bordered by rounded weakly projecting crest. Escutcheon lanceolate, elongate, with moderately deep wedge-shaped depression, bordered by rounded weakly projecting crest, and with moderately defined arch along crest near umbonal area; escutcheon 3/5 width of lunule.

Anterior adductor scar subovate, moderately large, strongly defined, becoming very deep dorsally and posteriorly, well impressed in ventral slope of hinge plate. Anterior pedal retractor scar small but well defined, placed posterodorsal of adductor scar just below ventral edge of hinge plate. Posterior adductor scar weak, shallow, subovate. Posterior pedal retractor scar not seen. Pallial line integripalliate.

Hinge plate moderately thick, with cardinal area relatively narrow dorsoventrally below beak; anterior hinge area relatively long, somewhat broad. Nymph moderately long, relatively narrow, surface covered by weak evenly spaced laminae parallel to posterodorsal margin.

Dentition with lateral teeth *AIII* and *AIV* relatively long, moderately thick, *AIII* strongly convex ventrally above adductor scar; lateral teeth *PII* and *PIII* moderately thick and long, both terminating well posterior of cardinal area; cardinal tooth 3b relatively strong, prominent, slightly elongate, with cardinal tooth



2 subequal and cardinal tooth 4b narrow and elongate; 2 and 4b separated by wide cardinal 3b socket (S3: min. = 41.2°; max. = 42°; av. = 41.6°).

COMPARISONS: *Neocrassina faceta* differs from most other species in the genus by having a relatively narrow cardinal area below the beak. Characters which also separate it from *N. densicostata* and *N. fessicostata* include a smaller lunule, less concave anterodorsal margin, a stronger ventral convexity above the adductor scar for lateral tooth *AIII*, a cardinal tooth 3b which is smaller and less elongate, and a cardinal tooth 3b socket with a greater apical angle.

Neocrassina ellsworthensis (Quilty, 1977), from the Heterian (Kimmeridgian) of Antarctica, differs from *N. faceta* in its more strongly curved margins, and in having a much wider cardinal area and a more posteriorly inclined cardinal tooth 3b. It differs further by having a deeper almost flat-bottomed lunule that is bordered by an acutely rounded ridge, and by having much stronger commarginal costae extending across the lunule.

Neocrassina unilateralis (J. de C. Sowerby, 1840) (Fig. 13: 4–6) differs from this species by having a more anteroventrally inclined and more concave anterodorsal margin. This results in the beaks being more anteriorly placed, and the dorsal region having a more projecting aspect. The cardinal area is wider below the beak, cardinal tooth 3b has slightly greater elongation, and the external shell surface between the anterodorsal and posterodorsal margins is more evenly rounded.

Neocrassina compressa (J. de C. Sowerby, 1840), from the Oxfordian to Early Kimmeridgian of India (Fig. 13: 7–9), differs from *N. faceta* by having considerably stronger commarginal costae over the entire shell surface on similarly inflated forms, and a more concave anterodorsal margin. The umbones are narrower on equivalent morphotypes, the nymph shorter, and the cardinal area wider below the beak. The external shell surface is more evenly rounded between the posterodorsal and anterodorsal margins, and the posterior hinge area is shorter, resulting in shorter and thinner lateral teeth *PII* and *PIII*.

Neocrassina ovata (Smith, 1817), from the Oxfordian to Early Kimmeridgian of England (Fig. 13: 1–3), is very variable in ornamentation and outline. Typically it has a posteroventrally subovate outline, and strong commarginal costae in early stages of growth, which fade during later growth stages into surface folds of low relief. These features together with a more elongate lunule, an almost evenly rounded external surface between the anterodorsal and posterodorsal margins, a stronger and basally wider cardinal tooth 4b, and a wider cardinal area below the beak, serve to distinguish it from *N. faceta* and other New Zealand species.

Neocrassina sowerbyana (Holdhaus, 1913), from the Late Oxfordian to Tithonian of India (Fig. 14: 2–6), is one of the largest species in the genus. It differs from New Zealand species by having more anteriorly placed beaks, a cardinal area which is considerably wider below the beak, a larger

and more elongate cardinal tooth 3b, and an anterior hinge area together with anterior lateral teeth *AIII* and *AIV* that are shorter. *Neocrassina sowerbyana* differs further in that the lunular depression is almost flat in the width direction, gently concave anteroposteriorly, and is bounded by a strongly rounded crest which is almost semicircular in cross-section. The relief of the lunular depression on New Zealand specimens is uniformly concave in length and width and consistently bordered by a rounded weakly projecting crest.

Neocrassina recki (Dietrich, 1933) from the Late Kimmeridgian of east Africa (Fig. 14: 1) is distinguished from *N. faceta* by its very broad posteroventrally subovate outline, and by having a more convex posterodorsal margin. It has a considerably wider cardinal area below the beak, a much shorter anterior hinge area, and shorter lateral teeth *AIII* and *AIV*. The lunule also differs by being bounded by a prominently projecting crest.

REMARKS: Trechmann (1923) referred large astartid bivalves, from the Late Temaikan–Heterian (Callovian–Kimmeridgian) of New Zealand, to *Neocrassina spitiensis* (Stoliczka, 1865) and *Neocrassina* cf. *sowerbyana* (Holdhaus, 1913), from the Late Oxfordian–Tithonian of India. However, an examination of shells has shown that *N. spitiensis* is conspecific with *Neocrassina unilateralis* (J. de C. Sowerby, 1840), from the Callovian–Oxfordian of India (Appendix 1).

DISTRIBUTION: Late Temaikan to Middle Heterian (Callovian to Early Kimmeridgian). *Neocrassina faceta* has been recorded from the Late Temaikan sequence of Opuatia Stream, Port Waikato, and is also common in Captain King's Shellbed of the Middle Heterian at Ohineruru Bay, Kawhia Harbour.

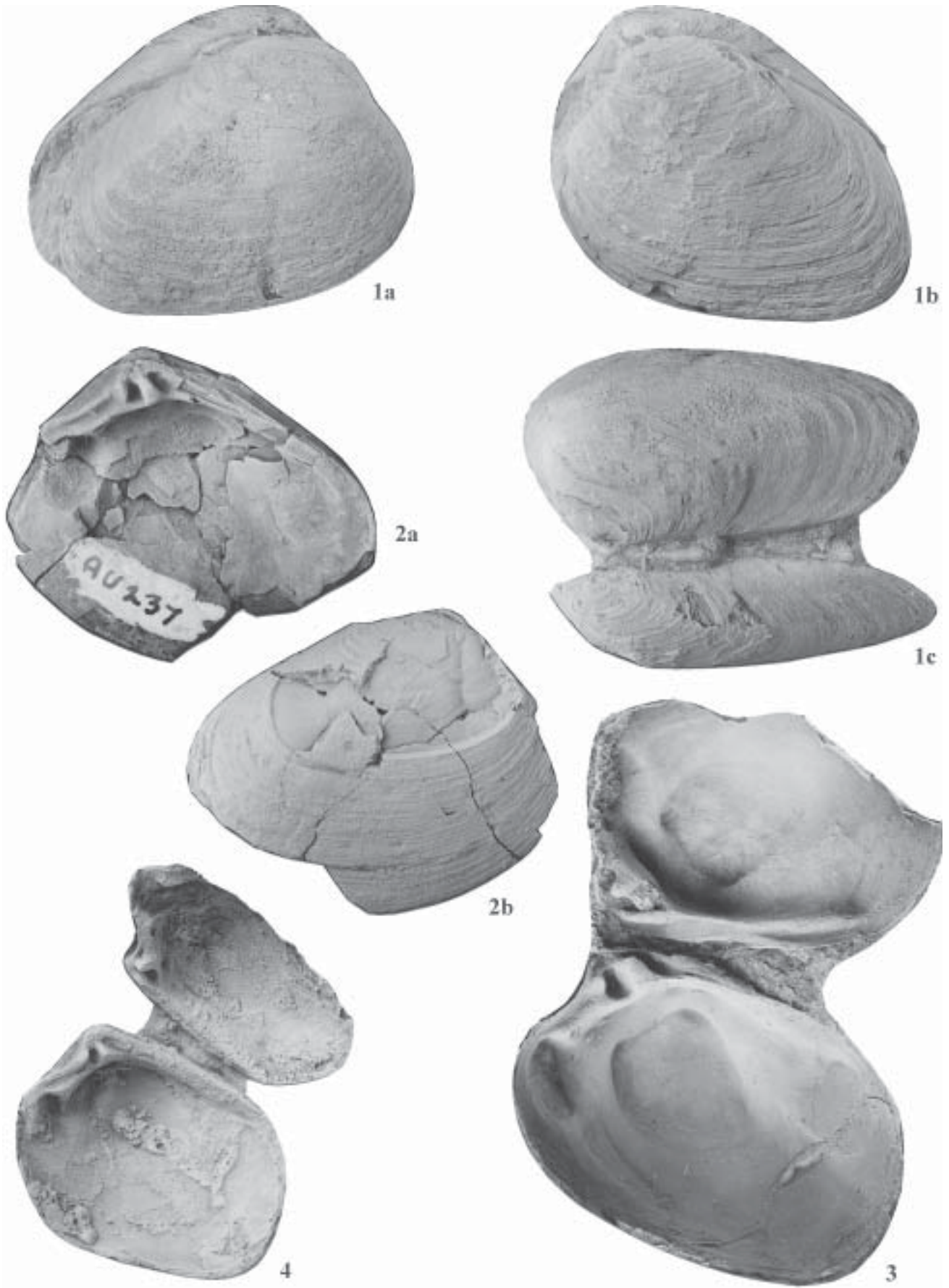
Subfamily TRIGONOPINAE n. subfam.

