

## *Praecypridea*: a new non-marine ostracod genus from the Jurassic and Early Cretaceous of Europe, North and South America, and Africa

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**ABSTRACT** – The genus *Praecypridea* gen. nov. (Cypridoidea, Family Cyprideidae Martin, 1940) is described and thus far comprises four species: the type species *Praecypridea acuticyatha* (Schudack, 1998) comb. nov., *Praecypridea postelongata* (Oertli, 1957) comb. nov., *Praecypridea suprajurassica* (Mojon, Haddoumi & Charrière, 2009) comb. nov. and *Praecypridea acuta* (Moos, 1959 in Wicher, 1959) comb. nov. Representatives of the new genus have been described from the Middle to Late Jurassic of Europe, North America and Africa and the Early Cretaceous of South America, with other presumed representatives also occurring in the Early Cretaceous. Species of *Praecypridea* are considered to represent members of the ancestral lineage of the extinct genus *Cypridea* Bosquet, representatives of which flourished in non-marine habitats of latest Jurassic to Early Cretaceous age and account for the first period of abundance of the non-marine Cypridoidea. *J. Micropalaeontol.* 29(2): 163–176, December 2010.

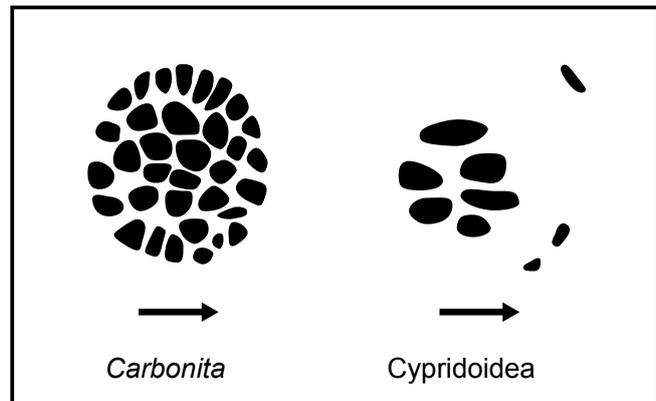
**KEYWORDS:** *Ostracoda, non-marine, Middle–Late Jurassic, Early Cretaceous, systematics, Cyprideidae*

### INTRODUCTION

Representatives of the Family Cypridoidea (cyprids) are the dominant ostracod group in Recent freshwater environments. Recognizing fossil non-marine Cypridoidea is difficult due to the lack of (preserved) diagnostic information. The usually weak calcification and fragility of the cyprid carapace is the reason why single valves are rarely preserved, and that preservation is often moderate to poor. Complete carapaces or, occasionally, single valves that are completely filled with sediment are usually found. Thus, useful internal characteristics, such as the typical muscle scar pattern (a central to antero-central group of roundish and elongate spots, not radially or linearly arranged, see Fig. 1), or the ridge-and-groove type hinge, are often not observable. We, therefore, have to use our experience to determine fossil cyprids by their outline, shape and – usually lacking or weakly developed – surface ornamentation.

The difficulties in finding and correctly identifying and differentiating early fossil cyprids has resulted in numerous misinterpretations and, thus, led to taxonomical inconsistencies in the literature. This includes the presumption of the existence of early non-marine cyprids prior to the Triassic, for example, a view not shared by the present authors. Here we present new data on the early evolution of the Cyprideidae Martin, 1940, an extinct family of the non-marine Cypridoidea that led to their first period of abundance in the latest Jurassic to Early Cretaceous.

For the reasons given above, the origin and early evolution of the non-marine Cypridoidea remain largely obscure to date; a detailed overview of the matter is in preparation. In summary, the early attempts of cyprid colonization of freshwater environments possibly took place in the Triassic of western Argentina (Las Cabras Formation, Mendoza Province, Hünicken & Chaia, 1992; Whatley & Ballent, 1996) more or less contemporaneously with another one in the Asiatic former USSR (Baskunchak Series, Precaspian Depression, Schleifer, 1966). The next younger faunas we know of are Early Jurassic in age. Whatley & Ballent



**Fig. 1.** Muscle scar differences between *Carbonita* Strand, 1928 and the typical cypridoidean pattern with an adductor muscle scar field consisting of a vertical row of 4 anterior scars and 2 behind it, as well as a frontal scar and 2 mandibular scars. Modified and supplemented from Retrum and Kaesler (2005).

