Neocrania n. gen., and a revision of Cretaceous–Recent brachiopod genera in the family Craniidae

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Synopsis

The new generic name *Neocrania*, type species *Patella anomala* Müller 1776, is proposed for the Recent and some Cenozoic inarticulate brachiopod species formerly included in the late Cretaceous genus *Crania* Retzius 1781. The history of the genus *Crania* is discussed, and new diagnoses and brief descriptions are given for *Crania* s.s., *Ancistrocrania*, *Craniscus*, *Isocrania*, *Danocrania*, *Valdiviathyris*, and *Neocrania*, the Cretaceous to Recent genera now contained in the family Craniidae Menke 1828. The new name *Neocrania reevei* is proposed for *Crania suessii* Reeve, non Bosquet, and lectotypes selected for this species and for *Craniscus tripartitus* (Münster).

Introduction

The punctate, calcareous-shelled inarticulate brachiopod genus *Crania*, which was established by Retzius (1781: 72), has undergone few major revisions in the past two centuries in comparison with other brachiopod genera described before 1800. Originally based on a late Cretaceous species from Sweden, *Crania brattensburgensis* Retzius 1781 (= *Anomia craniolaris* Linnaeus 1758), the genus expanded to include dozens of species ranging in age from Ordovician to Recent. Since the publication of Part H of the *Treatise on Invertebrate Paleontology* (Williams *et al.* 1965) most Palaeozoic species have been placed in separate genera, although *Crania* has still been widely used in a general sense for many species of Cretaceous to Recent age.

During a revision of living species included in the genus it became apparent that there were several major points of difference between living forms and the late Cretaceous type species *C. craniolaris*. These differences, which include shell structure, type of attachment, form of growth, and musculature, are sufficient to justify the establishment of a new genus, based on *Patella anomala* Müller, for many Recent and some Tertiary species formerly placed in *Crania*.

Historical survey of the Genus *Crania*

Twenty-three years after Linnaeus had described the first craniacean brachiopod, *Anomia craniolaris*, in the tenth edition of his *Systema Naturae* (1758), Retzius published his description of the new genus *Crania* (1781). He based the genus partly on the 'Brattensburg pennies' described by Stobaeus (1732) from the late Cretaceous of Sweden, with which he was familiar, and partly on a modern species from Philippine waters which he thought might be the same as *Anomia craniolaris*.

A general translation of Retzius' Latin diagnosis of *Crania* is as follows: 'Shell bivalved, subequilateral, subequivalved, orbicular. Hinge edentulous. Lower valve with three scars as pits intruding into the valve, two of which are hemispherical with their bases inserted within the hinge margin: the third situated in the centre is larger and subtriangular and surrounded by the

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elevated margin. Upper valve with two prominent scars placed within the hinge margin, corresponding with the scars of the lower valve. The third scar does not correspond and is deep within the internal convexity situated beneath a pair of small oblique ridges'.

Retzius described two species, *Crania brattensburgensis*, within which he cited *A. craniolaris* Linnaeus, and *C. egnabergensis*, in which he included the non-binomial *Nummulus minor* Stobaeus. The localities for the former were the Recent seas of the Philippines (for the specimen which he had called *C. craniolaris*) and the Isle of Ivö, Balsberg, and Ignaberga, southern Sweden, for the fossil specimens. The chalk pit at Ignaberga was also the type locality for *C. egnabergensis*. Thus in proposing *Crania*, which like Linnaeus' species name *craniolaris* referred to the skull or face-like appearance of the ventral valve interior, Retzius included living as well as his more local late Cretaceous species in his concept of the genus.

In the early nineteenth century, Lamarck (1819) introduced alternative names for some previously described species of *Crania*. These names, which included *C. nummulus* for *Crania craniolaris* (Linnaeus 1758), and *C. striata* for *Crania egnabergensis* Retzius 1781, were followed by a number of later workers including Nilsson (1826), Hoeninghaus (1828), and Münster (*in* Goldfuss 1840), and were the source of a great deal of confusion which was compounded by apparent unawareness of Müller's (1776) name of *Patella anomala* for the common Recent north Atlantic species.

In his comparison of the principal classifications in use at the time, Schmidt (1818) recorded the 'type' of *Crania* as *Anomia craniolaris* as figured by Chemnitz (1785: fig. 687), who was redescribing Linnaeus' specimens. This has been taken, under ICZN Rules (1985: 133), as the valid assignment of the type species. Some of the best and most easily identifiable illustrations of craniacean brachiopods are those of Hoeninghaus (1828), who described thirteen living and fossil species. Some of these plates were used again by Münster (*in* Goldfuss 1840), when he described species of Jurassic to Recent *Crania*.

The first comprehensive account of the various Recent species of *Crania* was that of Reeve (1862), who described with clear illustrations the living species *Crania anomala* (Müller) from the north Atlantic, *C. turbinata* Poli from the Mediterranean, *C. rostrata* Hoeninghaus from west Africa, and a new species from Australia, *C. suessii* Reeve (but see *Neocrania*).

In 1871 Dall discussed *Crania* at length, providing extensive synonymies. He was, however, incorrect in writing (1871: 30) that the Recent specimen from the Philippines discussed by Retzius (1781) was probably the same species as that 'previously described by Müller (1776) under the name of *Patella anomala*', from Scandinavian seas. *Crania anomala* (Müller) is a locally common constituent of north Atlantic benthic faunas and has been studied anatomically and developmentally by, for instance, Blochmann (1892) and Rowell (1960). Dall himself much later described a new species from Philippines waters as *Crania philippinensis* (Dall 1920). Dall (1871) was, however, correct in demonstrating how Recent species names, such as *anomala*, were often confused by late eighteenth and nineteenth century authors with fossil species, mainly from the Cretaceous.

Between 1818 and 1885 numerous species of Cretaceous to Recent age were attributed to the genus *Crania* by many authors including Defrance 1818, Sowerby 1823, Nilsson 1826, 1827, Hoeninghaus 1828, Münster (*in* Goldfuss 1840), Hagenow 1842, d'Orbigny 1847, Davidson 1852, 1856, Bosquet 1854, 1859, and Lundgren 1885.

An early attempt to subdivide the genus *Crania* was made by Dall (1871) when he proposed a new genus *Craniscus* (type species *Crania tripartita* Münster 1840), and a new subgenus *Craniopsis* (= *Ancistrocrania* Dall 1877) (type species *Crania parisiensis* Defrance 1818). Two further subdivisions, designating *Crania egnabergensis* Retzius 1781 as type species of the new genus *Isocrania*, and *Crania tuberculata* Nilsson 1826 as the type of a new subgenus *Danocrania*, were carried out this century by Jaekel (1902) and Rosenkrantz (1964) respectively.

Unlike the subdivisions of most of the other broadly defined 'sack' genera of brachiopods, such as *Rhynchonella* and *Terebratula* which have long since been subdivided into more restricted genera, those separated off from *Crania* do not seem to have been generally accepted. For example, although *Ancistrocrania* and *Isocrania* have been in the literature for well over fifty years, they were not accepted by Carlsson (1958) in his revision of *Crania* from Sweden,

and were recognized only as subgenera by other revisers of this group including Rosenkrantz (1964) and Kruytzer (1969).

Further problems have arisen where a figured type species of one genus has been placed inadvertently in another. For example, Roger (*in* Piveteau 1952), although listing *Isocrania* as a full genus, named an excellent figure of the type species, *I. egnabergensis*, as *Crania* s.s. More recently, Cocks (*in* Murray 1985) figured the type of *Danocrania*, *D. tuberculata*, under the name *Ancistrocrania*.

Systematic descriptions

In this paper revised diagnoses, descriptions and figures of the type species are provided for the Cretaceous to Recent genera now included in the family Craniidae. Species we have inspected, and believe to be well authenticated, are assigned to the appropriate genera and marked in the species lists with an asterisk (*). Other species are assigned on the basis of the literature. All specimens figured are in the collections of the Department of Palaeontology, British Museum (Natural History), unless otherwise stated. Genera are described in chronological order.

Order **CRANIIDINA** Waagen 1885

Superfamily **CRANIACEA** Menke 1828

Family **CRANIIDAE** Menke 1828

DIAGNOSIS. Shell calcareous, punctate, puncta in dorsal valve branching in some Recent genera. Dorsal valve usually conical, ventral valve subconical or convex when free, conforming to shape of attachment surface when fixed.