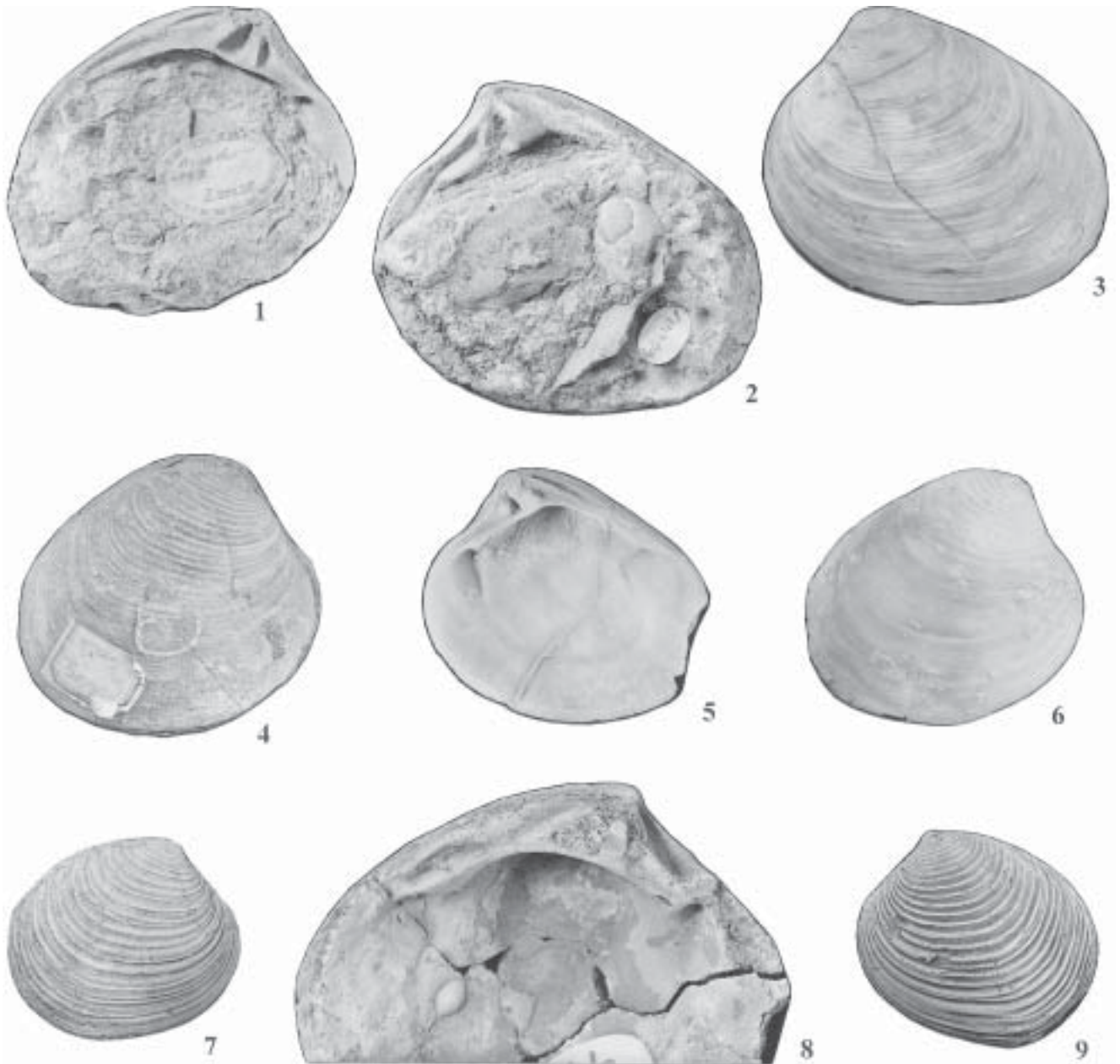
DIAGNOSIS: Subtrigonal or subtrapezoidal to posteroventrally subelliptical shells. Height commonly greater than or equal to length. Umbones positioned above beaks. Cardinal dentition robust, strongly projecting, with cardinal tooth 3b pyramidal in form. Anterior and posterior lateral teeth functional and variably defined, but lateral teeth *AI* and *AII* absent or obsolete. Lateral tooth *AIII* positioned along ventral edge of right valve anterior hinge area; lateral tooth *PIII* lies along right valve posterodorsal margin; lateral tooth *AIV* placed along, and equal in width to, left valve anterior hinge area; lateral tooth *PII* situated along ventral edge of left valve posterior hinge area. Hinge formula:

<i>AIII</i>	(3a)	3b	<i>PIII</i>
<i>AIV</i>	2	4b	<i>PII</i>

REMARKS: In his diagnosis of the subfamily Opinae, Chavan (1969) stated that anterior lateral teeth are obsolete. *Opis* and *Coelopsis* species lack an anterior hinge area, and have posterior lateral teeth that are either absent, very weak, or obsolete. However, in *Trigonopsis*, anterior and posterior lateral teeth are functional, and the anterior hinge area is well defined. There is a large degree of intraspecific variation in length of the anterior hinge area. Some species, such as *Trigonopsis similis* (J. Sowerby, 1819) from the Bajocian–Bathonian of England, have an extremely short anterior hinge area that is narrow on the right valve, with short lateral teeth *AIII* and *AIV*. Other species, such as *Trigonopsis morgani* (Trechmann, 1923) from the Middle Heterian (Early Kimmeridgian) of New Zealand, have a moderately long anterior hinge area, with

◀ **Fig. 11**
1–3 *Neocrassina fessicostata*, Early Temaikan (Bajocian–Bathonian), Rauroa Stream, Awakino valley, New Zealand: **1a, b**, paratype L4045, exterior of articulated valves, posteroventrally subovate form, $\times 1.46$; **2a–d** paratype L4049, exterior and interior of disarticulated valves, $\times 1.66$; **3a, b**, paratype L4048, exterior of articulated valves, posteroventrally subovate form, $\times 1.5$.



**Fig. 13**

1–3 *Neocrassina ovata* (Smith, 1817): **1**, BM L20228, Oxfordian, Marcham near Abingdon, Berkshire, England, interior of left valve, posteroventrally subovate form, $\times 1.0$; **2**, BM 44031, Oxfordian, Weymouth, Dorset, England, interior of right valve, subtrapezoidal form, $\times 1.0$; **3**, BM LL23777, Ringstead Coral Bed, Oxfordian, Weymouth, Dorset, England, exterior of left valve, subtrapezoidal form, $\times 1.0$.

4, 5, *Neocrassina unilateralis* (J. de C. Sowerby, 1840), Middle Callovian, Lonji Stream, Mandawa-Mahokondo Anticline, southeastern Tanzania, Africa: **4**, BM LL28260, exterior of right valve, posteroventrally subovate form, $\times 1.0$; **5**, BM LL28261, interior of right valve, posteroventrally subovate form, $\times 1.0$.

6, *Neocrassina unilateralis* (J. de C. Sowerby, 1840), BM LL1270, Callovian, west of Jumara, Kachh, India, exterior of right valve, transitional to subtrapezoidal form, $\times 1.0$.

7, *Neocrassina compressa* (J. de C. Sowerby, 1840), specimen 1 (47A/49) = BM LL28262, Oxfordian, Kachh, India, exterior of right valve, transitional between the posteroventrally subcircular and posteroventrally subovate form, $\times 1.0$.

8, 9, *Neocrassina compressa* (J. de C. Sowerby, 1840), Bed 3, Lower Dhosa Oolite, Oxfordian, east of Badi, Kachh, India: **8**, BM LL1263, interior of left valve showing lateral tooth *AIV* extending upward to form lamella *IV*, resulting in the formation of cardinal tooth 4b, $\times 2.0$; **9**, BM LL1257, exterior of left valve, posteroventrally subovate form, $\times 1.0$.

Fig. 12

1, 4, *Neocrassina faceta* n. sp., Captain King's Shellbed, Middle Heterian (Early Kimmeridgian), Ohineruru Bay, Totara Peninsula, Kawhia Harbour, New Zealand: **1a, b**, paratype TM8119, slightly disarticulated valves, subtrapezoidal form; **1c**, dorsal view showing fossilised ligament, $\times 0.9$; **4**, paratype L4052, interior of disarticulated valves, posteroventrally subrectangular form, $\times 0.95$.

2, 3, *Neocrassina faceta*, Late Temaikān (Early–Middle Callovian), Opuatia Cliff, Waikato, New Zealand: **2a, b**, paratype L4051, interior and exterior of right valve, posteroventrally subovate form, $\times 2.0$; **3**, holotype L4050, interior of disarticulated valves, transitional between the posteroventrally subrectangular and posteroventrally subovate form, $\times 1.9$.



