New data on the ostracod genus *Aratrocypris* Whatley *et al.* 1985, with descriptions of species from the Upper Cretaceous of Europe and the Cainozoic of the North Atlantic.

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ABSTRACT - *Paradoxostoma ? cretacea* Bonnema (1941), is shown to belong to the deep sea cyprid genus *Aratrocypris* Whatley *et al* (1985). The implications of the discovery of this genus, hitherto known only from the Palaeocene to Recent, in the Upper Cretaceous of the Netherlands are discussed with respect to the palaeodepth of the Dutch Chalk Sea and to the origin and palaeozoogeographical history of *Aratrocypris*. The new species *Aratrocypris gigantea*, from the Recent and *Aratrocypris maddocksae* from the Cainozoic, are described from the North Atlantic and other, *nomina nuda* species are described or discussed from the same area.

INTRODUCTION

In June 1987, while perusing the Ellis and Messina ostracod catalogue for early records of *Paradoxostoma*, the senior author encountered the subsurface Cretaceous record from the northeast Netherlands of *Paradoxostoma*? cretacea Bonnema (1941). Although the original illustrations are small, they and Bonnema's description are suggestive of *Aratrocypris* Whatley *et al.* (1985). The subsequent request for assistance in tracking down the original material was met by an immediate reply from LW who provided details of the original borehole, some of the cores of which are housed in the Netherlands Geological Survey, and who also sent specimens which clearly belong to *Aratrocypris*. In subsequent correspondence and at a meeting in October 1987, the two authors decided to collaborate and subsequently GC was also invited to contribute.

In 1969, Maddocks described a strange cyprid ostracod with an anterior flange-like projection from the sub-Recent of the eastern Pacific. She ascribed it to the genus *Australovcia*. Subsequently, Whatley *et al.* (1985), having discovered a number of species with the same curious 'plough'-like structure anteriorly, in DSDP cores of Upper Palaeocene to Pleistocenes age in the S.W. Pacific, erected the genus *Aratrocypris* to accommodate them. These authors also noted the record of the genus from Recent sediments in the North West Atlantic by Cronin (1983) as *Australoecia*. sp. G. and Whatley and Coles (1987) subsequently recorded it from the early Pliocene of the central North Atlantic.

On the basis of its then known fossil occurrence, Whatley *et al.* (1985) suggested that *Aratrocypris* evolved in the S.W. Pacific/Australasian area during the early Palaeocene, probably from a common ancestor which it shared with *Australoecia* McKenzie, 1967 and *Maddocksella* McKenzie, 1983. They suggest that this may have been *Argilloecia* Sars, 1866.

The late Palaeocene and early Eocene representatives of *Aratrocypris* in the S.W. Pacific/Australasian region seem to have lived in shelf environments in that they occur in association with the thermophylic genus *Cytherelloidea*

Alexander and also with ornate species with well developed eye tubercles. However, from the late Palaeogene onwards, all records of *Aratrocypris* are from deep water bathyal and abyssal (greater than 1000m) environments, where they occur in association with typically deep water ostracod taxa.

Whatley *et al.*, (1985) also suggest that not only did *Aratrocypris* originate in the S.W. Pacific/Australasian area, but that this was the locus of its involuntary induction into the deep sea by means of tectonic processes as outlined in Whatley *et al.* (1983), Whatley (1983). They also suggest that from this initial locus, the genus migrated by bathyal and abyssal pathways to other parts of the worlds oceans, arriving late in the North Atlantic.

Although Bonnema's original illustrations of *Paradoxos*toma? cretacea are very small, they are unmistakably of *Aratrocypris*. Together with the anteroventral 'plough'. other features typical of post-Cretaceous species of the genus are already well developed in *A.cretacea*. Most of these were noted by Bonnema (1941) in his original description. The most important, as discussed in Whatley *et al.* (1985) are:

i) The hingeline is short and is situated very posteriorly and inclined at a steep angle towards the posterior. It is also more or less parallel with the blade of the 'plough'.

ii) The smaller left valve is very strongly overlapped antero-dorsally by the right.

iii) The anterior and ventral surfaces of the 'plough' are strongly reinforced and dentate.

iv) The 'plough' has a deep concavity in its ventral surface.

v) The adductor scars seem to be situated well back in the carapace, thus allowing the valves to gape anteriorly.