Genus ***CRANIA*** Retzius (1781: 72)

DIAGNOSIS. Posteriorly-attached, posteriorly-directed muscle pits, with pseudointerarea in *C. antiqua*. No strongly developed dorsal muscle scars.

TYPE SPECIES. *Anomia craniolaris* Linnaeus (1758: 700), by subsequent designation of Schmidt (1818: 71). The lectotype, a ventral valve selected by Brunton & Cocks (*in* Brunton *et al.* 1967), a second ventral valve, and a dorsal valve, are in the collection of the Linnean Society, London, 183 A–C (numbered from Linnaeus, 1758). The type specimens were first figured by Chemnitz (1785: pl. 8, fig. 687a, b).

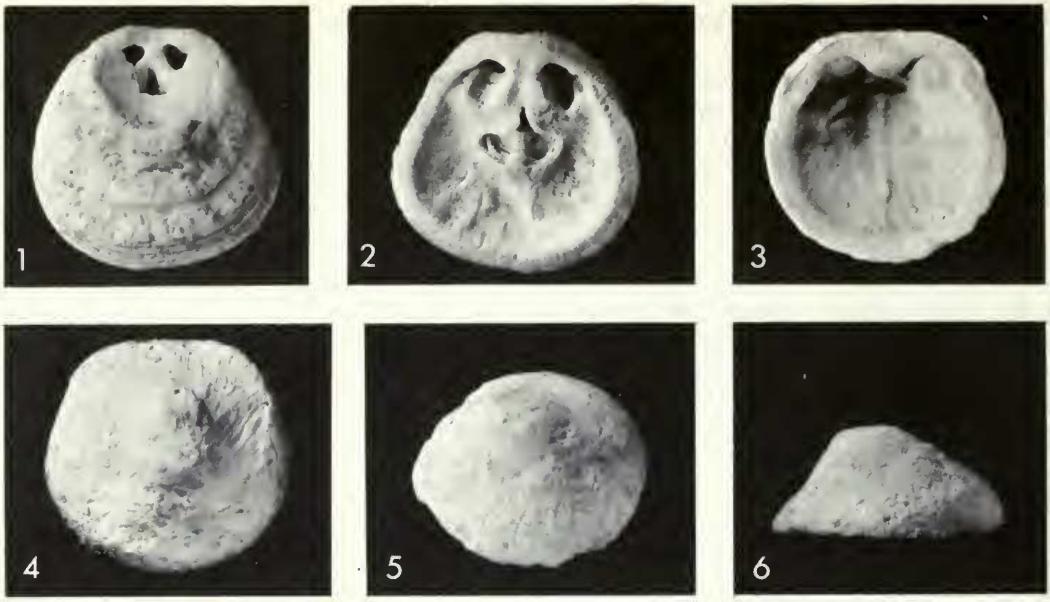
The type locality is Ivö (Ugnsmunnarna), Scania, Sweden. In both 1758 and 1767 Linnaeus described the locality of *A. craniolaris* as Ivö and Balsberg, Scania. There is no indication which locality yielded the three specimens in the Linnaean Collection so it would seem correct to designate the former as the type locality. The locality known to Linnaeus and Retzius as Ivö, 'a cliff section with natural caves' on Ivö Island in Lake Ivö, is now known as Ugnsmunnarna, *sensu* Christensen (1975). The locality now referred to as Ivö Klack was discovered in the latter part of the nineteenth century (W. K. Christensen, personal communication 1985). According to Lundegren (1934) and Christensen (1975) the Ivö localities are all of latest Lower Campanian age.

INCLUDED SPECIES. **Anomia craniolaris* Linnaeus 1758 (= *Crania brattensbergensis* Retzius 1781). Figs 1–6, 40–41.
**Crania antiqua* Defrance 1818. Figs 42–45.

GEOGRAPHICAL RANGE. Sweden, Denmark, France, Netherlands, Belgium, U.S.S.R.

STRATIGRAPHICAL RANGE. Upper Cretaceous, Campanian–Maastrichtian.

DESCRIPTION. Shell of medium size (maximum length 20 mm), subcircular in outline with maximum width towards shell anterior. Ventral valve attached only posteriorly, scar up to $\frac{1}{3}$ shell length. Mixoperipheral growth slight to well-developed, often producing a pseudo-



Figs 1–6 *Crania craniolaris* (Linnaeus). Lectotype and paralectotype from Ivö, Scania, of Lower Campanian age, in the collections of the Linnean Society of London. Specimens are numbered from Linnaeus, 1758. Figs 1, 2, lectotype, 183A, ventral valve exterior and interior respectively. Note medium-sized posterior attachment cicatrix, the perforations of the valve exterior by the posteriorly-directed muscle pits, and the 'face-like' appearance of the valve interior. × 3. See also Fig. 38. Figs 3–6, paralectotype, 183C, respectively interior, exterior, oblique and lateral views of dorsal valve. × 3. See also Figs 40–41.

interarea. Internally planar to concave with deeply incised muscle scars originating posteromedially, often perforating the valve externally (Figs 1, 2). Valve thickened with tuberculate marginal rim.

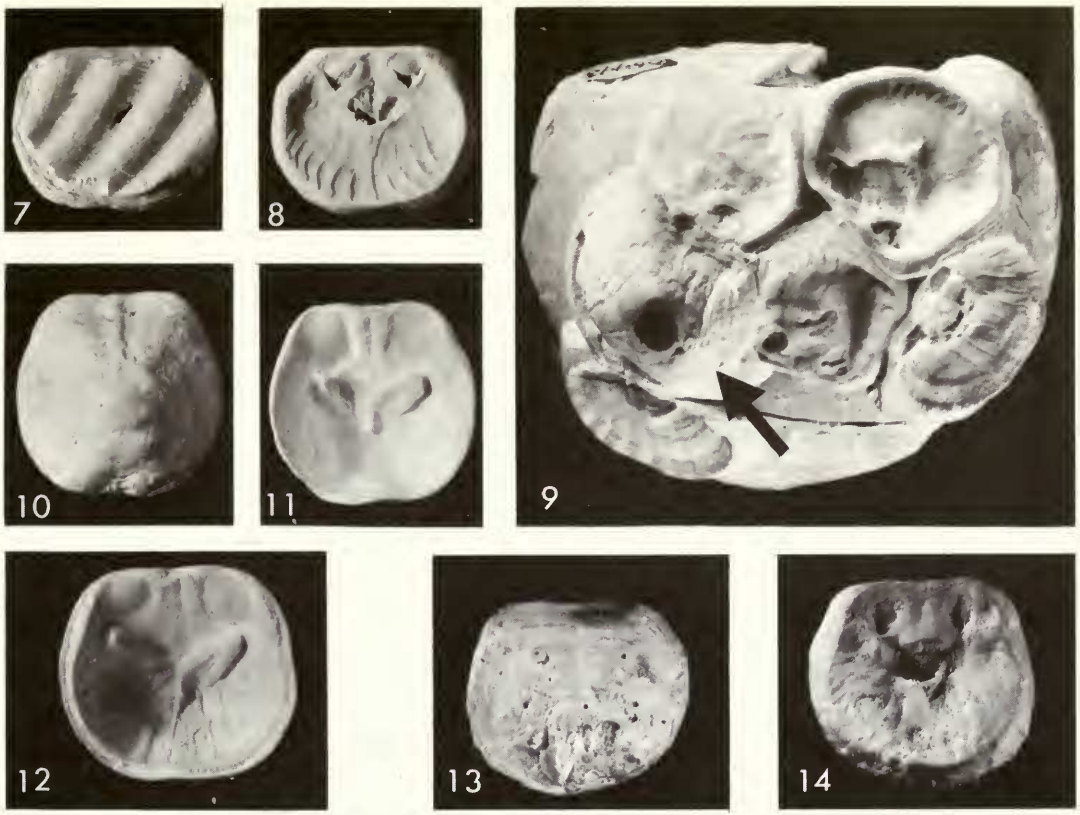
Dorsal valve with almost straight posterior margin and posteriorly directed umbo. Shell exterior smooth or with slightly pustulose ornament. Well-defined posterior muscle scars, in front of which there is a weak median ridge.