Fig. 14

1, *Neocrassina recki* (Dietrich, 1933), BM L51186, Nerinea beds, Late Kimmeridgian, Tendaguru, Tanzania, Africa, exterior of right valve, posteroventrally subovate form, $\times 1.0$.

relatively elongate lateral teeth *AIII* and *AIV*. *Trigonopsis anaton* n. sp., from the Middle Heterian (Early Kimmeridgian) of New Zealand, has an anterior hinge area that falls midway in length between that of *T. morgani* and that of *T. similis*. The size of the anterior hinge area in *Trigonopsis* species, together with the length and position of anterior lateral teeth, is similar to what is found in *Neocrassina* (subfamily Astartinae). *Trigonopsis* cannot be placed in Astartinae as it has an opine form, umbones which are elevated above the beaks, very strongly projecting cardinal teeth, and a pyramidal cardinal tooth 3b. *Trigonopsis* is raised to generic level as type of the new subfamily Trigonopinae, which is introduced here to accommodate bivalves with characters that fall midway between Astartinae and Opinae.

Genus *Trigonopsis* Munier-Chalmas, 1887

TYPE SPECIES: By original designation, *Cardita similis* J. Sowerby, 1819, Middle Jurassic, western Europe.

DIAGNOSIS (emended): Shell of medium size for subfamily, moderately inequilateral, posteroventrally elongate; subtrigonal or subtrapezoidal to posteroventrally subelliptical in outline. Beaks prominent, relatively low above cardinal area, 0.3–c. 0.5 of shell length from anterior margin; umbones very high and usually erect above beaks. Commarginal costae subtrigonal in cross-section, apically well rounded, and increasing slightly in width and spacing throughout growth. Costae and interspaces of constant width across flank, decreasing in width across anterior and posterior areas, and extending across lunule and escutcheon in form of costellae. Lunule broad, well defined, length and width usually subequal. Escutcheon elongate, narrow, well defined; escutcheon crest rounded in cross-section. Dorsal margin bordering cardinal area subtrigonal in outline. Right valve anterior hinge area short and broad. Cardinal tooth 3a either absent, or weakly defined and obsolete; cardinal tooth 2 subtrigonal and short, cardinal 4b very elongate and stronger than 2, both cardinals strongly projecting and not subequal in form with cardinal tooth 3b; lateral teeth *AIII* and *AIV* short; lateral teeth *PII* and *PIII* moderately elongate. Hinge formula:

<i>AIII</i>	(3a)	3b	<i>PIII</i>
<i>AIV</i>	2	4b	<i>PII</i>

COMPARISONS: The genus *Trigonastarte* Bigot, 1895, currently placed in the subfamily Opinae, is somewhat similar to *Trigonopsis*. However, characters that separate *Trigonastarte* from it include much larger size (largest recorded specimen 75 mm long), its strongly trigonal outline, its moderately convex posterodorsal margin, and its more weakly defined anterior lateral teeth. *Trigonastarte* is here transferred to the subfamily Trigonopinae.

Trigonopsis morgani (Trechmann, 1923) Fig. 15
1923 *Astarte* (*Opis?*) *morgani* Trechmann; p. 280, pl. 13, fig. 4a, 4b, 5.
1953 *Astarte morgani* Trechmann; Marwick, p. 107, pl. 10, fig. 22, 25.

TYPE MATERIAL: Lectotype BM L48047, Trechmann Collection (The Natural History Museum), Captain King's Shellbed, Middle Heterian (Early Kimmeridgian), Murihiku Supergroup. Locality probably R15/f8027 [660411], Ohineruru Bay, Totara Peninsula, Kawhia Harbour, New Zealand.

Figured specimens L4053, L4055, and L4057 (Fig. 15: 1, 3, 4), Captain King's Shellbed, Middle Heterian (Early Kimmeridgian), Murihiku Supergroup. Locality R15/f8027 [660411], Ohineruru Bay, Totara Peninsula, Kawhia Harbour. L4055 collected by R. H. Barron, 1953.

Figured specimens L4054 and L4056 (Fig. 15: 2, 5), locality unknown, Captain King's Shellbed, by matrix identification.

DIMENSIONS (in millimetres):

		L	H	I	LA/L	I/L
L4053	(LV)	22.4	23.2	16.0	0.41	0.69
L4054	(RV)	21.9	21.0	14.6	0.36	0.66
L4055	(LV)	18.4	–	12.8	0.49	0.69
L4056	(RV)	20.7	21.0	16.0	0.39	0.76
L4057	(DV)	22.5	21.9	15.4	0.31	0.68

DIAGNOSIS: Medium size shell, subtrapezoidal in outline, posterior area moderately inclined, posteroumbonal ridge well defined. Lunule elongate, depression concave in width and length, bordered by weakly defined ridge; escutcheon $\frac{1}{2}$ width of lunule. Adductor scars moderately large, anterior broadly subovate. Cardinal area moderately wide dorsoventrally below beak with stout cardinal tooth 3b. Anterior hinge area and lateral teeth *AIII* and *AIV* elongate. Apical angle S3: 48–51°.

DESCRIPTION: Medium size for genus (largest specimen recorded 22.5 mm long), variably subtrapezoidal in outline. Umbonal ridge well defined, prominent, extending from posterior of beak to posteroventral margin. Ridge strongly rounded from beak to mid-flank, then becoming progressively weaker posteroventrally. Posterior area moderately inclined. Beaks pointed, moderately prosogyrate, slightly projecting and low above cardinal area. Umbones relatively broad, moderately high, and moderately to strongly incurved. Inflation variable (I/L = 0.66–0.76). Anterior, ventral, and posterior margins with moderately strong internal crenulations.

Ornamentation consisting of well-rounded primary commarginal costae increasing in strength throughout growth. Commarginal costae and associated interspaces increasing in width during early stages of growth but becoming irregular during later growth stages. Angular interspaces infrequently bearing 1 or 2 intercalated secondary costellae that coalesce with previous primary costa over anterior or posterior area.

Lunule broadly cordate, length and breadth subequal, with moderately deep concave depression bordered by well-rounded projecting crest. Escutcheon lanceolate, moderately elongate with relatively deep wedge-shaped depression, bordered by rounded slightly projecting crest; escutcheon about $\frac{1}{2}$ width of lunule.

Anterior adductor scar of moderate size, broadly subovate, deepening posteriorly and dorsally; on right valve very strongly

2, *Neocrassina sowerbyana* (Holdhaus, 1913), specimen 5 (252) = BM LL28266, Kimmeridgian, Kachh, India, exterior of right valve, transitional between the posteroventrally subovate and subtrapezoidal form, $\times 1.0$.

3, 4, 6, *Neocrassina sowerbyana* (Holdhaus, 1913), Late Oxfordian to Early Kimmeridgian, Kachh, India: 3, specimen 2 (W39) = BM LL28263, exterior of right valve, posteroventrally subovate form, $\times 1.0$; 4, specimen 3 (W39) = BM LL28264, interior of right valve, posteroventrally subovate form, $\times 1.0$; 6, specimen 4 (W39) = BM LL28265, exterior of left valve joined to a separate specimen showing left valve hinge, $\times 1.0$.

5, *Neocrassina sowerbyana* (Holdhaus, 1913), BM LL1372, Tithonian, west of Soorkha, Kachh, India, interior of left valve, posteroventrally subovate form, $\times 1.0$.