(1996) cited two non-marine faunas of seemingly undoubted cyprids from the Lower Jurassic of western Argentina, both of which are pre-Toarcian and probably late Pliensbachian in age. Both deposits contain Darwinuloidea (darwinulids) as well as cyprids but remain undescribed. Schudack (2006) reported 150 poorly preserved valves and carapaces of unidentified Cypridoidea from the basal Jurassic Whitmore Point Member of the Moenave Formation (Utah, USA), associated with abundant darwinulid taxa. Kietzke and Lucas (1995) described *Scabriculocypris* n. sp. from the Early Jurassic (Sinemurian to Pliensbachian) Kayenta Formation of Arizona (USA) associated with darwinulids which, overall, looks more like a possible representative of the Limnocytheridae (Superfamily Cytheroidea) instead of a cyprid.

Thus, neither the Triassic nor the Lower Jurassic records of non-marine cyprids are of well-known faunas. Indeed, the

Argentinian material remains to be described, the North American material is of poor preservation or doubtful, while the Russian material is in need of modern study. In addition, there is still the problem that the Triassic/Early Jurassic age non-marine cyprids occur in South America, North America and Asia, whilst the earliest European records are from the Middle Jurassic.

#### Early evidence of the Cyprideidae Martin, 1940

The oldest European non-marine cyprids are from the Middle Jurassic (Upper Bajocian) of France (Oertli, 1957) where they occur in association with darwinulids, and non-marine cytherids (Cytheroidea). The original material of the fauna reported by Oertli (in Bernard *et al.*, 1957) was thought to be from the Lower Bathonian. However, the horizon from which the French material came is now considered Upper Bajocian (Colin & Carbonel, 1996, p. 188) on ammonite evidence, in that this horizon is overlain by a level containing *Parkinsonia parkinsoni* (Sowerby) (Colin pers. comm., October, 1998). One of the cyprids described in Bernard *et al.* (1957) is *Cypridea postelongata* Oertli, 1957 (*Praecypridea postelongata* Oertli comb. nov. herein). This is a very large (1.4–1.6 mm) ostracod clearly belonging to the Family Cyprideidae Martin, 1940 and conforms to the diagnosis of our new genus *Praecypridea*. It is the earliest and, presumably, either the ancestral taxon of the Family Cyprideidae or an early descendant of that hypothetical species. A paratype of this species was re-illustrated by Dépêche (1985, pl. 28, fig. 16) using the scanning electron microscope (SEM) and is redescribed and its figure reproduced herein (Pl. 1, fig. 9; by kind permission of TOTAL S.A.).

The record of the earliest English cyprid material supposedly including *Praecypridea postelongata* (Oertli) was extracted from the Forest Marble Formation of Gloucestershire, UK (Ware & Windle, 1981). Since this material is certainly Upper Bathonian, it appears that the non-marine colonization in France pre-dates that of southern England by an entire stage (*c.* 8 Ma, Gradstein *et al.*, 2004). However, grave doubt has to be cast on this oft-cited evidence regarding the occurrence of early Cyprideidae in England for several reasons. First, Ware & Windle (1981, p. 417) just mention the occurrence of cyprids that ‘closely resemble the lacustrine forms’ having been described by Oertli (1957), one of which they designated ‘*Cypridea postelongata*’. Yet, this publication (Ware & Windle, 1981) is a preliminary report and gives neither description nor illustration of the specimens. Second, Timberlake (1982, pl. 7, figs T–Y), in an unpublished study of material from this locality, illustrated four cyprids, all of which he (incorrectly) attributed to ‘*Cypridea*’ Bosquet. This includes a species he identified as ‘*Cypridea postelongata*’ Oertli with *Cypridea postelongata* of Ware & Windle (1981) in its synonymy list. A note in the relevant remarks is revealing in that it states ‘It is here considered that the ... species in fact belongs to an ancestral genus to *Cypridea* Bosquet, which for the moment is to be considered as ‘*Cypridea sensu lato*. This will be discussed at a later date by Ware ...’ (Timberlake, 1982, p. 211). Ware never published this planned successor paper. Third, after personal inspection of Timberlake’s (1982) material by BS, it became clear that the specimens are taxa of the Cypridoidea and remain to be identified more accurately, yet we do not believe that the species of Timberlake

(1982, pl. 7, figs T–Y) from the Bathonian belongs to either *Cypridea* or *Praecypridea*. We also presume the same to apply to the specimens mentioned by Ware & Windle (1981) since their material comes from the same locality and horizon. Consequently, the English record of Bathonian Cyprideidae is very doubtful and remains to be reassessed.

The next oldest presumed members of the Cyprideidae are reported from the continental mid- to upper Oxfordian of the Swiss Jura by Mojon (1989, p. 3), including *Cypridea* cf. *postelongata* Oertli. However, the material which he illustrates (Mojon, 1989, pl. 3, figs H–J) is indeed not typical of *Cypridea*, differs from *Praecypridea postelongata* comb. nov. and does not match many of the diagnostic characters of *Praecypridea* gen. nov.