Whatley *et al.* speculate on the possible function of the 'plough' and conclude that it must be associated with feeding. Whatever the particular feeding adaptation was, *Ara-trocypris cretacea* was already employing it in the Upper Cretaceous.

The discovery of *Aratrocypris* in the Dutch Chalk throws new light on the original and migrational history of the genus. While it does not necessarily negate the suggestion that the genus first entered the deep sea in the antipodes and spread into other oceans from there, it does demonstrate that its origins were not necessarily in that region and that they may best be sought in the Upper Cretaceous of Europe. Only the discovery of further fossil material of the genus will resolve this paradox. Unfortunately, the small size and fragile nature of *Aratrocypris* renders it likely to be overlooked or not preserved.

Of the four wells in the eastern Netherlands which Bonnema (1941) examined for Ostracoda, only one yielded *Paradoxostoma? cretacea*. This well, De Krim NNIV (Noord Netherland IV), is located near Coevorden, a township that was later to become well known for discoveries of natural gas.

Unfortunately, Bonnema placed all specimens of one species, irrespective of their stratigraphical provenance, in a single slide. The species was reported to be abundant in the 'Mergel', and no more detailed age or level was indicated, neither in the text nor on the slide with the original material.

In slide no. 0.2243 of Bonnema's ostracod collection, which is now housed in the Geological Survey of the Netherlands in Haarlem, some tens of specimens of the species are present. Three specimens are stored in a separate slide, no. 0.2360, and were apparently used for the original illustrations.

In order to obtain more detail on the distribution of the species through the Chalk, fifteen additional samples were taken from the original core material. The depth range of the samples was 325m (top of the Chalk is at 315m) to 582m. *Aratrocypris cretacea* was found in only four of the samples, the lowest occurrence being the sample at 493-499m and the highest the top sample at 325m.

Well preserved planktonic and benthonic foraminifera occur abundantly in these samples which, together with other elements of the rich microfauna enable the section of the core from which *Aratrocypris* has been recovered to be dated as Coniacian to Santonian.

Explanation of Plate 1

The associated ostracod fauna is rich and diverse and

Figs. 1-6 Aratrocypris maddocksae sp. nov.

Figs. 1, 2 Holotype, carapace, OS 13241, Middle Eocene, Site 549, Hole 549, core 8, section 4, Fig. 1 left ext. lat.; Fig. 2 right ext. lat. (both x 135).

Figs. 3, 6 Paratype, L.V., OS 12242, Upper Eocene, Site 549, Hole 549A, core 27, section 1, Fig 3 ext. lat.: Fig. 6. int. (both x 116)

Figs. 4, 5 Paratype, R.V., OS 12343, Upper Eocene, Site 549, Hole 549A, core 17, section 1, Fig. 4, ext. lat.; Fig. 5. int. (both x 109)

Figs. 7, 10 Aratrocypris prealta Whatley et al. 1985

Fig. 7. LV GC/NA/535, Upper Oligocene, Site 558, core 25, section 1, ext. lat. (x 140).

Fig. 10 RV., GC/NA/358, Upper Oligocene, Site 558, hole 558, core 25, section 1, ext. lat. (x 140).

Figs. 8, 9 Aratrocypris sp.A.

Figs. 8, 9. R.V., GC/NA/539, Upper Oligocene, Site 558, hole 558, core 22, Section 1, Fig. 8, ext. lat.; Fig. 9, int. (both x 97). Figs. 11, 12 *Aratrocypris gigantea* sp.nov.

Fig. 11 Holotype, L.V., FO-88-001, Recent, Meteor Station 357, ext. lat. (x 74).

Fig. 12 Paratype R.V., FO-88-002/1, Recent Meteor Station 357, ext. lat. (x 85).

among the more abundant taxa are Parvacythereis subparva, Phacorhabdotus semiplicatus, Xestoleberis ovata, Imhotepia marssoni, Cardobairdia minuta, Cytherelloidea circumvallata, Aversovalva vscripta and Krithe bonnemai, together with species of Cytherella, Neonesidea and Bythoceratina. This ostracod association indicates a shallow water environment. Many of the species have eyes, indicating deposition on the shelf. Some of the genera present in this Upper Cretaceous assemblage have subsequently migrated downslope and many or all of their species are deep water indicators in the Cainozoic (e.g. Krithe, Phacorhabdotus, Aversovalva, Cardobairdia, Bythoceratina). The principle of shallow water ostracods subsequently invading deeper water is well documented (Whatley, 1983). Aratrocypris which, in the Cainozoic and Recent, has only once (Cronin 1983), 454-783m) been encountered in palaeodepths less than 1000m (and usually much deeper) is a striking example.