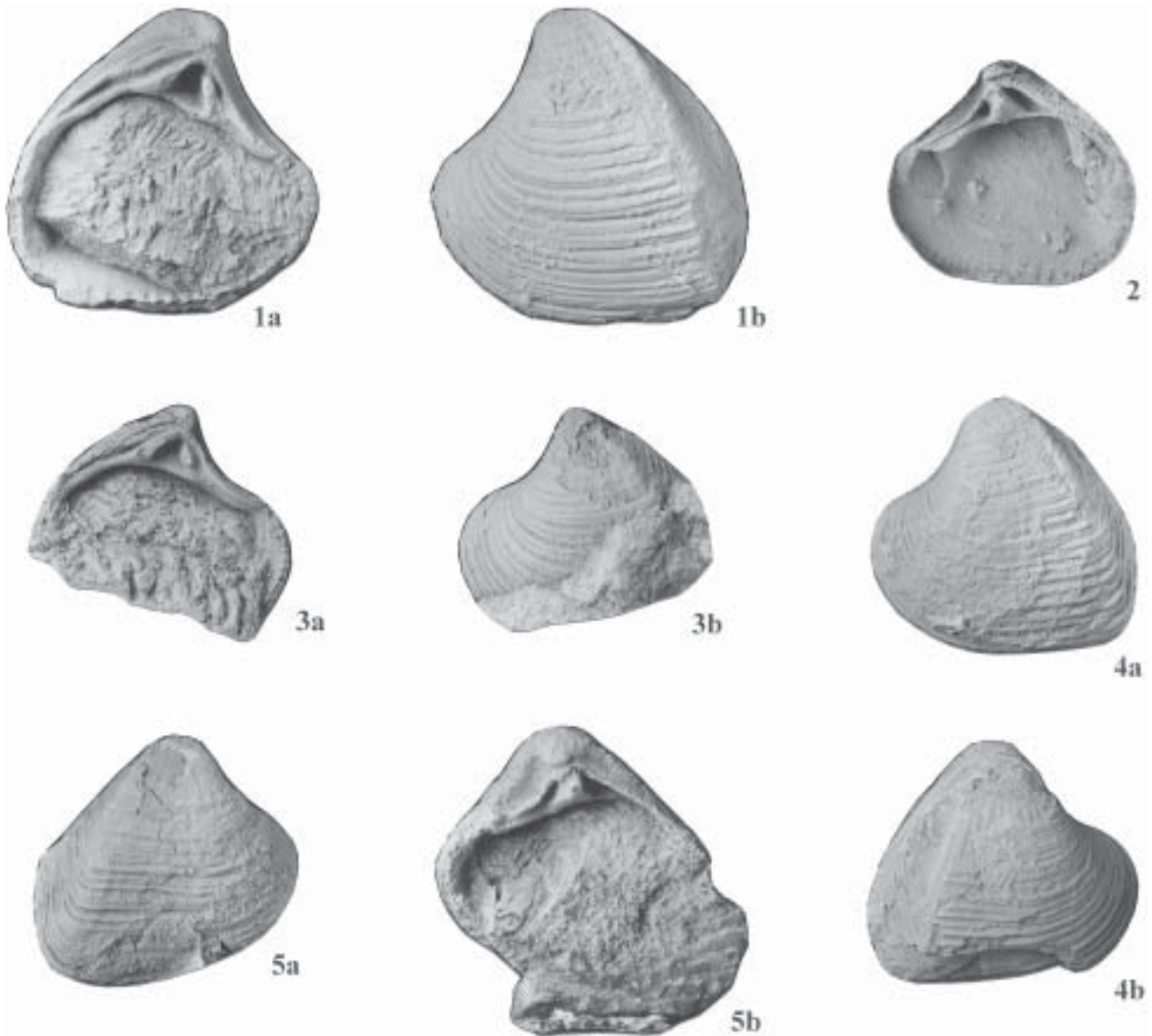


Fig. 15

1, 3, 4, *Trigonopsis morgani* (Trechmann, 1923), Captain King's Shellbed, Middle Heterian (Early Kimmeridgian), Ohineruru Bay, Kawhia Harbour, New Zealand: **1a, b**, L4053, interior and exterior of left valve, $\times 2.0$; **3a, b**, L4055, interior and exterior of left valve, $\times 2.0$; **4a, b**, L4057, exterior of articulated valves, $\times 1.7$.

2, 5, *Trigonopsis morgani*, Captain King's Shellbed by matrix identification, Middle Heterian, locality unknown, New Zealand: **2**, L4056, interior of right valve, $\times 1.7$; **5a, b**, L4054, exterior and interior of right valve, $\times 1.8$.

impressed in ventral slope of anterior hinge area. Anterior pedal retractor scar small but well defined, positioned posterodorsal of adductor scar below ventral edge of hinge plate. Posterior adductor scar shallow, but equal in size and shape to anterior adductor scar. Posterior pedal retractor scar not seen. Ligament suture narrow and deep, opisthodontic, slightly incurved.

Hinge plate thick, with cardinal area moderately wide dorsoventrally below beak, ventral edge with well-defined slant anteriorly; right valve anterior hinge area relatively broad, elongate for genus with moderate ventral convexity; posterior hinge area of right valve and anterior hinge area of left valve forming a thickening along ventral slope of dorsal margin; left valve posterior hinge area relatively broad, about equal in length to anterior hinge area. Nymph short, narrow, slightly rounded in section.

Dentition with lateral teeth *AIII* and *AIV* thick and elongate, *AIII* slanting inward near cardinal area to form a lamella or a weak obsolete cardinal tooth 3a; lateral tooth *PIII* elongate and slender; lateral tooth *PII* elongate and thick; cardinal tooth 3b very large, stout, and strongly projecting; cardinal tooth 2 short, narrow, with cardinal tooth 4b much stronger and very elongate, both cardinals separated by deep and very wide cardinal 3b socket (S3: min. = 48° ; max. = 51° ; av. = 49.5°).

VARIATION: *Trigonopsis morgani* exhibits a considerable amount of variation in ornamentation. All specimens examined have commarginal costae and associated interspaces gradationally increasing in width during early stages of growth. There is a gradual increase in the strength of costae

throughout growth. During later growth stages, ornamentation is highly variable. This ranges from a regular to an irregular ornament pattern. Specimens with an irregular pattern demonstrate the greatest degree of variation. Commarginal costae and interspaces are variable in width, and interspaces variable in depth. Where interspaces are shallow, the two associated costae appear to be fused. Commarginal costae are frequently intercalated by one or two secondary costellae, which frequently fuse to the previous primary costa, normally over the anterior or posterior area. Foliation of primary costae has not been observed during this study.

Shell form is considerably less variable than ornamentation. There is some variation in the height:length ratio, obliquity of the ventral margin, and curvature of the anterior margin. Due to a narrow range of inflation, and the absence of shells with smooth lower margins, *Trigonopsis morgani* is unlikely to have been sexually dimorphic.

COMPARISONS: *Trigonopsis morgani* may be compared with *T. corallina* (Damon, 1860), from the Oxfordian to Early Kimmeridgian of England (Fig. 17: 2). The New Zealand species is similar in size and outline, with almost identical lunule and escutcheon details, but differs by having a more oblique ventral margin, stronger commarginal costae, narrower umbones, and a weaker posteroumbonal ridge.

Trigonopsis stevensi (Quilty, 1977) from the Heterian (Late Callovian to Early Kimmeridgian) of Ellsworth Land, Antarctica, is one of the largest species in the genus. This character, together with its well-defined growth halts with interspaced finer commarginal ornamentation, wider cardinal area below the beak, stronger more elongate cardinal teeth 2 and 4b, and a longer anterior hinge area, distinguishes it from *Trigonopsis morgani*.

DISTRIBUTION: Middle Heterian (Early Kimmeridgian). *Trigonopsis morgani* is common in Captain King's Shellbed at Ohineruru Bay, Kawhia Harbour, New Zealand. This species has also been recorded from road cuttings in Ohineruru Formation along Whakapirau Road, south of Kawhia Harbour (Meesook & Grant-Mackie 1995).

Trigonopsis anatona n. sp.

Fig. 16

ETYMOLOGY: From the Greek *anatonos*, meaning stretching upward, referring to the dorsal margin of this species.

TYPE MATERIAL: Holotype L4058 (Fig. 16: 1), paratype L4059 (Fig. 16: 2), fine-coarse-grained medium brown tuffaceous sandstone, Ohineruru Formation, Middle Heterian (Early Kimmeridgian), Murihiku Supergroup. Locality R17/f8595 [691936], Palmer Creek, Awakino valley, New Zealand. Collected by J. A. Grant-Mackie, 1956.

Paratype L4060 (Fig. 16: 3), Captain King's Shellbed, Middle Heterian (Early Kimmeridgian), Murihiku Supergroup. Locality R16/f8832 [672190], Paraohanga Steam, Marokopa, New Zealand. Collected by D. MacFarlan, 1973.

DIMENSIONS (in millimetres):

		L	H	I	LA/L	I/L
L4058	(DV)	22.5	24.0	16.8	0.31	0.70
L4059	(LV)	24.0	26.6	17.4	0.34	0.65
L4060	(RV)	13.7	17.0	12.0	0.45	0.71

DIAGNOSIS: Shell large, subtrapezoidal in outline, posterior area strongly inclined, posteroumbonal ridge strongly defined. Lunule

elongate with almost flat-bottomed depression, bordered by well-defined acutely rounded ridge; escutcheon $\frac{3}{4}$ width of lunule. Adductor scars small, anterior with narrow subelliptical outline. Cardinal area wide dorsoventrally below beak with large cardinal tooth 3b. Anterior hinge area and lateral teeth *AIII* and *AIV* short. Apical angle S3: 43°.

DESCRIPTION: Large for genus (largest specimen recorded 24 mm long), subtrapezoidal in outline. Umbonal ridge strongly defined and well projecting, extending from posterior of beak to posteroventral margin. Ridge sharply rounded between flank and posterior area to near posteroventral margin, then becoming increasingly weaker. Posterior area strongly inclined, with inclination decreasing posteroventrally. Beaks rounded, moderately prosogyrate, slightly projecting, positioned low above cardinal area. Umbones broad, high, and erect, steeply incurved. Inflation slightly variable ($I/L = 0.65-0.71$). Anterior, ventral, and posterior margins with moderately strong internal crenulations.

Ornament consisting of well-rounded primary commarginal costae that increase in strength throughout growth, costae and interspaces increasing in width during early stages of growth, but of constant width during later growth stages. Angular interspaces infrequently bearing intercalated secondary costella that fuses to previous primary costa over anterior or posterior area.