Mojon *et al.* (2009), described *Cypridea suprajurassica* Mojon, Haddoumi & Charrière from the Oxfordian? to Kimmeridgian in Morocco which is here considered a representative of *Praecypridea* and refigured (Pl. 1, figs 10–13).

There is a citation of *Cypridea* sp. by Helmdach (1971, in German, and 1974, basically an English republication of the 1971 paper) from the Upper Jurassic of Portugal (locations Porto Pinheiro and Porto das Bacas). Among other Ostracoda (*Cetacella armata* Martin, 1958 and *Cetacella inermis* Martin, 1958), Helmdach reports that *Cypridea* sp. occurs rarely in his samples (Helmdach, 1971, p. 648; 1974, p. 9) and states that the sediments are ‘... almost certainly Kimmeridge, probably upper Kimmeridge’ (Helmdach, 1974, p. 9). However, these beds are now thought to be much younger. Mohr (1989), based on palynological data, indicates an early Berriasian age for microvertebrate-bearing beds for Porto Pinheiro, which is supported by Hahn & Hahn (1999) based on the level of development of the Multituberculata (Mammalia). Martin (1999) gives an age of around the Jurassic-Cretaceous boundary based on the Dryolestida (Mammalia). One of the present authors (MES) examined the remains of Helmdach’s collection at the Freie Universität Berlin (the whereabouts of some parts of his collection are unknown) and was unable to find any specimens of *Cypridea* from the localities mentioned. Without the material, the lack of descriptions in Helmdach’s publications, and the different age determinations we cannot assess the taxonomic affinities of his material.

There are more possibilities because representatives of *Cypridea* are now known to occur in pre-‘Purbeckian’ (i.e. pre-latest Jurassic) strata (Schudack & Schudack, 2002; Sames, 2008; Mojon *et al.*, 2009). Whatley (1990b, 1992) stated that *Cypridea* did not seem to have evolved prior to the very latest Jurassic. However, new results from East Africa (Kimmeridgian, Tendaguru Formation, SE Tanzania – Schudack & Schudack, 2002; Schudack & Sames, 2003; Sames, 2008) and Western Europe (Lower Tithonian of the Island of Oleron, France, J.-P. Colin, pers. comm., July 2006) suggest that *Cypridea* existed prior to the uppermost Tithonian and probably evolved in (East?) Africa.

Schudack & Schudack (2002, fig. 7) and Sames (2008, pl. 1, fig. 1) altogether recovered four different (new?) species of ‘true’ *Cypridea* from the (?upper) Kimmeridgian of the Middle Saurian Member (see Bussert *et al.*, 2009) of the Tendaguru Formation, SE Tanzania, but only one possible representative of *Praecypridea*. The specimen designated as *Paracypris* sp. in

Schudack & Schudack (2002, p. 330, fig. 8 therein) is questionably included in *Praecypridea* gen. nov.

The ostracods of the Upper Jurassic Morrison Formation of the Western Interior of the USA have recently been studied by Schudack (1998), while the senior author (BS) is currently re-examining the Lower Cretaceous non-marine ostracods from the USA. Schudack (1998) recovered a rich non-marine ostracod fauna comprising darwinulids, limnocytherids including *Theriosynoecum* and cyprids including taxa of the Cyprideidae. The *Cypridea* species described in that publication (*C. acuticyatha*) is the type species of *Praecypridea*. Another taxon, undescribed and referred to as ?*Cypridea* sp. in Schudack (1998), is considered here not to belong to *Praecypridea* or *Cypridea*. Considerable confusion has surrounded the age of the continental Morrison Formation in the past. It is now considered to extend from the latest Oxfordian, through the Kimmeridgian to the Early Tithonian. Although no part of the formation is believed to be Cretaceous this cannot be completely excluded, because the uppermost parts of the Morrison are devoid of fossils. There is, also, potential evidence for an Early Cretaceous (Early Berriasian?) age for the upper part of the Morrison Formation in the southern Black Hills, South Dakota, USA (Sames *et al.*, 2010). As shown by Sohn (1958, 1979) in his extensive revision, and subsequently confirmed by BS, the ostracod fauna of the Black Hills, USA is referable to the Lower Cretaceous Lakota Formation rather than to the underlying Morrison Formation, as stated by Roth (1933), Branson (1935) and Harper & Sutton (1935). The Black Hills fauna contains representatives of true *Cypridea* which are post-uppermost Jurassic. However, in contrast to the interpretation of Schudack (1998), the senior author now believes that the fauna of the Morrison Formation as reported therein (Schudack, 1998) has no taxa in common with the overlying Early Cretaceous Formations at species level. There are marked unconformities between the Morrison Formation and the overlying (Lower Cretaceous) formations; however, both the timespan represented by the hiatuses, plus the exact minimum/youngest age of the Morrison Formation and the maximum/oldest age of the Lower Cretaceous formations are controversial (Sames, 2010; Sames *et al.*, 2010).