Genus *ANCISTROCRANIA* Dall (1877: 13)
(nom. nov. for *Cranopsis* Dall, 1871: 27, non *Cranopsis* Adams 1860)

DIAGNOSIS. Dorsal valve with two raised anterior adductor scars not united medially. Ventral valve attachment scar central to whole surface.

TYPE SPECIES. *Crania parisiensis* Defrance (1818: 313; not figured), by original designation. The type specimens probably no longer exist; according to Cleevely (1983), the Defrance fossil invertebrate collection in the Musée d'Histoire Naturelle, Caen, was destroyed in June, 1944. Kruytzer (1969) noted that the first illustration, which did not however show the diagnostic processes in the dorsal valve, was that of Cuvier & Brongniart (1822). The types were from Chalk of Campanian age at Meudon, near Paris (Diffre & Pomerol 1979).

INCLUDED SPECIES. **Crania parisiensis* Defrance 1818. Figs 7–9, 39.
C. abnormis Defrance 1818
C. nodulosa Hoeninghaus 1828
**C. comosa* Bosquet 1854
C. bredai Bosquet 1854
**C. davidsoni* Davidson 1856. Figs 10–14, 46–47.
C. mulleri Bosquet 1859



Figs 7–9 *Ancistrocrania parisiensis* (Defrance). Topotypes from the Campanian chalk of Meudon, France. Figs 7, 8, exterior and interior views of a ventral valve attached in life to an inoceramid shell. B53203, × 1. See also Fig. 39. Fig. 9, six specimens attached to an echinoid; note the nearly complete dorsal valve in life position on the arrowed individual. B5993, × 1·5 (figured by Davidson 1853: pl. 1, fig. 7).

Figs 10–14 *Ancistrocrania davidsoni* (Davidson). Figs 10–11, exterior and interior views of dorsal valve showing diagnostic raised processes on anterior muscle scars. Maastrichtian chalk, Ciply, Belgium. BD3354, × 1·5. Fig. 12, interior of second dorsal valve from Ciply. BD3355, × 1·5. Figs 13–14, exterior and interior views of an anteriorly attached ventral valve from Vetschau, near Aix-la-Chapelle, of Campanian age. Note the anteriorly-directed muscle pits. Davidson Collection. B5990, × 1. See also Figs 46–47.

**C. suessi* Bosquet 1859
C. quadrangularis Lundgren 1885
C. retzii Lundgren 1885
?*C. bromelli* Lundgren 1885
?*C. stobaei* Lundgren 1885
Craniscus hesperius Cooper 1955

GEOGRAPHICAL RANGE. France, Belgium, Netherlands, Sweden, England, North America.

STRATIGRAPHICAL RANGE. Upper Cretaceous, Senonian–Maastrichtian, (?Danian).

DESCRIPTION. Ventral valve medium- to large-sized with central to anterocentral initial attachment area and scar of variable size. Planar to concave or conical internally with much thickened shell. Muscle scars, especially anterior ones, deeply sunken in pits originating anteriorly. Slightly pustulose crest to submarginal rim, with smooth outward facing surfaces.

Dorsal valve relatively thin-shelled. Umbo slightly posterior of central with low ridge to mid-posterior margin. Internally with large posterior muscle scars. V-shaped ridges, bearing anterior adductor scars, widen posteriorly to form short, slender processes near posterior scars; a small median ridge extends anteriorly from their apex. Shell exterior smooth or with pustulose ornament.

Remarks. Davidson (1856) figured a new species of *Crania* using a manuscript name of Bosquet three years before the latter's publication appeared, and thus inadvertently became the author of a species named after himself.

Genus ***CRANISCUS*** Dall (1871: 27)

Diagnosis. Dorsal valve with three ridges joined medially.

Type species. *Crania tripartita* Münster (1840: 297), by original designation. The dorsal valve figured by Münster is here selected as **lectotype** (Figs 15, 16); it is housed in the Bavarian State Museum, Munich, number AS VII 171. (There are three paralectotypes). The lectotype was newly figured by Rowell (*in* Williams *et al.*, 1965: fig. 181.3a–c). It is from coral limestone of Jurassic (Lower Oxfordian) age (pebbles in a stream), near Thurnau, northern Bavaria, Germany (Barczyk 1968).

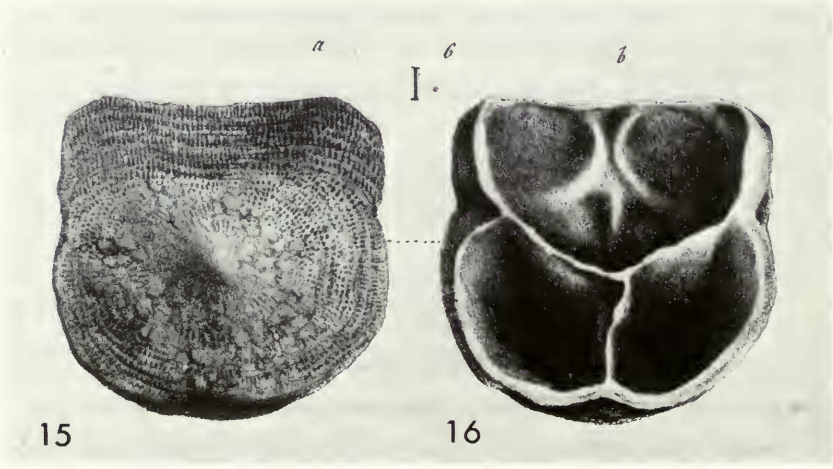
Included species. **Crania tripartita* Münster 1840. Figs 15–16.
**C. suevica* Quenstedt 1857
**C. japonica* Adams 1863. Figs 17–18.
C. quadrangularis Tate 1893 (*non* Lundgren 1885)
= *Ancistrocrania skeatsi* Allan 1940

Several other species from the Jurassic were placed in *Craniscus* by Rollier (1915–16) and Barczyk (1968). Nekvasilova (1982) has recently assigned a new species from the Lower Cretaceous of Czechoslovakia to this genus.

Geographical range. Europe, Australia, Japan, Indo-Pacific seas.

Stratigraphical range. Upper Jurassic–Recent.

Description. Small to medium-sized shell; ventral valve attached by entire surface. Dorsal valve relatively thin-shelled, weakly to strongly convex, margins of valves not thickened. Anterior adductor muscle scars variable, raised on ridges or platforms; united with a raised median myophore or short ridge which partially divides valves into three sections.



Figs 15–16 *Craniscus tripartitus* (Münster). Copy of the original illustration of the **lectotype** (herein selected) of the species, after Münster (*in* Goldfuss 1840: pl. CLXII, fig. 6a, b). The lectotype is a poorly preserved silicified specimen in the Bavarian State Museum, Munich, number AS VII 171. Note that its length is about 4·7 mm, and that most of the anterolateral margin of the shell appears to be broken or worn away.

Figs 17–18 *Craniscus japonicus* (Adams). Exterior and interior views of a dorsal valve of a small Recent specimen from Japan. Cuming Collection. ZB132, × 5.

Remarks. In describing the new genus *Craniscus*, Dall (1871) noted that 'the differences between the genera *Crania* and *Craniscus* are fully as great as any existing between the acknowledged genera of the Terebratulidae'. His original diagnosis of *Craniscus* wrongly stated that it was the 'fixed' or ventral valve which was divided into three parts, but he subsequently corrected this (Dall 1877, 1920). In fact, although the type specimen displays three chambers in the dorsal valve interior separated by three vertical wall-like septa (Figs 15–16), few other specimens attributed to *Craniscus* show this feature. It is worth noting that the type locality is a streambed, and we suspect that the valve margins of the lectotype are broken or worn away. If so, then the dorsal valve ridges do not normally reach the valve margins. This is certainly true for specimens of the closely related *Craniscus suevica* of late Oxfordian age in the collections of the British Museum (Natural History).

Genus ***ISOCRANIA*** Jaekel (1902: 1062)

Diagnosis. Strong radial ribbing on both valves, biconvex, small to no attachment scar.

Type species. *Crania egnabergensis* Retzius (1781: 75), by subsequent designation of Schuchert & LeVene (1929: 69). The type specimens are unknown (Surlyk 1973), but the locality is given as Ignaberga, Scania, southern Sweden. The age is Lower Campanian (Christensen 1975).