Lunule cordate, elongate, moderately broad, with deep almost flat-bottomed depression, bordered by well-rounded projecting crest. Escutcheon lanceolate, moderately elongate with shallow wedge-shaped depression, bordered by weakly projecting rounded crest; escutcheon about $\frac{3}{4}$ width of lunule.

Anterior adductor scar small, with narrow dorsoventrally elongate subelliptical outline, deepening posteriorly and dorsally. Anterior pedal retractor scar very small but well defined, placed posterodorsal of adductor scar below ventral edge of hinge plate. Posterior adductor scar shallow, broadly subovate, about equal in size to anterior adductor scar. Posterior pedal retractor very small but well defined, positioned posterodorsal of adductor scar below ventral edge of hinge plate. Ligament suture not seen.

Hinge plate thick, with cardinal area wide dorsoventrally below beak, ventral edge with moderate anteriorly directed slant; right valve anterior hinge area broad, short, with strong ventral convexity; posterior hinge area of right valve and anterior hinge area of left valve forming a thickening along ventral slope of dorsal margin; left valve posterior hinge area relatively broad, about equal in length to anterior hinge area. Nymph short, narrow, slightly rounded in section.

Dentition with lateral teeth *AIII* and *AIV* thick and short, *AIII* slanting inward near cardinal area to form weak obsolete cardinal tooth 3a; lateral tooth *PIII* elongate and slender; lateral tooth *PIII* short and weakly defined; cardinal tooth 3b very large, stout, and strongly projecting; cardinal tooth 2 moderately strong and elongate, with cardinal tooth 4b much stronger and very elongate, both cardinals separated by deep and wide cardinal 3b socket ($S3 = 43^\circ$).

COMPARISONS: This new species is similar to *Trigonopsis similis* (J. Sowerby, 1819), from the Bajocian-Bathonian of England (Fig. 17: 1), but is distinguished by its larger size, broader subtrapezoidal outline, less oblique ventral margin, and less prominent posteroumbonal ridge. In addition, the lunule is shorter and more depressed, with a more prominently rounded crest. Both species have similar hinge characters, but *T. anatona* has a cardinal tooth 2 which is more elongate, and cardinal tooth 4b is weaker, less elongate, with a less posteriorly directed slant.

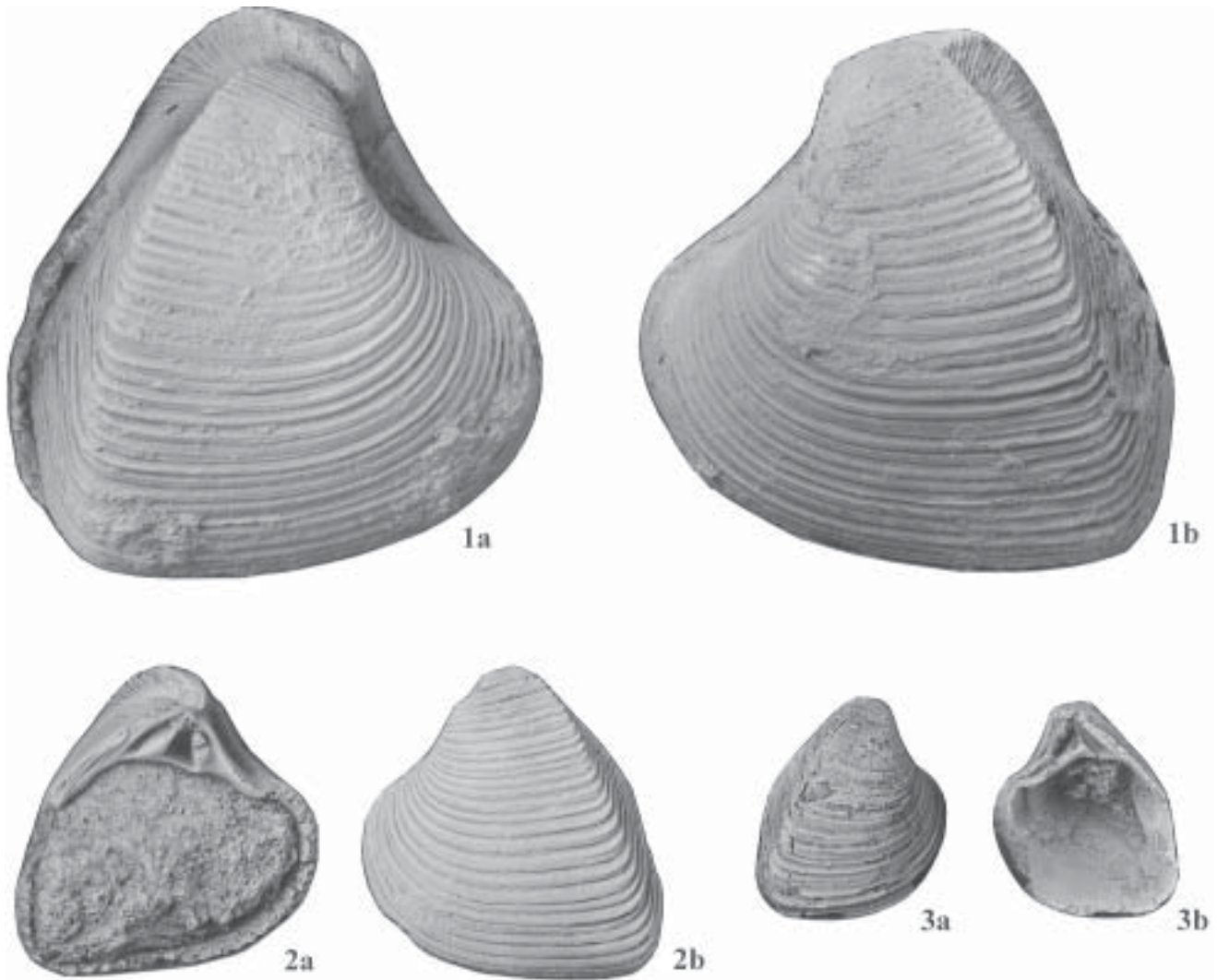


Fig. 16

1, 2, *Trigonopsis anatona* n. sp., Ohineruru Formation, Middle Heterian (Early Kimmeridgian), Palmer Creek, Awakino valley, New Zealand: **1a, b**, holotype L4058, articulated valves, $\times 3.2$; **2a, b**, paratype L4059, interior and exterior of left valve, $\times 1.8$.
3a, b, *Trigonopsis anatona*, Captain King's Shellbed, Middle Heterian, Paraohanga Stream, Marokopa, New Zealand. Paratype L4060, exterior and interior of right valve, $\times 1.9$.

Trigonopsis gibbosus (Wright, 1860) from the Bajocian of England (Fig 17: 4) highlights the large degree of variation in commissural outline between species. Typically it has a subtrapezoidal outline with a ventral margin that is only gently curved and very slightly oblique. These characters together with a more strongly inclined posterior area, and the fact that growth halts appear randomly on the shell surface, distinguish this species from *T. anatona*.

This new species is almost identical in commissural outline and shell form to an undescribed species of *Trigonopsis*, recorded from the Dumortieria zone, Upper Lias, England (Fig 17: 3). Externally, *T. anatona* differs only by having a less oblique ventral margin. The hinge plate was not exposed on any of the specimens examined of the Upper Lias *Trigonopsis* sp.

Trigonopsis anatona differs from its New Zealand congener *T. morgani* by its broader umbones and relatively greater height. The lunule is shorter, broader, and almost flat-bottomed, with a greater depression, and is bordered by a more projecting and more prominently rounded crest. The hinge

plate differs considerably, with the cardinal area being shorter along the ventral edge, and wider below the beak. Cardinal tooth 2 is weaker, and cardinal tooth 4b more elongate than their equivalents in *T. morgani*.

Trigonopsis torinosuensis (Kimura, 1956) from the Kimmeridgian–Tithonian of Japan highlights the considerable differences between Japanese species and those from Europe, Antarctica, and New Zealand. It differs by having strongly prosogyrate and incurved beaks, a longer and considerably broader lunule, and a weaker defined posteroumbonal ridge. This species is suitably placed in the genus *Trigonopsis* because of its short but well-defined anterior hinge area, and functional anterior and posterior lateral teeth.

DISTRIBUTION: Middle Heterian (Early Kimmeridgian). *Trigonopsis anatona* is relatively common in Captain King's Shellbed at Paraohanga Stream, Marokopa, New Zealand. It has also been recorded from beds in Ohineruru Formation at Palmer Creek in the Awakino valley.

**Fig. 17**

- 1a, b**, *Trigonopsis similis* (J. Sowerby, 1819), BM 81187, Ferruginous Oolite, Bajocian, Les Moutiers (Calvados), France, interior and exterior of left valve, $\times 2.0$.
2, *Trigonopsis corallina* (Damon, 1860), BM L70466, "Shell-cum-Pebble Bed", Oxfordian, Headington, Oxfordshire, England, exterior of right valve, $\times 1.5$.
3, *Trigonopsis* sp., BM L84883, ?Upper Lias, Dumortieria zone, garden of "Hollies", Nailsworth, Gloucestershire, England, exterior of right valve, $\times 1.5$.
4, *Trigonopsis gibbosus* (Wright, 1860), BM L6861, Inferior Oolite, Bajocian, Cold Comfort, England, exterior of right valve, $\times 1.5$.