Colin (pers. comm., January 2007) provided the information and showed us SEM pictures of whole specimens of *Praecypridea acuticyatha* (Schudack, 1998) comb. nov., occurring in the Late Jurassic (probably Kimmeridgian) Stanleyville Formation of the Democratic Republic of the Congo, Central Africa. This species was first mentioned by Grekoff (1957, pp. 87–88, illustrated with a small line drawing of a single specimen in table 1) as ‘Ostracode 12089’. Grekoff (1957) noted the acute postero-ventral end, related this specimen to *Stenocypris* Sars and even stated that ‘. . . une forme analogue se retrouve dans la Morrison Formation de l’Oklahoma et de New Mexico, U.S.A. . . .’ (translation: a similar form is present in the Morrison Formation of Oklahoma and New Mexico, USA, *op. cit.*, p. 88). The specimens of Colin (pers. comm., January 2007) are topotypic with those of Grekoff (1957).

Thus, by the Kimmeridgian the differentiation of the non-marine Cypridoidea, including the Cyprideidae, had proceeded apace, as shown by Schudack *et al.* (1998) for the USA, and as shown for East Africa by Schudack & Sames (2003), Schudack & Schudack (2002), and Sames (2008). In China, Jurassic

non-marine sediments commonly occur yielding numerous ostracods. For as yet unknown reasons, the Cypridoidea are extremely rare or absent, while *Cypridea* and its allies are absent (e.g. Xu, 1983) prior to the uppermost Jurassic (Gou & Cao, 1983; Pang & Whatley, 1990), which is probably approximately equivalent to the Upper Purbeckian of southern England.

The first major adaptive radiation of the non-marine Cypridoidea took place in the Late Tithonian/Early Cretaceous (‘Purbeck/Wealden’) interval, associated with a major global regression (Whatley, 1986; 1988; 1990a, b; 1992) and the inception of the ‘Purbeck’ facies in Europe (Horne, 2002), but may have started earlier (Kimmeridgian). The main part of the Early Cretaceous cypridoidean diversity has been attributed to the now-extinct Cyprideidae Martin, 1940 (Horne & Martens, 1998), i.e. *Cypridea* and its close relatives, which includes some taxa of *Praecypridea* gen. nov. The Cyprideidae are also considered to have dominated most latest Jurassic to Early Cretaceous non-marine habitats in terms of diversity (not abundance, see Whatley, 1992). Ongoing revisions of *Cypridea* and some of its taxa, however, revealed that the hypothesis of mixed reproduction, i.e. a combination of sexual and parthenogenetic reproductive modes, is likely in taxa of the Cyprideidae (BS, research in progress). This is presumed to have had strong effects on the intraspecific genetic and morphological variability, which, in turn leads to the assumption that the diversity (more than 600 taxa) in *Cypridea* may have been highly overestimated in the past.

Irrespective of their potential degree of faunal domination, *Cypridea* and its allies flourished during the Early Cretaceous within the ‘Purbeck/Wealden’-like facies throughout much of the world. However, with the principal exceptions of China, Mongolia and India, the rich and varied *Cypridea* faunas were widely rendered extinct by the cumulative Cretaceous marine transgression, starting as early as the Aptian/Albian. In these Asian areas, however, *Cypridea* and its allies survived through the Late Cretaceous and, possibly in northern China, into the Paleocene (Ye, 1994) or Eocene (Guan *et al.*, 1997).