Included species. **Crania egnabergensis* Retzius 1781. Figs 19–22.
**C. costata* Sowerby 1823
C. barbata Hagenow 1842
**C. paucicostata* Bosquet 1859
**Isocrania faxensis* Nielsen 1911
I. posselti Rosenkrantz 1920

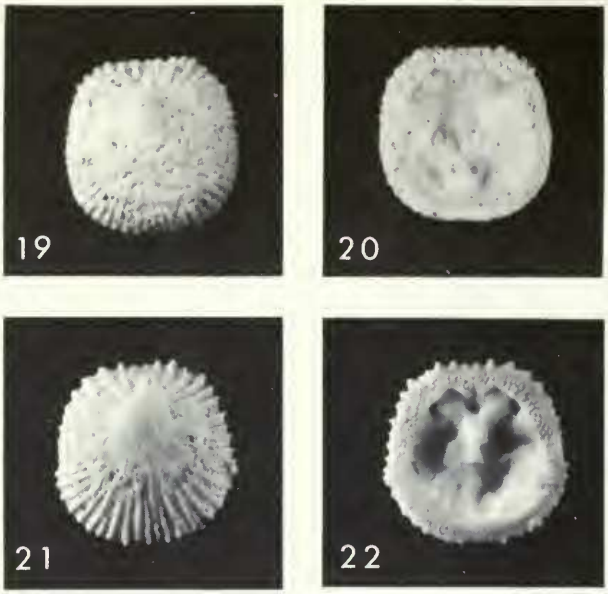
Geographical range. Sweden, Denmark, Netherlands, England, Africa, Asia.

Stratigraphical range. Upper Cretaceous–Lower Tertiary, Campanian–Danian.

Description. Small, biconvex shell with little or no ventral valve attachment, strongly costellate with additions by intercalation. Marginal rims flattened and papillose in both valves.

Ventral valve interior rounded with slightly raised posterior muscle scars. Anterior scars small, separated by a prominent short median ridge (nose).

Dorsal valve interior with slightly raised posterior scars and two pairs of anterior scars; one widely separated median pair and the other smaller pair set close together anteriorly.



Figs 19–22 *Isocrania egnabergensis* (Retzius). Both specimens are from Oretorp, 1 km south-east of Ignaberga, Sweden, of Campanian age. Figs 19–20, exterior and interior views of a dorsal valve. Note the extreme anterior position of the anterior muscle scars. BD3373, × 3. Figs 21–22, exterior and interior views of a ventral valve. BD3372, × 3.

Genus ***VALDIVIATHYRIS*** Helmcke (1940: 237 (23))

TYPE SPECIES. *Valdiviathyris quenstedti* Helmcke (1940), by original designation. Known by a single dorsal valve, specimen No. 198, Humboldt University, Berlin (Rowell 1962: 542). From Station 165, Deutschen Tiefsee Expedition 1899, near St Paul I., south Indian Ocean, in 672 m. Recent.

REMARKS. Rowell (1962) re-examined the single valve known for this genus, and concluded that it was a juvenile (length 2·5 mm, width 4·7 mm), and possibly related to *Ancistrocrania*. Until further specimens are found, the relationship of this species to other craniids is not determinable.

Genus ***DANOCRANIA*** Rosenkrantz (1964: 515)

SYNONYM. *Westalicrania* Cockbain (1967: 75; type species *W. allani* Cockbain, by original designation.

DIAGNOSIS. Exterior pustulose to spinose, ventral valve interior commonly tuberculate and muscle scars in shallow pits.

TYPE SPECIES. *Crania tuberculata* Nilsson (1826, emended 1827) (= *Craniolites brattenburgicus* Schlotheim 1820), by original designation. Nilsson's type material in Lund University Geological Institute cannot now be found (K. Lindholm, personal communication 1985). From Scania, southern Sweden; of Danian age.

INCLUDED SPECIES. **Crania tuberculata* Nilsson 1826 (emended 1827). Figs 23–28.
**C. spinulosa* Nilsson 1827. Figs 29–31.
**C. hagenowi* Davidson 1852
C. kressenbergensis Gümbel 1861
C. austriaca Traub 1938
C. geulhemensis Kruytzer & Meijer 1958
Danocrania polonica Rosenkrantz 1964
Westalicrania allani Cockbain 1967

Figs 23–25 *Danocrania tuberculata* (Nilsson). All specimens are from the Danian Saltholm Limestone, South Harbour, Copenhagen, presented by Dr A. Rosenkrantz. Fig. 23, finely spinose dorsal valve exterior. B80856, × 3. Fig. 24, slightly damaged ventral valve exterior. B80850, × 3. Fig. 25, highly tuberculate ventral valve interior. B80858, × 3. See also Figs 26–28.

GEOGRAPHICAL RANGE. Sweden, Denmark, Belgium, Netherlands, Austria, Ukraine, Crimea, Australia.

STRATIGRAPHICAL RANGE. Upper Cretaceous–Paleocene, Maastrichtian–Danian, (?Thanetian).

DESCRIPTION. Shell small to large, mostly thin-shelled. Shell exterior, especially on dorsal valve, pustulose to spinose with quincuncial/radial arrangement.

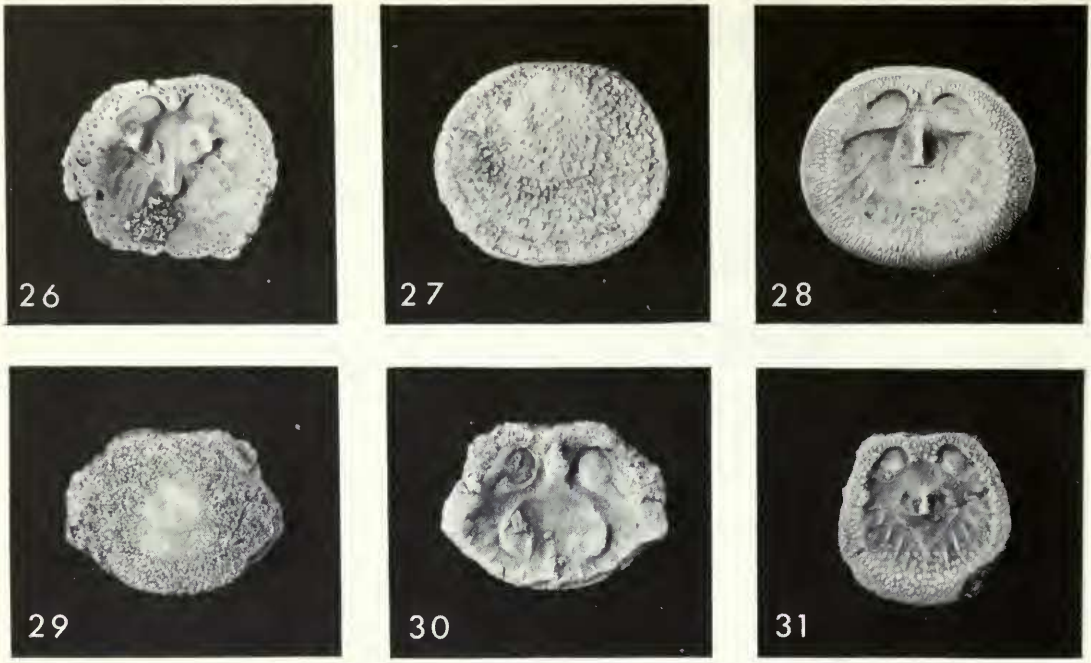
Ventral valve with small, posteriorly positioned attachment scars. May develop small pseudointerarea. Internally, a strongly tuberculate rim may form an extension between the well-defined posterior muscle scars, which may be raised. Anterior scars separated by a prominent short median ridge ('nose') with the rest of the 'face' being tuberculate to radially ridged.

Dorsal valve interior with flattened articulatory ridge between the posterior muscle scars. Anterior muscle scars broad, widely separated but converging anteriorly. Weak anteromedian ridge and slight radial ridging within the marginal rim.