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REFERENCES

- Adams, H.; Adams, A. 1853–58: The genera of recent Mollusca arranged according to their organisation. *1*, 1853–54, 484 p.; *2*, 1854–58, 661 p.; *3*, 1853–58, 138 p. London, John van Voorst.
- Agrawal, S. K. 1956: Sur un nouveau sous-genre et deux espèces nouvelles d'Astarte du Jurassique de Kutch (Inde). *Bulletin Société Géologique de France, Series 6*, 5 (7–9): 433–439.
- Arkell, W. J. 1927: The Corallian rocks of Oxford, Berks, and north Wilts. *Royal Society of London, Philosophical Transactions and Proceedings (B)* 216: 67–181.
- Arkell, W. J. 1929–37: A monograph of British Corallian Lamellibranchiata. Monograph of the Palaeontographical Society of London.
- Arkell, W. J. 1933: The Jurassic System in Great Britain. Oxford, 681 p.
- Bayle, E. 1878: Fossiles principaux des terrains. In: *Explication de la carte géologique de la France 4 (1)*.
- Bigot, A. P. D. 1895: Contributions à l'étude de la faune jurassique de Normandie. Sur les Opis. *Mémoires de la Société Linnéenne de Normandie* 18: 153–191.
- Blake, J. F.; Hudleston, W. H. 1877: The Corallian rocks of England. *Quarterly Journal of the Geological Society of London* 33: 393.
- Boden, K. 1911: Die faunas des unteren Oxford von Popilany in Lithauen. *Geologische und Paläontologische Abhandlungen* 10: 125–200.
- Böhm, G. 1893: *Coelastarte und Heteropis*. *Berichte Naturforschender Gesellschaft zu Freiburg* 7 (2). 174 p.
- Brassier, M.; Geleta, S. 1993: A planktonic marker and Callovian–Oxfordian fragmentation of Gondwana; data from Ogaden Basin, Ethiopia. *Palaeoecology, Palaeoclimatology, Palaeoecology* 104: 177–184.
- Chavan, A. 1945: Les lamellibranches hétérodontes des Sables Astartiens de Cordebugle (Calvados). *Journal de Conchyliologie* 86: 41–86.
- Chavan, A. 1952: Les pélécytopodes des Sables Astartiens de Cordebugle (Calvados). *Schweizerische paläontologische Gesellschaft, Abhandlungen* 69: 1–132.
- Chavan, A. 1969: In: Moore, Raymond C. ed. *Treatise on invertebrate paleontology, part N, vol. 2 (of 3), Mollusca 6, Bivalvia*. Geological Society of America, Inc. and University of Kansas. N562–N573.
- Contejean, C. 1860: Étude de l'étage Kimmeridgien dans les environs de Montbéliard et dans le Jura. *Mémoires de la Société d'Émulation du Doubs* 4. 352 p.

- Cottreau, J. 1925–32: Types du Prodrome de Paléontologie stratigraphique universelle d'Alcide d'Orbigny. 2, Callovian–Portlandien. *Annales de Paléontologie* 14–21: 1–222.
- Cox, L. R. 1930: "On British fossils named by William Smith". *Annals and Magazine of Natural History* 6 (10): 287–304.
- Cox, L. R. 1965: Jurassic Bivalvia and Gastropoda from Tanganyika and Kenya. *Bulletin of the British Museum (Natural History), Geology Supplement 1*: 1–213.
- Cox, L. R. 1969: In: Moore, Raymond C. ed. *Treatise on invertebrate paleontology, part N, vol. 1 (of 3), Mollusca 6, Bivalvia*. Geological Society of America, Inc. and University of Kansas. N1–N129.
- Cox, L. R.; Arkell, W. J. 1948: A survey of the Mollusca of the British Great Oolite Series, primarily a nomenclatorial revision of the monograph by Morris & Lycett (1851–1855), Lycett (1863), and Blake (1905–1907). Monograph of the Palaeontographical Society of London.
- Dall, W. H. 1903: Synopsis of the family Astartidae, with a review of the American species. *Proceedings of the United States Natural History Museum* 26: 933–951.
- Damon, R. 1860: Handbook to the geology of Weymouth and the Isle of Portland. London. 199 p.
- Defrance, M. J. L. 1825: Nucule (fossiles). *Dictionnaire des Sciences naturelles nat.* 35: 216–219.
- Deshayes, G. P. 1830: Histoire naturelle des ver. Tome seconde, "Encyclopédie Méthodique". 256 p.
- Dietrich, W. O. 1933: Zur stratigraphie und paläontologie der Tendaguru-schichten. *Palaeontographica Supplement* 7: 1–42.
- Dollfus, A. 1863: La faune kimmeridienne du Cap de la Hève. Paris.
- Duff, K. L. 1978: Bivalvia from the English Lower Oxford Clay (Middle Jurassic). Monograph of the Palaeontographical Society of London. 137 p.
- Etheridge, R. 1910: Oolitic fossils of the Grenough River district, Western Australia. *Geological Survey Western Australia Bulletin* 36 (3): 29–50.
- Ferussac, A. E. de 1822: Tableaux systematiques des animaux mollusques. Paris and London. 111 p.
- Fischer, P. H. 1886: Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossils. Paris, Librairie F. Savy.
- Gardner, R. N.; Campbell, H. J. 2002: Middle to Late Jurassic bivalves of the subfamily Astartinae from New Zealand and New Caledonia. *New Zealand Journal of Geology and Geophysics* 45: 1–51.
- Goldfuss, G. A. 1826–44: Petrefacta Germaniae. Vol. 2. 1833–40, 1–312.
- Gottsche, C. 1925: Contribuciones a la paleontologia de la República Argentina. Sobre fósiles jurásicas de la Cordillera Argentina (Paso del Espinacito, prov. de San Juan). *Acta Academia Nacional Ciencias Cordoba* 8: 229–296.
- Grant-Mackie, J. A.; Aita, Y.; Balme, B. E.; Campbell, H. J.; Challinor, A. B.; MacFarlan, D. A.; Molnar, R. E.; Stevens, G. R.; Thulborn, R. A. 2000: In: Wright, A. J.; Talent, J.; Young, G. ed. Palaeobiogeography of Australasian faunas and floras. *Australasian Association of Palaeontologists Memoir* 23: 311–353.
- Guppy, R. J. L. 1874: On the West Indian Tertiary fossils. *Geological Magazine* 1 (2): 433–446.
- Hallam, A. 1983: Early and mid-Jurassic molluscan biogeography and the establishment of the central Atlantic seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology* 43: 181–193.
- Holdhaus, K. 1913: Fauna of the Spiti Shales (Lamellibranchiata and Gastropoda). *Memoirs of the Geological Survey of India, Palaeontologia Indica, series 15 (part 4 no. 2)*: 397–456. Calcutta.
- Hudleston, W. H. 1878: *Geological Society of London, Proceedings* 5: 486.
- Jaitly, A. K. 1992: Neocrassinid bivalves (Heterodonta) from the Middle Bathonian (Jurassic) of Kachchh, Western India. *Paläontologische Zeitschrift* 66: 67–79.
- Kanjilal, S.; Pathak, D. B. 1998: Spiti Shale bivalves from Chichim and Gata, Spiti Valley, Himachal Pradesh, India. *Himalayan Geology* 19 (1): 29–37.
- Kimura, T. 1956: Some pelecypods from the Upper Jurassic Torinosu group in Kochi Prefecture, Japan. *Journal of Earth Sciences, Nagoya University* 4 (2).
- Lamarck, J. B. de 1818–19: Histoire naturelles des animaux sans vertébrés: 5, 1818, 612 p.; 6, 1819, 343 p.
- Linnaeus, C. 1758: Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum... Tomus I. Editio decima, reformata. Holmiae, impensis Direct. Laurentii Salvii 1. Stockholm. 824 p.
- Loriol, P. de 1874–75: Description des fossils. In: Loriol, P. de; Pellat, E., Monographie paléontologique et géologique des étages supérieurs de la formation jurassique des environs de Boulogne-sur-Mer. *Société de Physique et d'Histoire Naturelle de Genève, Comptes Rendus, Mémoires* (24): 1–326.
- Loriol, P. de 1896–1901: Étude sur les mollusques et brachiopods de l'Oxfordien supérieur et moyen du Jura bernois. *Schweizerische Paläontologische Gesellschaft, Abhandlungen, Zurich*, 23, 24, 28: 1, 1896, 1–77; 2, 1897, 78–158; suppl. 1, 1901, 1–119.
- Loriol, P. de 1898–99: Étude des mollusques et brachiopods de l'Oxfordien inférieur ou Zone à Ammonites renggeri du Jura bernois. *Société Paléontologique de la Suisse, Mémoires* 25–26: 1, 1898, 1–116; 2, 1899, 117–220.
- Maithani, J. B. P. 1968: Some new species of Jurassic gastropods and lamellibranchs from Habo Dome and their usefulness in correlation. *Geological Survey of India Records* 95 (2): 491–524.
- Marwick, J. 1953: Divisions and faunas of the Hokonui system (Triassic and Jurassic). *New Zealand Geological Survey Paleontological Bulletin* 21. 142 p.
- Meesook, A.; Grant-Mackie, J. A. 1995: Upper Jurassic stratigraphy, south Kawhia region, New Zealand. *New Zealand Journal of Geology and Geophysics* 38: 361–373.
- Moore, C. 1870: Australian Mesozoic geology and palaeontology. *Quarterly Journal of the Geological Society of London* 26: 226–261.
- Morris, J.; Lycett, J. 1851–55: A monograph of the Mollusca from the Great Oolite. Monograph of the Palaeontographical Society of London.
- Munier-Chalmas, E. 1887: In: Fischer, P. H. (1880–87). Manuel de conchyliologie et de paléontologie conchyliologique. Paris. P. 28.
- Neumayr, M. 1884: Zur Morphologie des Bivalvenschlösses. *Bayerische Akademie der Wissenschaften, mathematisch-physikalische Klasse, Abhandlungen, Sitzungsberichte, München*, 88: 385–418.
- Oppel, A. 1863–65: Ueber ostindische fossilreste aus den secundären ablagerungen von Spiti und Gnari-Khorsum in Tibet. *Palaeontologische Mitteilungen aus dem Museum des Königlich-Bayerischen-Staates* 1 (4): 267–322.
- Orbigny, A. d' 1844: Description des mollusques et rayonnés fossiles. Terrains crétacés. *Paléontologie Française* 3, *Lamellibranches*: 1–288.