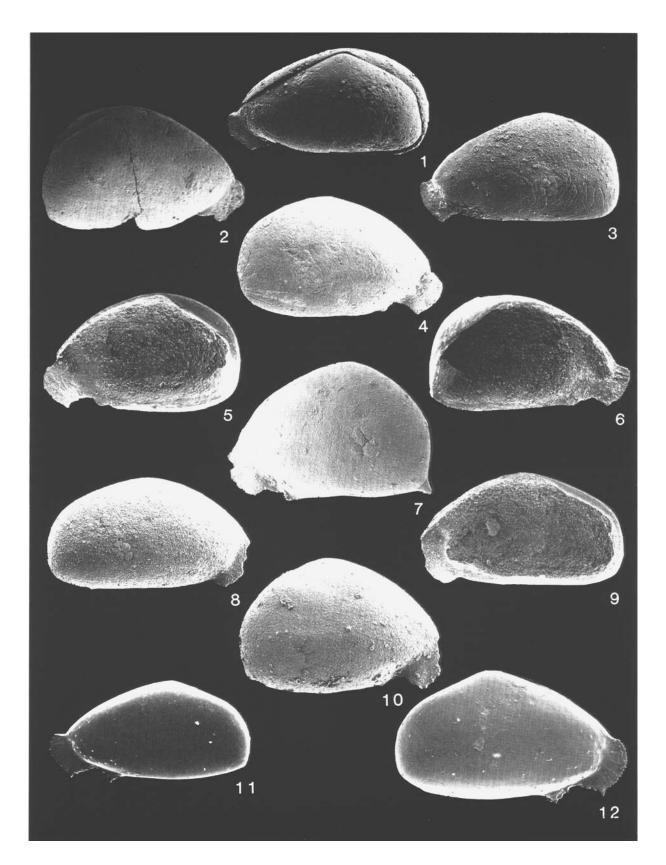
SYSTEMATIC DESCRIPTIONS

The type material of *A. cretacea* (Bonnema) and *A.gigantea* sp. nov. is deposited in the Rijks Geologische Dienst, Haarlem, The Netherlands, under the serial numbers prefixed BvV-0.2360/1 and FO-88-001 respectively. The type material of *A. maddocksae* sp. nov. is deposited in the Department of Palaeontology, British Museum (Nat. Hist.) with the prefix OS and other material, prefixed GC/NA is housed in the Micropalaeontology Museum at Aberystwyth.

Order Podocopida Müller, 1894 Suborder Podocopina Sars, 1866 Superfamily Cypridacea Baird, 1845 Family Pontocyprididae Müller, 1894 Genus Aratrocypris Whatley et al., 1985 Aratrocypris cretacea (Bonnema), 1941 (Pl. 2, figs 4-5, 7-10).

1941 Paradoxostoma? cretacea Bonnema, 43, pl. 7, figs 51-54.

Diagnosis. A small, smooth species of Aratrocypris with rounded or subrounded posterior margin and strongly den-



tate 'plough'

Description. Small, thin-shelled, subovate to sub-elliptical in lateral view. In dorsal view, widest in the posterior third and tapering regularly towards the laterally compressed anterior. Anterior margin with straight to slightly convex antero-dorsal slope extending from the anterior cardinal angle (at or just behind mid-length) to the tip of the 'plough'. 'Plough' like process well developed, dentate and with ventral incurvature. Posterior margin rounded or subrounded. Dorsal margin short, straight and steeply inclined towards the posterior. Ventral margin posterior of the 'plough' straight. Greatest length below mid-height; greatest height at the anterior cardinal angle; greatest width in the posterior third. Right valve larger than and strongly overlapping the left valve, especially antero-dorsally and ventrally. Surface smooth, internal features as for genus.