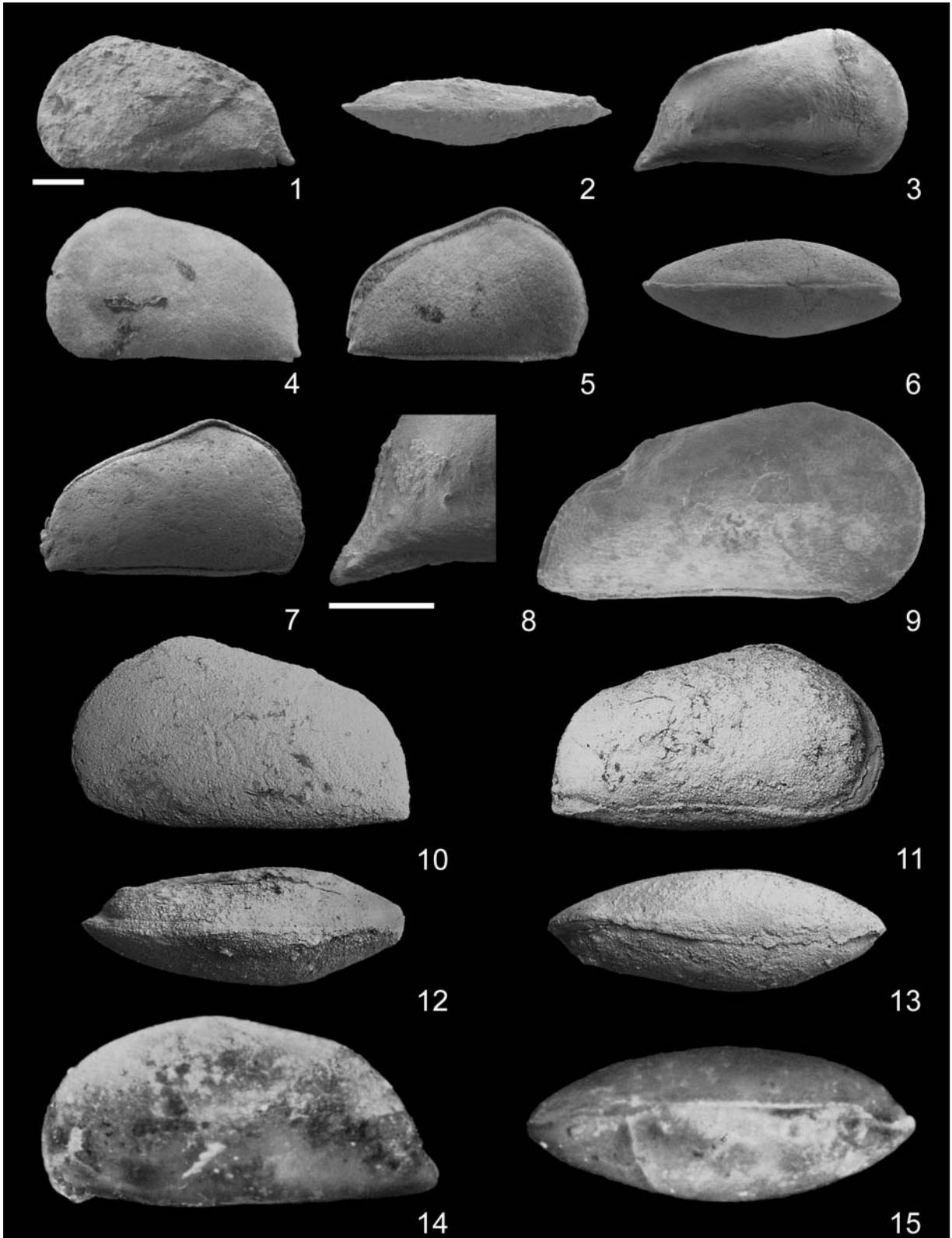
## SYSTEMATIC DESCRIPTIONS

### Terminology

Abbreviations: LV, left valve; RV, right valve. For illustrations of the following terms see Figure 2.

*Equi-, infra- and supracurvate*. Lüttig (1962) introduced these useful terms to define the curvature of anterior or posterior margins. Equicurvate (German ‘äquikurvat’) means equally rounded, infracurvate (German ‘infrakurvat’) narrowly rounded towards venter, and supracurvate (German ‘suprakurvat’) narrowly rounded towards dorsal margin.

*Alveolus (small trough)*. An indentation (*alveolar notch*) commencing behind the rostrum, which (in *Cypridea*) usually extends upwards as an *alveolar furrow* (narrow and elongate) or *alveolar groove* (large, broad, either elongate or with a subtriangular shape, being broad at the base and pointed in a dorsal direction) in both valves. Depth, width and length of the furrow/groove vary considerably between different species. In most cases the alveolar notch and its adjoining furrow/groove