- Orbigny, A. de 1850: Prodrôme de paléontologie stratigraphique universelle des animaux mollusques et rayonnés. 1, 394 p.; 2, 428 p.
- Phillips, J. 1829: Illustrations of the geology of Yorkshire. xvi +192 p.
- Quenstedt, F. A. 1856–58: Der Jura. Tübingen (Laupp & Siebeck). 842 p.
- Quilty, P. G. 1977: Late Jurassic bivalves from Ellsworth Land, Antarctica; their systematics and paleogeographic implications. *New Zealand Journal of Geology and Geophysics* 20: 1032–1080.
- Roemer, F. A. 1836–39: Die Versteinerungen des Norddeutschen Oolithengebirges. 1, 1836, 218 p.; 2, Nachtrag, 1839, 59 p.
- Rouillier, C.; Vossynski, A. 1847: Études progressives sur la paléontologie des environs de Moscou. *Bulletin Société Impériale des Naturalistes de Moscou* 20: 371–447.
- Salter, J. W.; Blanford, H. F. 1865: Palaeontology of Niti. Calcutta.
- Singh, C. S. P.; Kanjilal, S. 1982: On some astartid bivalves from the Habo Hill in Kutch. *Journal of the Palaeontological Society of India* 27: 49–61.
- Skwarko, S. K. 1974: Jurassic fossils of Western Australia, 1: Bajocian bivalves of the Newmarracarra limestone and the Kajarena sandstone. *Bureau of Mineral Resources of Australia* 150: 1–54.
- Smith, W. 1816: Strata identified by organic fossils, Kimmeridge Clay, North Wiltshire Canal, Oak Tree Clay. Plate, fig. 8.
- Smith, W. 1817: Stratigraphical system of organised fossils with reference to the specimens of the original geological collections in the British Museum. London. 113 p.
- Sowerby, J. 1818: *The Mineral Conchology of Great Britain* 2: 195–239.
- Sowerby, J. 1819: *The Mineral Conchology of Great Britain* 3: 41–98.
- Sowerby, J. de C. 1835: *The Mineral Conchology of Great Britain* 6: 239–250.
- Sowerby, J. de C. 1840: Description of fossils from the Upper Secondary Formation of Cutch collected by C. W. Grant. *Geological Society of London, Transactions* 5 (2): 21–23.
- Stevens, G. R. 1987: The influences of palaeogeography, tectonism and eustasy on faunal development in the Jurassic of New Zealand. Atti del secondo convegno internazionale. Fossili, Evoluzione, Ambiente. Pergola 25–30 ottobre 1987. Estratto: Pp. 441–457.
- Stoliczka, F. 1865: Geological sections across the Himalayan Mountains from Wangto Bridge on the River Sutluj to Sungdo on the Indus with an account of the formations in Spiti accompanied by a revision of all known fossils from that district. *Geological Survey of India Memoirs* 5 (1): 1–154.
- Tamura, M. 1959: Trigoniidae, Ostreidae, Bakevelliidae, Pteriidae, Cardiidae and Astartidae from the Upper Jurassic Sakamoto Formation in central Kyushu, Japan. *Palaeontological Society of Japan, Transactions and Proceedings* 33: 23–32.
- Trechmann, C. T. 1923: The Jurassic rocks of New Zealand, with an appendix on ammonites from New Zealand by L. F. Spath. *Quarterly Journal of the Geological Society of London* 79: 246–312.
- Waagen, W. 1865: Versuch einer allgem. Classification. Weymouth. P. 10.
- Wright, T. 1860: On the subdivisions of the Inferior Oolite in the south of England, compared with the equivalent beds of that formation on the Yorkshire coast. *Quarterly Journal of the Geological Society of London* 16: 1–48.
- Young, G.; Bird, J. 1822: A geological survey of the Yorkshire coast. Whitby. 235 p.
- Zakharov, V. A. 1970: Late Jurassic and Early Cretaceous bivalves of the Siberian north and their ecology. Part 2. Family Astartidae. *Académie Impériale des Sciences U.S.S.R. Siberian branch, Institute of Geology and Geophysics, Transactions* 113: 1–144.
- Zieten, C. H. von 1830–33: Les pétrifications de Wurtemberg. 1, 1830, 1–16; 2, 1831, 17–32; 3, 1832, 33–64; 4, 1833, 65–96.

(Appendix 1 on following page)

APPENDIX 1 Synonymies of Jurassic astartid species referred to in this work.

Neocrassina ovata (Smith, 1817)

- 1816 *Venus* sp.; Smith: pl., fig. 8.
 1817 *Astarte ovata* Smith; p. 44, 51, 105; reference to figure in previous work (1816).
 1822 *Tellina crassa* Young and Bird; p. 227, pl. VIII, fig. 2.
 1829 *Crassina aliena* Phillips; pl. III, fig. 22.
 1839 *Astarte crassitesta* Roemer; p. 39, pl. XIX, fig. 18.
 1850 *Astarte Michaudiana* d'Orbigny; vol. II, p. 50, no. 115 (figured 1932).
 1860 *Astarte patens* Contejean; p. 263, pl. XI, fig. 4.
 1860 *Astarte bruta* Contejean; p. 264, pl. XI, fig. 11, 12.
 1860 *Astarte Thompsonii* Damon; suppl., pl. IV, fig. 3.
 1860 *Astarte modiolaris* var., Damon (*non* Lamarck); pl. IV, fig. 4.
 1863 *Astarte michaudiana* d'Orbigny; Dollfus: p. 61, pl. XI, fig. 20–22.
 1865 *Astarte michaudiana* d'Orbigny; Waagen: p. 10.
 1874 *Astarte michaudiana* d'Orbigny; d' Loriol & Pellat: p. 95, pl. XV, fig. 8.
 1874 *Astarte bruta* Contejean; d' Loriol & Pellat: pl. XV, fig. 9a, 9b.
 1878 *Astarte megalomorpha* Hudleston; vol. V, p. 486.
 1901 *Astarte matheyi* d' Loriol; p. 232, pl. XXVI, fig. 1, 2.
 1911 *Astarte lituanica* Boden; p. 62, pl. VII, fig. 1, 1a, 2.
 1927 *Astarte ovata* Smith; Arkell: vol. CCXVI B, p. 165.
 1930 *Astarte ovata* Smith; Cox: vol. VI, p. 298.
 1930 *Astarte aliena* (Phillips); Cox: vol. VI, p. 298.
 1932 *Astarte michaudiana* d'Orbigny; Cottreau: vol. XX, p. 192, pl. LXV, fig. 19, 20.
 1933 *Astarte ovata* Smith; Arkell: pp. 400 ff.
 1929–37 *Astarte ovata* Smith; Arkell: p. 231, pl. XXXII, fig. 1–12.
 1945 *Astarte* (*Neocrassina*) *ovata* (Smith); Chavan: p. 56, fig. 6, 7.

DISTRIBUTION: Oxfordian–Kimmeridgian of England, and the Kimmeridgian of France.

Neocrassina elegans (J. Sowerby, 1818)

- 1818 *Astarte elegans* J. Sowerby; p. 82, fig. 3.
 1829 *Astarte elegans* J. Sowerby; Phillips: pl. XI, fig. 41.
 1830 *Astarte elegans* J. Sowerby; Zieten: pl. LXI, fig. 4.
 1839 *Astarte elegans* J. Sowerby; Goldfuss: pl. CXXXIV, fig. 12.
 1850 *Astarte elegans* J. Sowerby; d'Orbigny: p. 277, ét. 10, n. 298.
 1855 *Astarte elegans* J. Sowerby; Morris & Lycett: p. 86, pl. XIV, fig. 14.
 1858 *Astarte elegans* J. Sowerby; Quenstedt: p. 763, pl. XC111, fig. 31.
 1899 *Astarte elegans* J. Sowerby; d' Loriol: p. 84.
 1948 *Astarte* (*Neocrassina*) *elegans* (J. Sowerby); Cox & Arkell: (revised explanation of Morris & Lycett bivalves, pl. XIV).