Dimensions. (mm). All specimens from Bonnema's slide No. BvV-O.2243.

i	Length	Height	Width
Carapace BvV-O.2360/1 (lectotype)	0.37	0.21	0.18
Carapace BvV-O.2360/3			
(paralectotype)	0.40	0.21	0.19
Adult RV BvV-O.2360/2			
(paralectotype)	0.41	0.22	0.11
Carapace BvV-O.2243/3	0.38	0.21	0.18
Carapace BvV-O.2243/4	0.40	0.22	0.17
Left valve BvV-O.2243/8	0.41	0.22	-
Carapace BvV-O.2243/9	0.40	0.21	0.18
Carapace BvV-O.2243/10	0.40	0.22	0.17
Carapace BvV-O.2243/11	0.39	0.21	0.17

Remarks. *Aratrocypris cretacea* is smaller than any previously described species of the genus. A size comparison of seven species of the genus is given below.

This indicates that there is an overall, if irregular, increase in the size of the genus from the Upper Cretaceous to the Recent.

The mean and range in size of adults.

		Length	Heig	ght	Width
A. cretacea Mea	n	0.39	0.21	0.17	
U. Cret.	Range	0.37	-0.41	0.21-0.22	0.16-0.18
A. praealta Mea	n	0.42	0.22		
U. Pal Mioc.	Range	0.36	-0.46	0.21-0.28	
A. maddocksae Mea	n	0.44	0.24		
U. Pal L. Olig.	Range	0.40	-0.49	0.21-0.30	
A. rectoporrecta Mea	n	0.48	0.26	_	
M. Eoc Rec.	Range	0.41	-0.56	0.23-0.30	_
Aratrocypris sp. A.Me	an	0.55	0.30	_	
U. Olig.	Range	0.55		0.30	
A. vaccamaris Mea	n	0.43	0.22		
Mioc.	Range	0.41	-0.44	0.21-0.23 -	
A. gigantea Mea	n	0.72	0.38	0.23	
Recent	Range	0.71-0.72		0.36-0.39	0.22-0.25

(Data from the present study and from Whatley *et al.* 1985. Note that the species with the longest stratigraphical ranges also have the greatest range in size. In almost all cases, the largest individuals are also the youngest).

Apart from being the smallest known species of genus, *A. cretacea* differs from the type species, *A. rectoporrecta*, in the shape of the 'plough' and in lacking the strongly truncated posterior margin and the postero-ventral spine on its left valve. *A. vaccamaris* differs in size and shape and also bears a weak ornament of ribs anteriorly. *A. praealta* is proportionally much higher and its left valve has a blunt postero-ventral spine which is either absent or only inconspicuously developed in *A. cretacea*. The most similar of previously illustrated species is *Aratrocypris* sp. of Whatley *et al.* (1985) which is herein subsumed within *A. maddocksae* sp. nov. This latter species, although considerably larger, is similar in overall shape, particularly in its subrounded posterior margin. The morphology of the 'plough' in the two species is also similar and it is probably that they are closely related.

Explanation of Plate 2

Fig. 1-3, 6. Aratrocypris gigantea sp. nov.

Figs. 1,6. Paratype R.V., FO-88-002/1, Recent, Meteor Station 357, Fig. 1, int; (x 75); Fig 6., ventral (x 79)

Fig. 2,3 Holotype L.V., FO-88-001, Recent, Meteor Station 357, Fig. 2, int. (x 75); Fig. 3, detail of antero-ventral 'plough', (x 210)

Figs. 4-5, 7-10 Aratrocypris cretacea (Bonnema) 1941.