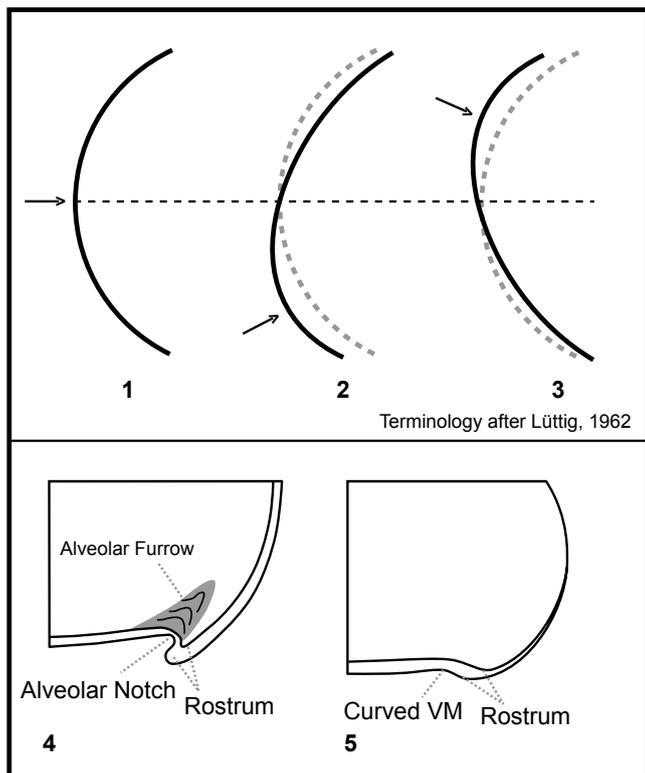


Fig. 2. (1–3) Terminology of curvature of anterior and posterior ostracod carapace margins after Lüttig (1962): 1, equicurvate; 2, infracurvate; 3, supracurvate. (4) Rostrum and alveolus in true *Cypridea*. (5) Rostrum and slightly upwards curved, but not incised, ventral margin (VM) in *Praecypridea postelongata* (Oertli, 1957) comb. nov.

are more or less larger and much more distinct in the larger valve (LV usually). Regarding *Praecypridea*, the alveolus is generally not developed, showing only a faint alveolar furrow (*Praecypridea acuticyatha* and *Praecypridea acuta* (Moos, 1959 in Wicher, 1959) herein) at maximum, but no anteroventral incision of the ventral margin. The important difference to *Cypridea* is that the alveolar notch does not exist in *Praecypridea*, i.e. its ventral margin is not or just very slightly curved upwards.

*Rostrum* (*beak of some authors*). As fully developed in *Cypridea* to different degrees, this is a more or less pointed triangular

prolongation (process) of the anteroventral angle, bounded by the anterior margin in front and by a notch and furrow (i.e. the *alveolus*) behind it. In representatives of *Praecypridea*, the rostrum is absent, or not fully developed and there is either a sharp anteroventral angle (e.g. *Praecypridea acuticyatha* herein) or a poorly developed rostrum (e.g. *Praecypridea postelongata* herein). In the latter case, no alveolar notch is developed in *Praecypridea*, rarely a faint alveolar furrow is present (*Praecypridea acuta*).

*Remarks*. The terms rostrum and beak are, so far, purely descriptive. The crucial point as to the usage of rostrum and beak is that, with regard to the Cypridae, some authors used it interchangeably for the anteroventral process while others (e.g. Horne & Colin, 2005) used the term beak in the sense of the combination of both, rostrum and alveolus. For reasons of clarity, particularly when discussing *Praecypridea* and *Cypridea* at the same time and because of the fact that *Praecypridea* lacks almost any sign of alveolar elements, we do not use the term ‘beak’ at all and apply the term rostrum for the anteroventral process (if developed) only.

Szczuchura (1981) discussed the importance of the development of the anteroventral region (i.e. the rostrum and alveolus) in combination with a ‘true’ cyathus (see below) for the taxonomy of *Cypridea* and demonstrated the importance of analysing both internal and external characters to distinguish between representatives of the Cypridae and the superficially (external view) similar genera with anteroventral rostrum-like processes.

The function of the rostrum and alveolus within the Cypridae Martin, 1940 (*Cyprideal/Praecypridea* and relatives) is as yet unknown and, thus, these terms remain purely descriptive. Horne and Martens (1998) speculated about a possible connection with feeding and/or swimming, or sensory perception. For marine ostracods such as the cypridoidean genus *Aratrocypris* Whatley *et al.*, and the cytheroidean genus *Acetabulastoma* Schornikov its function has been discussed at length by Whatley *et al.* (1985, 1989).

*Cyathus/Cyathus-like protrusion*. In the genus *Cypridea*, the cyathus (‘true cyathus’) is defined as a crescent, semi-circular or triangular extension of the posteroventral margin (at or close to the posteroventral angle) of the larger valve only. It is concave internally and strengthened by fine ribs, and the direction of its point may be ventral, posteroventral or posterior.