REMARKS: With the exception of rare morphotypes, *Neocrassina elegans* has an outline that ranges from slightly to strongly subquadrate, with slight projection in a posteroventral direction. Specimens examined have a regular ornament pattern throughout growth, and costal density is variable between shells. This species is suitably placed in *Neocrassina* due to its anteriorly placed beaks, its short anterior hinge area, and by having posteroventral elongation.

Neocrassina rotunda (J. de C. Sowerby, 1835) from the Bathonian of England and France is very similar to *N. elegans* in outline, ornamentation, and most hinge plate characters. It differs by its thicker shell, and by having a slightly wider right valve anterior hinge area. Analysis of populations is expected to show that *N. rotunda* is a Bathonian development from *N. elegans*.

DISTRIBUTION: Inferior Oolite, Bajocian, England and France.

Neocrassina sowerbyana (Holdhaus, 1913)

- 1840 *Astarte major* J. de C. Sowerby; pl. 61, fig. 1 and explanation, (*non Astarte elegans major* Zieten).

- 1913 *Astarte sowerbyana* Holdhaus; p. 443, pl. 99, fig. 12, 13, 15; pl. 100, fig. 1.
 1933 *Astarte krenkeli* Dietrich; p. 40, pl. 4, fig. 62, 64, 66.
 1982 *Neocrassina* (*Pruvostiella*) *sowerbyana* (Holdhaus); Singh & Kanjilal: p. 56.
 1998 *Neocrassina* (*Pruvostiella*) *sowerbyana* (Holdhaus); Kanjilal & Pathak: p. 36, pl. 1, fig. 9.

REMARKS: Cox (1965) recorded this species from the Late Oxfordian to Late Kimmeridgian of Tanzania, East Africa. The few available specimens from Tanzania resemble forms from India, but critical hinge plate details are not known.

DISTRIBUTION: This species occurs in the Late Oxfordian–Tithonian of Kachh, and in the Tithonian of Moondan, India. It is also present in the Late Oxfordian to Late Kimmeridgian of Tanzania, East Africa.

Neocrassina unilateralis (J. de C. Sowerby, 1840)

- 1840 *Astarte unilateralis* J. de C. Sowerby; p. 327, pl. 21, fig. 14.
 1863 *Astarte hermanni* Oppel; p. 272.
 1865 *Astarte unilateralis* J. de C. Sowerby; Salter & Blanford: p. 97, pl. 23, fig. 10.
 1865 *Astarte spitiensis* Stoliczka; vol. 5, p. 91, pl. IX, fig. 9.
 1913 *Astarte hermanni* Oppel; Holdhaus: p. 440, pl. 99, fig. 7–11, 14.
 1965 *Astarte unilateralis* J. de C. Sowerby; Cox: suppl. 1, p. 87, pl. 24, fig. 2, 3.
 1968 *Astarte* (*Pruvostiella*) *unilateralis* J. de C. Sowerby; Maithani: p. 513, pl. 32, fig. 6.
 1982 *Neocrassina* (*Pruvostiella*) *unilateralis* (J. de C. Sowerby); Singh & Kanjilal: p. 55, pl. 1, fig. 18, pl. 2, fig. 6.
 1998 *Neocrassina* (*Pruvostiella*) *unilateralis* (J. de C. Sowerby); Kanjilal & Pathak: pl. 1, fig. 8.

REMARKS: Jaitly (1992) placed *Neocrassina unilateralis* and *N. compressa* as synonyms of *Neocrassina ovata*. However, an examination of shells lodged with The Natural History Museum in London demonstrated that *N. unilateralis* and *N. compressa* are distinct species.

Neocrassina compressa differs from *N. unilateralis* by having narrower umbones, the adductor scars are larger, the escutcheon crest is less prominently arched, and the lunule has a flat-bottomed deeper depression; *N. unilateralis* has a shallow depression that is concave anteroposteriorly and in width.

Neocrassina unilateralis differs from *N. ovata* by having consistently broader umbones on equivalent morphotypes, a more prominent arch along the escutcheon crest, and longer and thinner anterior lateral teeth.

DISTRIBUTION: This species has been recorded from the Callovian of Tanzania in East Africa, and the Callovian–Tithonian of India.

Neocrassina compressa (J. de C. Sowerby, 1840)

- 1840 *Astarte compressa* J. de C. Sowerby; vol. V, pl. LXI, fig. 2.
 1968 *Astarte* (*Neocrassina*) *compressa* (J. de C. Sowerby); Maithani: p. 511, pl. 32, fig. 1, 2.

REMARKS: *Neocrassina compressa* differs from *N. ovata* by having strong commarginal costae throughout all stages of growth on similarly inflated forms, and by having a more depressed lunule with a flat-bottomed depression that is bounded by a more prominently rounded crest. Cardinal tooth 3b was observed to be basally narrower, and posterior lateral teeth shorter and thicker. Additionally, *N. compressa* has narrower umbones on equivalent morphotypes, and a more convex posterodorsal margin. In highly to very highly inflated Astartinae, the convexity of the posterodorsal margin is variable between shells (Gardner & Campbell 2002). For slightly to moderately inflated species, such as *N. ovata*, *N. compressa*, and *N. unilateralis*, the convexity of the posterodorsal margin remains fairly constant.

DISTRIBUTION: Oxfordian–Kimmeridgian of India.

Neocrassina recki (Dietrich, 1933)

1933 *Astarte recki* Dietrich; p. 40, pl. 4, fig. 60; pl. 5, fig. 69–71.
1965 *Astarte recki* Dietrich; Cox: suppl. 1, p. 91, pl. 14, fig. 4, 5.

DISTRIBUTION: Late Kimmeridgian, Tanzania, East Africa.

Neocrassina ellsworthensis (Quilty, 1977)

1977 *Astarte elleworthensis* Quilty; p. 1066, fig. 81, 82.

DISTRIBUTION: Heterian (Late Callovian to Early Kimmeridgian), Ellsworth Land, Antarctica.

Neocrassina cliftoni (Moore, 1870)

1870 *Astarte cliftoni* Moore; p. 26, 232, 249, 250, pl. 13, fig. 10.
1910 *Astarte cliftoni* Moore; Etheridge: p. 36–38, pl. 5, fig. 8 (*non*
fig. 5–7; *non* pl. 6, fig. 3).
1974 *Astarte cliftoni* Moore; Skwarko: p. 96, pl. 34, fig. 1–4, 10–
13, 15, 16.

DISTRIBUTION: Newmarracarra Limestone, Bajocian, Western Australia.

Neocrassina tibraddeni (Skwarko, 1974)

1974 *Astarte tibraddeni* Skwarko; p. 96, pl. 34, fig. 14, 17–19.

REMARKS: This species differs from *Neocrassina cliftoni* by its much wider cardinal area below the beak, and by its more prominent arch along the escutcheon crest in early stages of growth.

DISTRIBUTION: Newmarracarra Limestone, Bajocian, Western Australia.

Trigonopsis similis (J. Sowerby, 1819)

1819 *Cardita similis* J. Sowerby; p. 56, fig. 3.
1855 *Opis similis* (J. Sowerby); Morris & Lycett: p. 81, pl. V1, fig. 4, 4a.
1895 *Trigonopsis similis* (J. Sowerby); Bigot: p. 172, pl. IX, fig. 10–14.
1948 *Opis (Trigonopsis) similis* (J. Sowerby); Cox & Arkell: p. 28.

DISTRIBUTION: Bajocian–Bathonian of England, and also from the Bajocian of France.

Trigonopsis corallina (Damon, 1860)

1860 *Opis corallina* Damon; pl. IV, fig. 10.
1877 *Opis corallina* Damon; Blake & Hudleston: vol XXXIII, pp. 267 et seq.
1878 *Opis corallina* Damon; Hudleston: vol. V, p. 487.
1929–37 *Opis (Trigonopsis) corallina* Damon; Arkell: p. 259, pl. XXXIV, fig. 7–9.

DISTRIBUTION: Oxfordian to Early Kimmeridgian, England.

Trigonopsis stevensi (Quilty, 1977)

1977 *Opis (Trigonopsis) stevensi* Quilty; p. 1070, fig. 87–93.

DISTRIBUTION: Heterian (Late Callovian to Early Kimmeridgian), Ellsworth Land, Antarctica.

Trigonopsis torinosuensis (Kimura, 1956)

1956 *Opis (Trigonopsis) torinosuensis* Kimura; p. 87, pl. 1, fig. 10.
1959 *Opis (Trigonopsis) torinosuensis* Kimura; Tamura: p. 113, pl. 12, fig. 11–13.

DISTRIBUTION: Nakanosawa Formation, Kimmeridgian–Tithonian, Japan.