REMARKS. In 1820 Schlotheim figured, poorly and without description, a new 'genus' and species of brachiopod, *Craniolites brattenburgicus*, from a limestone (possibly also a reworked limestone) at Copenhagen. He noted that it differed from other species found in Denmark and contrasted it with *Crania craniolaris* from southern Sweden. Several years later, Nilsson (1826, emended 1827) described a number of new brachiopod species, including *Crania tuberculata* from Scania. From the time of the first revision of Schlotheim's specimens by Hoeninghaus (1828), the name *Craniolites brattenburgicus* was discarded in favour of Nilsson's *Crania tuberculata*. Lundgren (1885) suggested that *brattenburgicus* was a misspelling of *brattensburgensis* Retzius, a synonym of *C. craniolaris*. For more than 130 years *C. tuberculata* was in general use both as a species name and as the namebearer for the *Crania tuberculata* Zone (e.g. Różkowska 1955; Kongiel 1958).

In 1958 Carlsson, following a brief mention by Wind (1953), exhumed the name *C. brattenburgicus*, and his usage was followed by Kruytzer & Meijer (1958). In 1964 Rosenkrantz argued that Schlotheim's name should be discarded and that *C. tuberculata*, which he designated as the type species of a new subgenus (now a full genus) *Danocrania*, should replace it. We follow Rosenkrantz (1964) and Kruytzer (1969) in urging that Schlotheim's name should be discarded because he provided no species description and only a poor illustration, the species name was very similar to *C. brattensburgensis* Retzius (= *C. craniolaris* Linnaeus), the name had been out of general use for over a century, and its synonym *C. tuberculata* Nilsson is well understood and has been widely used as an informal zone name. An application for the suppression of Schlotheim's species name has been lodged with the ICZN.

In 1826 Nilsson described and figured four 'new' species of *Crania*, all of which, save *C. tuberculata*, were synonyms of previously described species. The following year he added to this list further species including *C. spinulosa* which he separated off from a redefined *C. tuberculata*.



Figs 26–28 *Danocrania tuberculata* (Nilsson). Specimens of Danian age from Faxe, Denmark. Fig. 26, interior of incomplete dorsal valve. BD3367, × 3. Figs 27–28, spinose ventral valve exterior and tuberculate valve interior. BD3366, × 3. See also Figs 23–25.

Figs 29–31 *Danocrania spinulosa* (Nilsson). Both specimens of Maastrichtian age from Inkerman, Crimea, U.S.S.R. Figs 29–30, exterior and interior of incomplete dorsal valve. BD3369, × 3. Fig. 31, ventral valve interior. BD3368, × 3.

In 1964, Rosenkrantz placed most spinose *Crania* in *Danocrania*, including all records of *C. spinulosa* save the original of Nilsson (1827). Since Nilsson's specimens are unavailable, and his figures closely resemble other *Danocrania* species, we have included *C. spinulosa* in this genus.

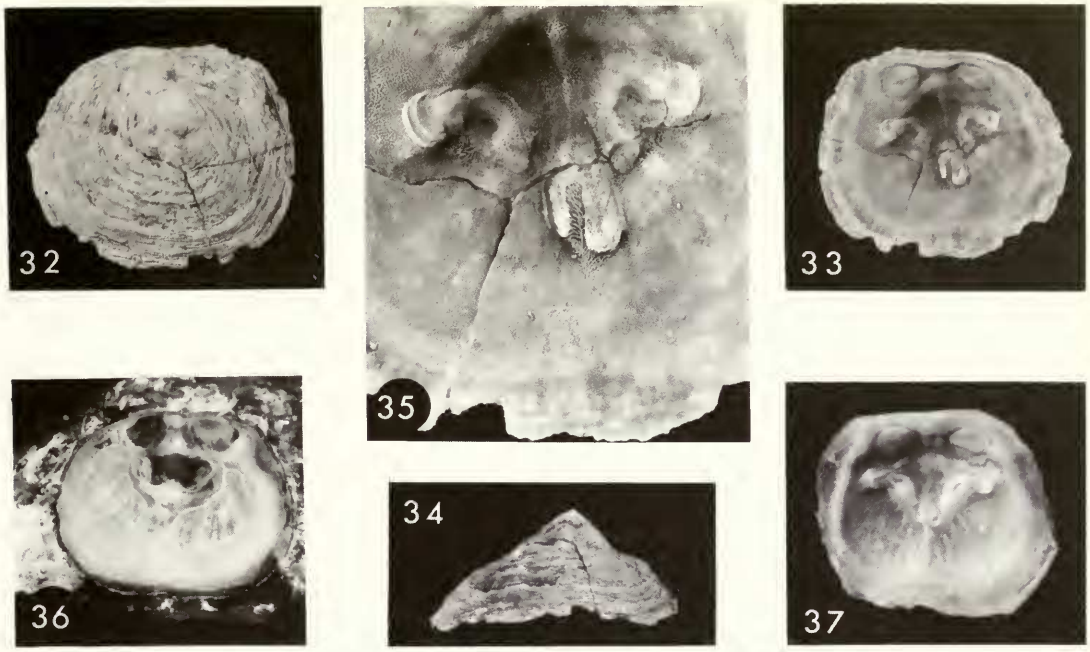
The new generic name *Westalicrania*, proposed by Cockbain (1967) for specimens closely resembling *Danocrania*, is here included in this genus.

Genus ***NEOCRANIA*** nov.

DIAGNOSIS. Ventral valve entirely cemented to substrate, often uncalcified, dorsal valve margins not thickened, with slightly raised muscle scars.

TYPE SPECIES. *Patella anomala* Müller (1776: 237; 1788: 4, pl. 5). Müller's original specimens are lost, but the species as it occurs in the North Atlantic is well known and undisputed. The title of Müller's monograph indicates that it occurs in the seas around Denmark or Norway, although he did not specify a locality for the species. We therefore do not select a neotype, in accordance with the recommendations of the ICZN (1985: 157–159; Article 75), but instead figure a specimen from off the Danish coast near where Müller's specimens may have been collected (Figs 32–36). Recent.

GENERIC NAME. There are extensive and confusing synonymies for the genus *Crania* (see for instance Dall 1871 and Williams *et al.* 1965). Two of the oldest available generic names are *Criopus* and *Criopoderma* of Poli 1791 and 1795 respectively. Following much of the contemporary practice of his day Poli used these two names for the soft parts and hard parts (the valves) of several brachiopods, with the result that inarticulates and articulates were united by him within these 'genera'. In modern taxonomy this is clearly unacceptable, and since the names



Figs 32–37 *Neocrania anomala* (Müller). Figs 32–36 are from 'Knähaken', south of Helsingborg, Øresund, Denmark, collected by the Elsinore Marine Laboratory, ZB3955a, b. Fig. 32, smooth dorsal valve exterior ornamented only by concentric growth-lines. × 2. Fig. 34, conical dorsal valve seen in lateral view. × 2. Figs 33, 35, dorsal valve interior showing details of anterior adductor muscle scars, and asymmetrical brachial protractor scar. × 2, × 5. Fig. 36, interior view of ventral valve with tissue still present, including posterior muscle fibres and mantle including gonadal ducts. × 2. Fig. 37, dorsal valve interior showing impressions of mantle canals. Cuming Collection, from the block figured by Reeve (1862: pl. 1, fig. 4). ZB134/23, × 2. North Atlantic. See also Figs 48–49.

have not been used (indeed Dall, 1871, did not accept them) other than as synonyms we are applying to the ICZN for their suppression.

Another old generic name, about which there has been considerable confusion, is *Orbicula* Cuvier 1798. The first description was very general in nature, but he mentioned *Patella anomala* Müller within the genus, so it became the type species. Illustrations were not provided until the third edition of Cuvier's *Règne Animal* (1845), at which time other species were added to *Orbicula* and the named species *O. lamellosa* (Broderip) was figured. That species is now the type of *Discinisca* Dall 1871, a chitinophosphatic-shelled impunctate discinid. *P. anomala* is a calcareous-shelled endopunctate craniid. Confusion as to whether *Orbicula* was a craniid or a discinid heightened when specimens sent by J. Sowerby to Lamarck were described (1819) as *Discina ostreoides*, and other examples from the same collection were described by G. B. Sowerby (in 1818, but not published until 1822) as *Orbicula norvegica*; all these specimens are discinids. Since then almost åll nineteenth century authors treated *Orbicula* as a discinid; Sherborne (1932) listed 68 species names of *Orbicula* published between 1800 and 1850, of which only four should be craniids. From 1902 the *Zoological Record* notes only one non-synonymy use of the name *Orbicula*, which has thus essentially been unused taxonomically for over a century. Eminent specialists such as Davidson (1853) and Dall (1871) have recommended against the use of *Orbicula*, while recognizing that its original link with *P. anomala* placed it as a junior synonym of *Crania*. Davidson (1853) went on to recommend the suppression of *Orbicula*.