**Explanation of Plate 1.**

figs 1–8. *Praecypridea acuticyatha* comb. nov.: 1, holotype MES 356, left view of carapace, sample 1340-2-32; 2, dorsal view of holotype, laterally compressed, anterior end to the left; 3, paratype MES 355, right lateral view of carapace, sample 1340-2-32; 4, specimen from slide MES 354, left lateral view of carapace, cyathus-like protrusion partly missing, 1342-1; 5, specimen from slide MES 354, right lateral view of carapace, 1342-1; 6, dorsal view, anterior end to the left, cyathus-like protrusion broken off, sample 1342-1; 7, right lateral view of carapace, cyathus-like protrusion broken off, sample 1342-1; 8, cyathus-like protrusion, detail, enlargement of figure 3. Photos taken by M.E. Schudack at Freie Universität Berlin, Fachrichtung Paläontologie. Sample numbers and locations from Schudack *et al.* (1998), all specimens from the Morrison Formation, Kenton Section, Cimarron County, Oklahoma, USA. Figures 1, 4 and 5 refigured from Schudack *et al.* (1998) by kind permission of Taylor & Francis (UK) Journals (<http://www.tandf.co.uk/journals>). fig. 9. *Praecypridea postelongata* (Oertli, 1957) comb. nov., refigured from ‘Atlas des Ostracodes de France’ (Oertli, 1985, p. 129, pl. 28, fig. 16, paratype BE 195). Posterodorsally slightly damaged. Reproduced by kind permission of TOTAL S.A. figs 10–13. *P. suprajurassica* (Mojon, Haddoumi & Charrière, 2009) comb. nov.: 10, holotype, MHNG 60562, dorsal view, anterior end above; 11, holotype, ventral view, anterior end above; 12, holotype, lateral left view of carapace; 13, lateral right view of carapace, holotype. Figures 10–13 reproduced from Mojon *et al.* (2009, pl. 2, figs G1, G2, G5, and G6, holotype) by kind permission of P.-O. Mojon (all rights reserved by the authors) and B. Granier, Publisher/Editor of ‘Carnets de Géologie’. figs 14, 15. *Praecypridea acuta* (Moos in Wicher, 1959) comb. nov.: 14, lateral left view of carapace, holotype T.-K.-Nr. 3179, refigured from Wicher (1959, pl. 9, fig. 3a); 15, dorsal view, anterior end to the right, holotype T.-K.-Nr. 3179, refigured from Wicher (1959, pl. 9, fig. 3b). Figures 14–15 reproduced by kind permission of E. Schweizerbart’sche Verlagsbuchhandlung OHG (Naegele u. Obermiller) Science Publishers (<http://www.schweizerbart.de>). Scale bar: 200 µm. Specimens to scale, except figure 8.

In *Praecypridea*, however, this posteroventral prolongation occurs in both valves and does not really resemble a ‘scooping cup’ (from Latin/Ancient Greek: *cyathus*). Consequently, for the reason of a presumed *Praecypridea*–*Cypridea* lineage but at the same time lacking internal features of *Praecypridea* for further confirmation, i.e. the differentiation of a potential cyathus occurring in both valves of the Cyprideidae and carapaces of other ostracods with pointed posteroventral corners in both valves, we apply the term cyathus-like protrusion for *Praecypridea* here. Its function remains unclear.

Class **Ostracoda** Latreille, 1802  
 Order **Podocopida** Müller, 1894  
 Suborder **Podocopina** Sars, 1866  
 Superfamily **Cypridoidea** Baird, 1845  
 Family **Cyprideidae** Martin, 1940

**Remarks.** Here we follow the view of keeping *Cypridea* and its close relatives with a rostrum and alveolus or a presumed precursor of these features, respectively, in a separate family of the Cypridoidea, the Cyprideidae Martin, 1940 (extinct; not to be confused with the extant cypridoid Family Cyprididae). This is based on the hypothesis of a *Cypridea*–*Bisulcoocypridea* lineage (see Horne & Colin, 2005, p. 27), which is extended to a presumed *Praecypridea*–*Cypridea*–*Bisulcoocypridea* lineage here. However, the ‘classic’ concept of keeping *Cypridea* and its close relatives in the Family Ilyocyprididae, then under the Subfamily Cyprideinae, is based on a possible *Cypridea*–*Bisulcoocypridea*–*Ilyocypris* lineage and cannot be ruled out thus far. The elevation of the Cyprideinae to family status supersedes the usage of the latter term (e.g. Sohn, 1979; Horne & Colin, 2005).

**Age.** Middle Jurassic (Bajocian) to Eocene, as confined by the occurrence of *Praecypridea postelongata* (Oertli, 1957) and *Cypridea (Cypridea) pingyiensis* Guan, 1997 (in Guan *et al.*, 1997).

Genus *Praecypridea* gen. nov.

**Type species.** *Cypridea acuticyatha* Schudack, 1998.

**Derivation of name.** Latin *prae* (adv. as prefix), early/ahead, plus *Cypridea*; alluding to its presumed phylogenetic status as the ancestor to the genus *Cypridea*.