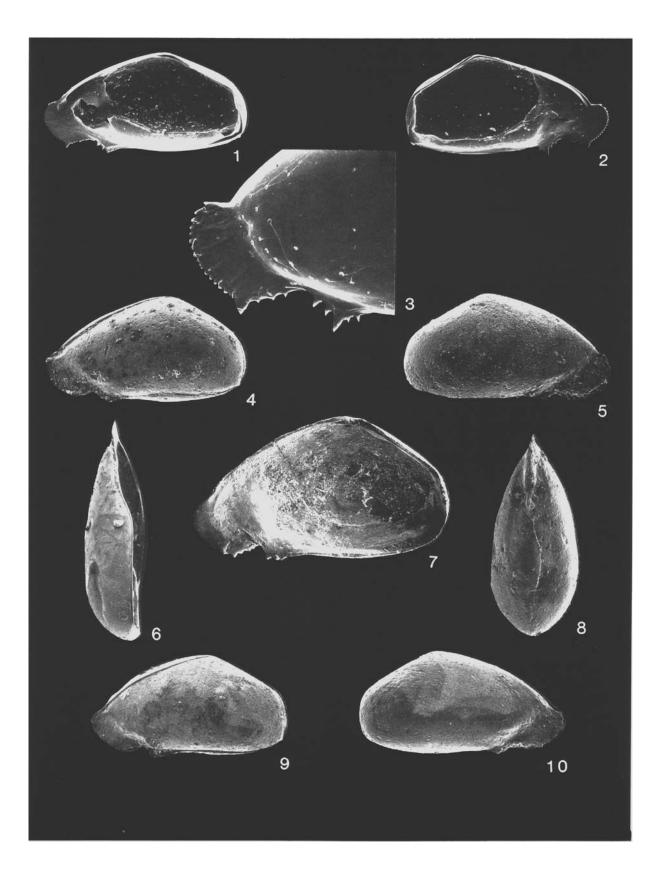
Fig. 4 Lectotype, carapace, BvV 2360/1, Upper Cretaceous, De Krim NNIV borehole, near Coevorden, The Netherlands, left ext. lat. (x 144).

Fig. 5 Paralectotype R.V., BvV 2360/3, Upper Cretaceous, De Krim NNIV borehole, near Coevorden, The Netherlands, ext. lat (x 136).

Fig. 7 R.V., BvV 2360/2, Upper Cretaceous, De Krim NNIV borehole, near Coevorden, The Netherlands, int. (x 166)

Fig. 8, 9 Carapace, BvV 2243/4, Upper Cretaceous, De Krim NNIV borehole, near Coevorden, The Netherlands, Fig. 8, dorsal (x 140); Fig. 9, left ext. lat (x 140)

Fig. 10 R.V. BvV 2243/3, Upper Cretaceous, De Krim NNIV borehole, near Coevorden, The Netherlands, ext. lat. (x 144).



Aratrocypris gigantea sp. nov. (Pl. 1, Figs 11,2: Plate 2, Figs 1-3,6)

Derivation of name. Latin, from the very large size of the carapace of this species with respect to other member of the genus.

Diagnosis. A large species of *Aratrocypris* with well developed plough-like structure. Valve surface smooth, posteroventral spines absent from both valves. Holotype Left valve, FO-88-001.

Material. Four specimens; two left valves, two right valves. **Type locality and horizon**. "*Meteor*' station 357, sample No. 16424-1. Corridor between Gambia Abyssal Plain and Sierra Leone Basin. Lat. 09° 01.8'N; Long. 19° 20.1'W. Water depth 3648m. Recent. Unconsolidated clay, rich in foraminifera.

Description. Very large for genus. Thin-shelled. Subovate to sub-triangular in lateral view. Right valve considerably larger than left, suggestive of strong overlap, particularly anterodorsally. Dorsal margin arched with rounded apex just behind mid-length. Ventral margin gently convex. Posterior margin tumid and forming a sharp angle at is junction with the ventral margin. Postero-ventral spines not developed. Plough-like antero-ventral structure well developed and consisting of two blades separated by a ventral crescentic incurvature. Frontal blade rounded, with four to five faint, elevated rays. The dorsal margin of this structure is almost horizontal in left valve, more rounded in right valve. Margin finely and regularly denticulate, except ventrally where a single large and three smaller denticles are developed from anterior to posterior. The posterior blade is triangular and coarsely dentate with one large central denticle and four smaller ones. A few crater-like normal pores bearing setae occur in the anterior part of the valves; otherwise surface smooth. Inner lamella wide anteriorly, much narrower posteriorly. Adductor scars situated behind mid-length and comprising 5 discrete scars in a rosette pattern. Hing adont, short and straight, inclined at a steep angle towards the posterior and situated entirely posterior of mid-length.

Dimensions. (mm)	Length	Height
Holotype LV FO-88-001	0.72	0.38
Paratype RV FO-88-002/1	0.72	0.39
Paratype RV FO-88-002/2	0.72	0.36
Paratype LV FO-88-002/3	0.71	0.381
) (and a first or a line halo of a		

¹ (specimen slightly damaged).

Remarks. Aratrocypris gigantea, in shape and outline, most closely resembles the Upper Cretaceous A. cretacea but it can be easily distinguished from this, and from all other species of the genus by its much greater size. It is almost twice as large a A. cretacea.