Thus in wishing to create a new genus based on *P. anomala* Müller, we are faced either with the need to reintroduce one of the above old named 'genera', a procedure which would create much confusion among zoologists and palaeontologists, or suppress these old names and start with a clean sheet using *Neocrania* gen. nov. We choose the latter course, and in addition to our application for the suppression of *Criopus* and *Criopoderma* we have applied to the ICZN for the suppression also of *Orbicula* Cuvier and for its inclusion on the Official Index of Rejected and Invalid Generic Names in Zoology.

INCLUDED SPECIES. **Patella anomala* Müller 1776. Figs 32–37, 48–49.
**Anomia turbinata* Poli 1795
Crania rostrata Hoeninghaus 1828
C. pourtalesi Dall 1871
C. nysti Davidson 1874
C. lecointei Joubin 1901
**C. huttoni* Thomson 1916
C. philippinensis Dall 1920
C. hawaiiensis Dall 1920
C. californica Berry 1921
**C. chathamensis* Allan 1940
C. valdiviae Helmcke 1940
C. roseoradiata Jackson 1952
C. indonesiensis Zezina 1981
**Neocrania reevei* nom. nov., pro *Crania suessii* Reeve 1862, non Bosquet 1859.

GEOGRAPHICAL RANGE. Cosmopolitan.

STRATIGRAPHICAL RANGE. Eocene–Recent.

DESCRIPTION. Shell of medium size (maximum length recorded 24 mm), subcircular to quadrangular in outline.

Ventral valve cemented to substrate by entire surface; valve varying from thin, uncalcified organic film to wholly calcified and thickened with anterolateral marginal rim. Valve interior with sometimes sunken posterior muscle scars with anterior scars united medially.

Dorsal valve smooth, slightly pustulose or finely ribbed, umbo centrally to posteriorly placed. Valve interior with large, widely separated pad-like posterior muscle scars and smaller diverging V-shaped anterior scars. Weak posterior submarginal rim, internal surfaces strongly endopunctate.

REMARKS. Although numerous names were applied to 'species' of living *Crania* between 1776 and 1862, most can be regarded as variants of *Neocrania anomala* (Müller) (Brunton & Curry 1979) or *N. turbinata* (Poli) (Logan 1979). Reeve (1862), in an important survey of living craniids, discussed the then known species and their distribution, and described a new species from Australia as *C. suessii*, a name which was unfortunately preoccupied by *C. suessi* of Bosquet (1859). We here propose the new name *Neocrania reevei* for the specimens from the Cuming collection (ZB 1520–1522) in the British Museum (Natural History) figured by Reeve (1862: pl. 1, fig. 2) and select ZB 1520 as the **lectotype**.

After the work of Dall (1871) no further comparisons between living and fossil craniid species of Cretaceous age were carried out until the present work, which follows a study of Recent and Tertiary *Neocrania* from New Zealand (Lee, in press).

Stratigraphical and geographical distribution

Although Rowell *in* Williams *et al.* (1965) gave a doubtful Carboniferous age for the oldest record of *Crania*, Williams & Wright (1970), following Rosenkrantz (1964), considered that '*Crania* s.s. is not reliably recorded in rocks older than the Cretaceous'. With the establishment

of the new genus *Neocrania* for Tertiary to Recent species formerly included in *Crania*, the stratigraphic range of *Crania* s.s. is reduced to the Upper Cretaceous (Senonian to Maastrichtian) in northwestern Europe and possibly the U.S.S.R. (Sobetskiĭ *et al.* 1982).

The oldest verified records of *Ancistrocrania*, *Isocrania* and *Danocrania* are also of Upper Cretaceous age, although Williams & Wright (1970) mentioned that '*Isocrania* . . . , like *Ancistrocrania* and *Craniscus*, is known from the Jurassic'. *Ancistrocrania* as presently defined may not extend into the Tertiary (Kruytzer 1969), but *Isocrania* and *Danocrania* continue up into the Danian and ?Thanetian respectively (Rosenkrantz 1964). It is worth noting that while the genera continue across the Cretaceous–Tertiary boundary, individual species disappear at the close of the Cretaceous (Surlyk & Johansen 1984). *Isocrania* is found as far afield as Africa and Asia, and *Danocrania* as Australia, though both are best known from the Chalk of Europe.

Ancistrocrania is recorded principally from Europe with one North American species. *Craniscus* ranges from the Jurassic through to the Recent, and appears to have had a wide distribution, although species records are poorly documented. As mentioned elsewhere in this paper, the differences between *Ancistrocrania* and *Craniscus* are small, and the somewhat puzzling dearth of Late Cretaceous records of *Craniscus* may be explained if some of the numerous species now assigned to *Ancistrocrania* should more correctly be placed in the former genus.

Neocrania appears to have had a cosmopolitan distribution from the Eocene to the present day.

Shell structure and form of growth

The shell structure of craniids has excited interest for well over a century and was studied by, for example, Carpenter (*in* Davidson 1853) and Blochmann (1892) and more recently, in great detail using the electron microscope, by Williams & Wright (1970). The early interest was aroused by the unusual endopunctation in living species, in which the distal ends of the puncta are branched. Williams & Wright (1970) illustrated the shell microstructure of *Neocrania anomala*, which they used to characterize the genus *Crania*; Mesozoic species of *Crania* s.s. were not knowingly studied. They also illustrated examples of *Isocrania egnabergensis* from Ignaberga; *Ancistrocrania parisiensis* from Ciply, Belgium; and '*Danocrania*' sp. from Ciply (we do not recognize the genus at this locality, and the specimen involved is, we believe, a *Crania antiqua*). These authors also discussed *Craniscus*, based on the living *C. japonicus* (Adams), as well as representative species from older Palaeozoic genera. Thus in terms of this paper Williams & Wright (1970) studied *Neocrania anomala*, *Isocrania egnabergensis*, *Crania antiqua*,

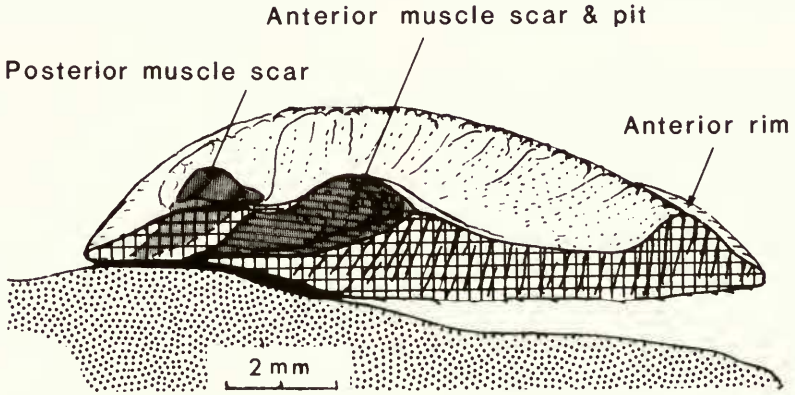


Fig. 38 *Crania craniolaris* (Linnaeus). Diagram of a ventral valve seen in median sagittal section, showing the anterior growth of the muscle scars, leaving pits behind them within the shell. (The posterior scars are not crossed by the median section.) An impression of the endopuncta is given on the sectioned and internal surfaces of the valve. See also Fig. 2.

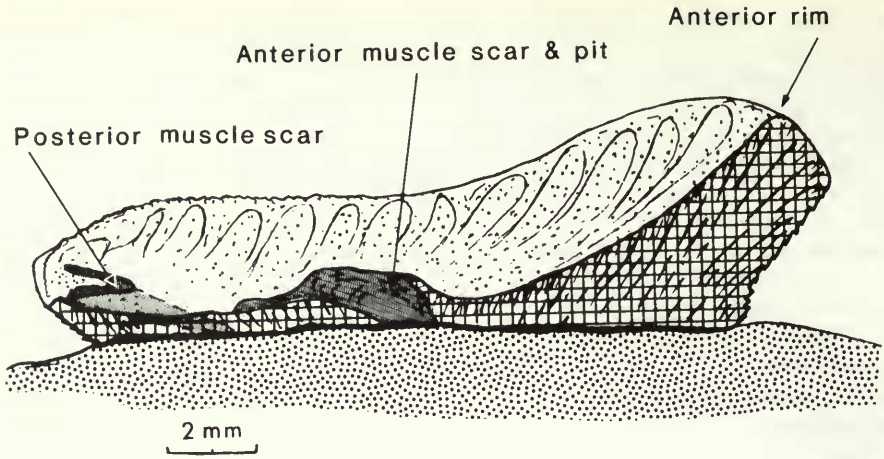


Fig. 39 *Ancistrocrania parisiensis* (Defrance). Diagram of a ventral valve seen in median sagittal section, showing the posterior growth of the muscle scars, leaving pits within the shell. An impression of the endopuncta is given on the sectioned and internal surfaces of the valve. See also Fig. 8.