Distribution. The species was found in two surface sediment samples, taken with an oversize box-corer in deep water off the coast of Sierra Leone. The samples are from depths of 3436m and 3648m and were collected during 'Geotropex 83'.

Aratrocypris maddocksae sp. nov (Pl. 1, figs 1-6)

1985 Aratrocypris sp. Whatley, Ayress, Downing, Harlow and Kesler, p. 72, pl. 2, figs 14, 15, 16?, 17.

Derivation of name. In honour of Dr. R. F. Maddocks in recognition of her important studies in marine Cypridacea and because she was the first author to illustrate *Aratrocypris* after Bonnema.

Diagnosis. A small subovate to subtriangular species of *Aratrocypris* with the apex of the dorsal margin at midlength. Hinge very short.

Holotype. Carapace, OS 13241.

Material. 42 specimens, 36 from the North Atlantic, 6 from the Southwest Pacific.

Locality and horizon. DSDP Site 549, Hole 549, Goban Spur, Lat. 49° 04.28'N; Long. 13° 05.88'W, PDWD 2513m. Core 8, section 4, interval 95-102cm. Middle Eocene, NP 15. Pale greenish-white nannofossil ooze.

Description. Small, subovate to subtriangular. Anterior margin with small, subcrescentic plough-like structure. Posterior margin bluntly truncate and narrowly rounded, postero-ventral spine absent. Dorsal margin convex with apex at mid-length in right valve or slightly posterior of midlength in left valve. Ventral margin almost straight in right valve, very slightly concave in left valve. Maximum width posterior of mid-length, tapering anteriorly. Right valve overlaps left on dorsal and posterior margins. Surface smooth, Anterior vestibulum small, hinge very short. Other internal features as for genus.

Dimensions. (mm)	Length	Height
Holotype Car., OS 13241, 549 8-4 M. Eocene	0.40	0.22
Paratype LV, OS 13242, 549A 27-1 U. Eocene	0.46	0.26
Paratype RV, OS 13243, 549A 17-1 U. Eocene	0.49	0.30
Paratype Car., OS 12243, 209 27-2 M. Eocene	0.40	0.21
Paratype RV, OS 12241, 209 1-1 U. Pleist.	0.47	0.25
Paratype Car., OS 12242, 209 27-2 M. Eocene	0.40	0.21

(The last three paratypes were illustrated by Whatley *et al.* (1985) as *Aratrocypris* sp.).

Remarks. This species differs from the type of the genus, *A. rectoporrecta* Whatley *et al.*, principally in its rounded rather than spinose posteroventral corner and in being much less umbonate dorsally. While similar in outline, the present species lacks the anterior ornament of A. vaccamaris Whatley et al. It shares its rounded posteroventral margin with *A. cretacea* (Bonnema), but the latter species is smaller and also differs in the outline of its dorsal margin. In including *Aratrocypris* sp. of Whatley *et al.* 1985 in the synonomy of this species, we have reservations only in respect of the single specimen from the Pleistocene (OS 12241, Pl. 2, Fig. 16). The Pacific Palaeogene specimens (Pl. 2, figs 14, 15, 17) are clearly conspecific with our Palaeogene material from the North Atlantic. We also note that one of the specimens

of *A. rectoporrecta* illustrated by Whatley *et al.* 1985 (Pl. 1, Fig. 11) is more similar to *A. maddocksae* than other members of the former species but the similarity is largely in the nature of the posterior margin and not, for example, in the dorsal margin.

Distribution. Whatley *et al.* (1985) recorded this species, as *Aratrocypris* sp., from the Lower and Middle Eocene and the Upper Pleistocene of DSDP Site 209 on the Queensland Plateau in the SW Pacific. The single Upper Pleistocene specimen (paratype OS12241), is only tentatively included within the species.