Ancistrocrania parisiensis and *Craniscus japonicus*, which we retain in that genus with some hesitation in view of the uncertainty surrounding the characteristics of *Craniscus tripartitus*—the type species—and its relationship with *Ancistrocrania.*

Using scanning electron microscopy we have studied examples of *N. anomala* from the Oban area of western Scotland; *C. craniolaris* from the type area of southern Sweden; *C. antiqua* from Ciply, Belgium; *A. parisiensis* from Ciply; and *D. tuberculata* from Faxe, Denmark. In general the attached ventral valves display more shell variation than dorsal valves, as noted by Williams & Wright (1970). This variation is principally linked with the degree of shell thickening in the ventral valve and involves the development of what the above authors termed 'canals'. These are tubular cavities (approximately 0·05 mm in diameter) with apertures up to twice that width on some interiors, and thus are several times wider than normal endopuncta. They are aligned obliquely to most external surfaces and extend inwards, roughly radially and anteriorly, so that their inner ends are more or less perpendicular to growth or internal surfaces. Such 'canals' are present in *Ancistrocrania parisiensis*, *A. davidsoni* (Davidson) and *Crania antiqua*;

Figs 40 to 45 are scanning electron micrographs taken in the Electron Microscope Unit of the British Museum (Natural History). Figs 40 and 41 are of uncoated specimens, taken using the environmental chamber, while the remainder are of specimens coated with gold-palladium.

Figs 40, 41 *Crania craniolaris* (Linnaeus). External views of the paralectotype 183B, of early Campanian age, Linnean Society Collection. Fig. 40, exterior of the complete ventral valve showing the posterior attachment scar (cicatrix) with concentric growth-lines anteriorly. × 8. Fig. 41, immediately anterolateral to the cicatrix (top right corner) showing secondarily enlarged crystals of the secondary layer. × 66. See also Figs 1–6.

Figs 42–45 *Crania antiqua* (Defrance). Ventral valves from Ciply, Belgium, of Maastrichtian age. Fig. 42, radial fracture surface of specimen B35519 showing inclined endopuncta. The exterior is to the top and the anterior to the right. × 85. Fig. 43, enlargement of an area with inclined endopuncta in the thickened shell anterior to the previous figure. × 600. Figs 44, 45. Two views of a mid-radial section (resin-mounted, polished and etched) showing what Williams & Wright (1970: pl. 11, fig. 2) called the 'micritic rubble junction between the secondary laminae . . . and the separation layer . . .'. Specimen B82746, × 1100. Fig. 44, near the cicatrix (bottom right), below the region of the posterior muscle scars, showing secondary laminae, the junction layer and the coarse fabric between the endopuncta. Fig. 45, similar coarse fabric near the posterior margin, beyond the cicatrix, showing the junction layer. Valve exterior is to the bottom right.

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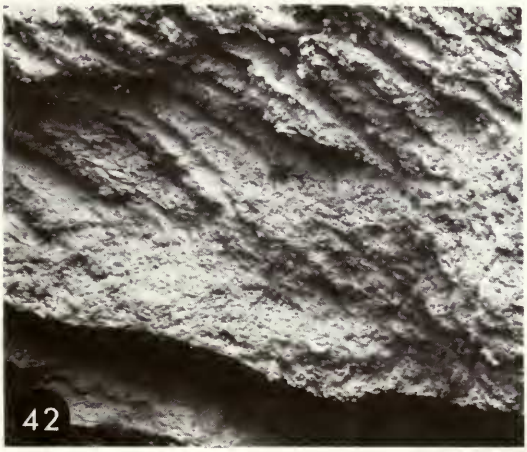

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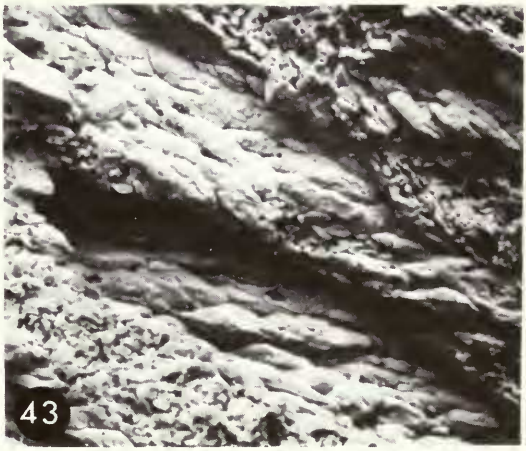

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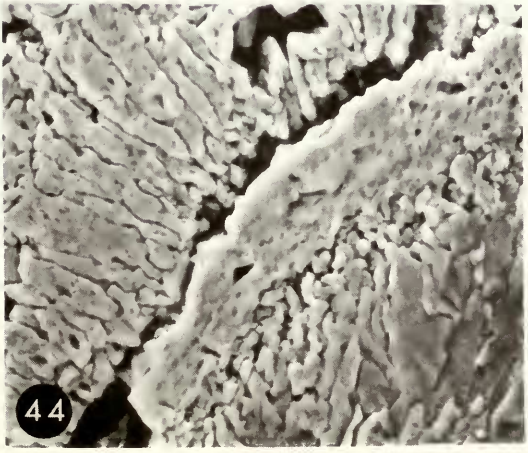

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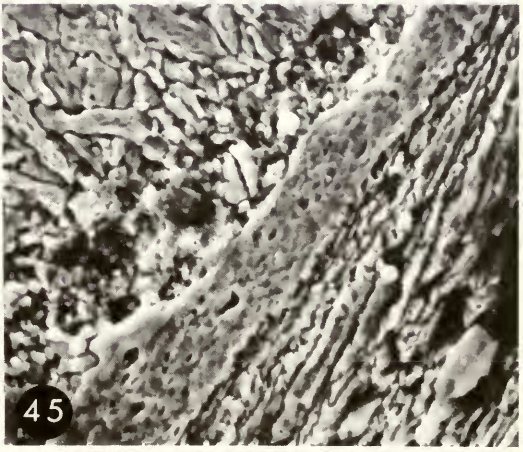

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see below for further discussion on these structures. We have not seen normally-sized endopuncta with these 'canals', nor have we distinguished external branching in these genera, such as occurs in the endopuncta of *Neocrania*.

In our view *Crania* s.s. and *Ancistrocrania* differ principally on their modes of growth away from their areas of initial attachment. Adult *Crania* species have posterior attachment scars and thus normally grew mainly anteriorly during life. Since the main muscles were inserted onto the ventral valve from its earliest stages, in valves which are heavily thickened they leave a trace or cavity from their adult internal surface positions back to their youthful positions within the attachment scar. Thus in *Crania* s.s. the anterior (and to a lesser extent also the posterior) scars trace into the shell posteriorly (Fig. 38).

In thick-shelled species of *Ancistrocrania* the adult attachment is positioned anterocentrally (*A. davidsoni*), or involves almost the complete external surface (*A. parisiensis*). Growth-lines show the initial attachment to have been anterocentral in all species, and thus growth was virtually holoperipheral, with a strong posterior component. The traces or cavities of the muscle scars within the shell, therefore, have their origins anterocentrally, and this resulted in anteriorly-directed muscle cavities (Fig. 39).

This marked difference in the extent of attachment areas in *A. parisiensis* and *A. davidsoni* is the only obvious difference between the species, and the possibility that it may have resulted by chance settlement of the spat onto large hard surfaces or onto small hard objects, respectively, must be recognized.

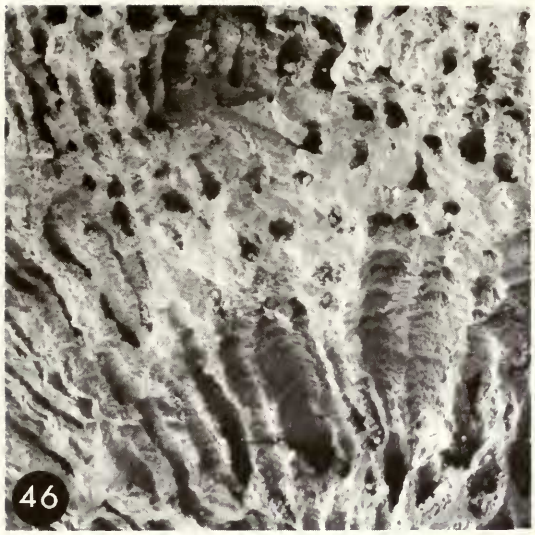
In general the degree of cemented attachment to the substrate of craniid ventral valves is variable, but consistent within species. All known species attach to the substrate at least initially, but those individuals surviving to adulthood vary as to the substrate type and degree of cementation. Surlyk (1973) showed how *Isocrania egnabergensis* and *I. costata*, although living on different substrates, became unattached during ontogeny and lived freely on, or slightly below, the sediment. It seems that some *Danocrania* species retained a small posterior attachment, while others may have become free-living as adults. The two species of *Crania* s.s. included here both attached by up to a third of their adult ventral valve area, while living *Neocrania* species attach the whole of their ventral valves to the substrate, as also seems to be the situation in *Craniscus*.

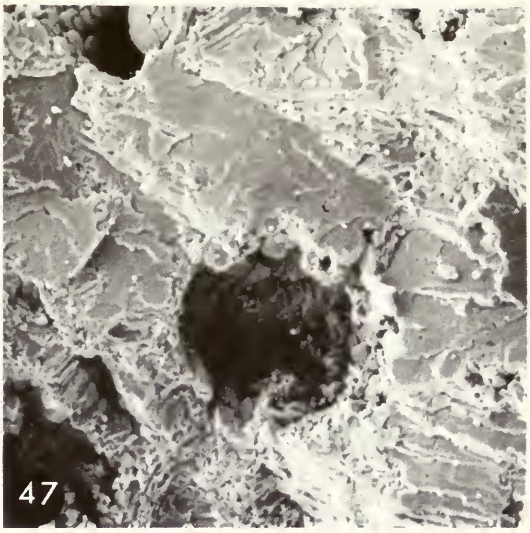
Endopuncta and 'canals'

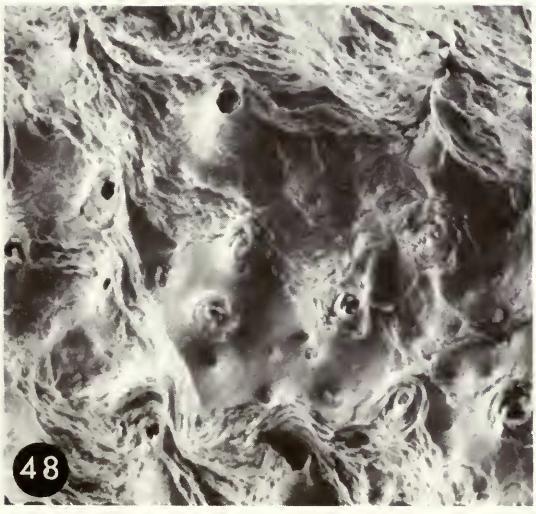
We believe the 'canals' recorded by Williams & Wright (1970) to be enlarged endopuncta, developed in the thickened ventral valves of some *Crania* and *Ancistrocrania* species, which may have been developed as a means of limiting the amount of calcium carbonate required for these thick valves.

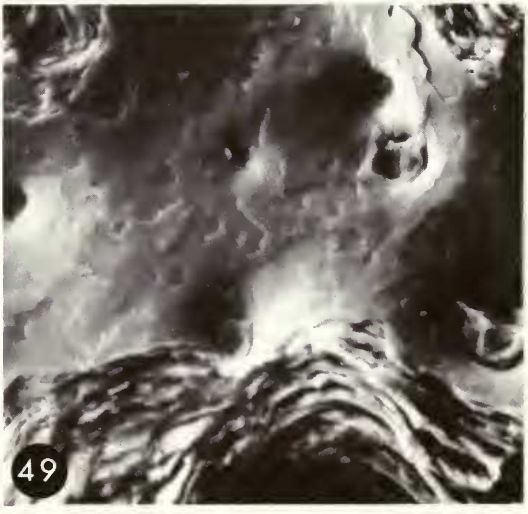
In *Ancistrocrania parisiensis* and *A. davidsoni* the diameter of the puncta increases with increased valve thickness, i.e. at the anterior rim and around the anterior muscle scars their diameters increase to the extent of allowing the elimination of up to 50% of the valve material (Figs 45, 46). The diameter of these puncta decreased considerably as the shell growth ceased, so that on mature internal surfaces they are much less obvious than on eroded, broken or younger specimens. Earlier we described the oblique nature of these wide puncta. This is especially clearly developed in an anterior direction and associated with highly thickened marginal rims. It resulted from the speed of growth and deposition of shell material in these thickened areas which, as it were, pulled the endopuncta in the principal direction of growth. As growth slowed, later in life, the puncta curved to the more usual orientation, approximately perpendicular to the inner surface. In thinner, median regions of the valve similar wide puncta remained perpendicular to both surfaces through growth, simply because less shell material was added to the valve, only increasing its thickness rather than also adding to its size.

As the thickness of ventral valves varies between species we do not find the absence or presence of wide puncta particularly helpful in defining genera. However, it is relevant that the puncta in species of *Danocrania*, *Isocrania* and *Neocrania* remain relatively narrow, seldom exceeding about 0·002 mm in diameter.









Figs 46 to 49 are scanning electron micrographs taken in the Electron Microscope Unit of the British Museum (Natural History). Specimens coated with gold-palladium.

Figs 46, 47 *Ancistrocrania davidsoni* (Davidson), from the Maastrichtian chalk of Ciply, Belgium. B3552. View showing a fractured mid-radial section of a ventral valve near the thickened anterior margin. Interior is to the top and anterior to the left. Fig. 46, at about the mid-thickness of the shell, showing the large, closely packed endopuncta. × 50. Fig. 47, enlargement from the middle of the previous figure showing the lamellose appearance of the fractured surface between the endopuncta. × 350. See also Figs 10–14.

Figs 48, 49 *Neocrania anomala* (Müller), from off the west coast of Scotland. Dorsal valve ZB3967, viewed on a fractured surface. The exterior is uppermost. Fig. 48, showing the outwardly deflected lamellae around endopuncta. × 290. Fig. 49, detail from the previous figure showing the pattern of screw dislocations on the laminae and small scale inwardly-directed cone-in-cone structures forming small tubercules on the internal surface. × 1100. See also Figs 32–37.

Shell fabric and relationships

Bearing in mind that Williams & Wright (1970) used living *Neocrania anomala* to characterize the shell of '*Crania*', all we can add to their description is that the ventral valves of some *Neocrania* species are thickened and display, at about × 200, a prismatic structure orientated with the endopunctation, which at over × 1000 can be seen to be composed of compact laminae similar to those figured in the dorsal valve of *Neocrania* (Figs 48–49).

The fabric of a ventral valve of *Crania antiqua* (Figs 44–45) was described by Williams & Wright (1970) as *Danocrania*, and their information, combined with our own observations on *Crania craniolaris* dorsal and ventral valves, shows an essentially laminar shell with endopuncta of varied size, including the so-called 'canals' in *C. antiqua*. The studied ventral valve of *Danocrania* has a uniformly endopunctate laminar shell, apparently lacking the 'crystalline' fabric of Williams & Wright (1970).

We have been unable to find Mesozoic *Craniscus* specimens with shell well preserved, and can add nothing further to the earlier studies using *C. japonicus*. We agree, however, with Williams & Wright (1970) that the dorsal valve morphology of *Craniscus* is close to that of *Ancistrocrania*. *Isocrania* species are distinctive, but are probably more closely related to *Danocrania* than to other genera. *Danocrania*, *Crania* and *Neocrania* form a grouping with species of the last two genera forming an evolutionary lineage.

Acknowledgements

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