In the NE Atlantic, this species is recorded from DSDP Site 549 on the Goban Spur, where it is present from the Upper Palaeocene to the Lower Oligocene (NP 9-22). The details of its distribution in the Palaeogene of the North Atlantic are as follows:

Hole	PDWD(m)	Core	Section Interval (cm) Age			Zone
549	2513	16	3	41-48	U. Pal.	NP 9
"	**	14	4	29-36	L. Eoc.	NP 11
		13	4	15-22		
		11	5	90-97		NP 12
	••	8	4	95-102	M. Eoc.	NP 15
	**	7	4	88-95	••	
••	••	6	1	96-103		NP 16
••	**	5	4	73-80		
	••	5	1	73-80		
	**	4	4	73-80	**	
549A		27	1	62-69	U. Eoc.	NP 20
		24	2	50-57	•	•
••		17	1	33-40	•	NP 21
	"	16	1	94-101	L. Olig.	••
••		11	2	80-87	,	NP 22

Aratrocypris sp. A. (Pl. 1, figs. 8, 9)

Material. 3 specimens: 1 adult valve, 2 juvenile valves. **Diagnosis**. A relatively large, elongate and inflated species of *Aratrocypris*, with a regularly convex dorsal margin and bluntly rounded posterior margin. Anteroventral ploughlike structure wide but short. Surface smooth. Greatest height at mid-length. Inner lamella narrow with short radial pore canals and moderately large anterior vestibulum.

Dimensions (mm).	Length	Height
Adult RV, GC/NA/539, 558 22-1	0.55	0.30

Remarks. This species is left in open nomenclature because only one adult specimen was recovered. It differs from *A*. *maddocksae* sp.nov. in being larger, more elongate and less convex dorsally. It resembles *A*. *vaccamaris* Whatley *et al*. (1985) but is larger, has a less umbonate dorsum and lacks the low ridges on the antero-lateral surface.

Distribution. *Aratrocypris* sp. A is known only from the Upper Oligocene of DSDP Site 558, in the N. Atlantic, SW of the Azores.

Hole	PDWD(m)	Core	Section Interval (cm) Age			Zone	
558	3754	23	1	30-37	U. Olig.	NP 24	
	22	1	75-82		"		
	21	2	111-118	••	NP 25		

OTHER ARATROCYPRIS SPECIES IN THE NORTH ATLANTIC

Aratrocypris sp. Cronin and Compton-Gooding, 1987

This species is represented by only 3 specimens from the Middle Eocene of DSDP Site 612 (PDWD 1404m) off New Jersey, USA. This is clearly distinct from all other known species of the genus. The single illustrated RV is small (length 0.43mm), elongates in outline with a very bluntly truncated posterior margin and a small, slightly upturned antero-ventral plough-like process. Unusually for the genus, the slope of the hinge margin is not parallel with the antero-ventral margin of the 'plough'.

Australoecia sp. G. Cronin 1983.

This represents another distinct species of *Aratrocypris* which was recorded from the Recent slope off Florida between 454-783m. Small (length 0.44mm), subovate in outline, very broadly rounded posteriorly, regularly convex dorsally. Antero-ventral 'plough' small, finely denticulate. Inner lamella wide and notched anteriorly. It is most similar in shape to *A. praealata* Whatley *et al.* (1985), but lacks the postero-ventral spine and differs in the shape of the antero-ventral 'plough'.

Aratrocypris praealta Whatley et al., 1985 (Pl. 1, Figs. 7, 10).

This species, which was originally recorded only from the Upper Palaeocene to Miocene of DSDP sites 56, 207 and 277 in the SW Pacific, has subsequently been recorded at Site 558 in the North Atlantic. The details of its occurrence are given below:

Hole	Core	Section	Zone		
558	26	3	57-64	L. Olig.	NP 22
••	25	1	10-17	U. Olig.	NP 23
••	24	3	113-120	U. Olig.	Np 23
••	23	1	30-37	U. Olig.	NP 24

PHYLOGENETIC CONSIDERATIONS

With respect to the phylogenetic relationships between the various species of *Aratrocypris*, we believe, largely based on the rounded nature of the posterior margin and particularly the postero-ventral corner, that there is probably a relationship between *A. maddocksae* and both *A. cretacea* and *A. gigantea*. The exact nature of this relationship is difficult to elucidate. However, we suggest that *A. maddocksae* may have evolved from *A. cretacea* or to have shared with it a

common ancestor. We do not believe, however, that *A.* maddocksae is ancestral to *A. gigantea* (and, therefore, possibly intermediate between *A. cretacea* and *A. gigantea*). Rather, we suggest that *A. gigantea* evolved from *A. cretacea*, possibly via an as yet undescribed intermediate species.

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