**Diagnosis.** Medium-sized (0.90–2 mm) representative of the Cyprideidae. Anterior margin slightly infracurvate; ventral margin very straight. Anteroventral rostrum absent and represented only by a slightly obtuse-angled intersection of the anterior and ventral margins, or barely to weakly developed. If rostrum present, the ventral margin is not or only slightly curved upwards, no alveolar notch is developed. Rarely with faint alveolar furrow. Dorsal margin sloping to the posterior. Well-marked anterior but weakly marked posterior cardinal angle. Maximum height anteriorly, mostly at 1/3 of length, measuring less than half the length. Posterior margin short and sloping steeply to a posteroventral sharply or bluntly pointed cyathus-like protrusion with an angle below 90°, slightly or distinctly extending beyond posterior margin. Cyathus-like protrusion

present in both valves. LV larger than RV, moderate overlap. Valve surface smooth to delicately punctate, potentially with tubercles. Internal features unknown. Sexual dimorphism not observed.

**Included species.** (1) *Cypridea acuticyatha* Schudack, 1998 – Kimmeridgian, Morrison Formation, Morrison Zones 3 and 4 of Schudack *et al.* (1998), Front Range Foothills, Oklahoma and Colorado, USA ⇒ *Praecypridea acuticyatha* (Schudack, 1998) **comb. nov.** [type species]. (2) *Cypridea postelongata* Oertli, 1957 – Late Bajocian (formerly considered to be Early Bathonian, Colin & Carbonel, 1996, p. 188), Vallée de la Vienne, Poitou, France ⇒ *Praecypridea postelongata* (Oertli, 1957) **comb. nov.** (3) *Cypridea acuta* Moos, 1959 (in Wicher, 1959, p. 46, pl. 9, figs 3 a, b) – Lower Cretaceous, Bahia Supergroup (Recôncavo Series), Itaparica Formation, Recôncavo Basin, NE Brazil ⇒ *Praecypridea acuta* (Moos, 1959) **comb. nov.** (4) *Cypridea suprajurassica* Mojon, Haddoumi & Charrière, 2009 (pp. 14–15, pl. 2, figs G1–G6, pl. 3, fig. E) – Upper Jurassic (Oxfordian?–Kimmeridgian), ‘Red Beds’ of the Moroccan Atlas, Morocco ⇒ *Praecypridea suprajurassica* (Mojon, Haddoumi & Charrière, 2009) **comb. nov.**

**Other possible species.** (1) *Cypridea modica* Lyubimova, 1956 (pp. 73–75, pl. 16, fig. 3a, b) – Lower Cretaceous, Baruunbayan District of Mongolia. (2) *Paracypris* sp. in Schudack & Schudack, 2002 (p. 329, fig. 8) – Kimmeridgian, Middle Saurian Member of the Tendaguru Formation, SE Tanzania. (3) *Daurina mongolica* Sinitza, 1986 (pl. 11, fig. 3) – Gurvan Eren Formation, Lower Cretaceous, western Mongolia. (4) *Salvadoriella? acuta* Krömmelbein & Weber, 1971 (pp. 45–46, pl. 8, figs 37a, b, c) – Lower Cretaceous, Bahia Supergroup (Recôncavo Series), São Sebastião Formation, Recôncavo Basin, NE Brazil. (5) *Cypridea aemulans* nom. nov. pro *Cypridea acuta* Anderson, 1971 (non Moos) (Anderson, 1971, p. 50, pl. 16, fig. 5) – Berriasian to Valanginian?, Durlston Formation (Purbeck Limestone Group) and Ashdown Bed Formation (Hastings Beds Group) Corfe to Nutfield faunicycles of Anderson (1985), *Cypridea granulosa* to *Cypridea menevensis* subzones of Horne (1995), England, UK.

There are several other potential forms from the English Purbeck and Wealden and Purbeck–Wealden-like deposits world-wide that superficially show some similarity to, or might be taken into consideration as, representatives of *Praecypridea*, only some of them can be discussed here by example (see paragraph Discussion for details), e.g. from the English Purbeck and Wealden *Eoparacypris abbreviata* Anderson, 1971 and *Cypridea blackbushensis* Anderson, 1967 (in Anderson *et al.*, 1967).

Except for *Paracypris* sp. in Schudack & Schudack (2002), we have not examined original material of the possible *Praecypridea* species listed above. With respect to *Cypridea acuta* Moos, 1959 (in Wicher, 1959) and *Salvadoriella? acuta* Krömmelbein & Weber, 1971, topotypes of these from Krömmelbein were examined by J.-P. Colin and considered to be closely related to each other and, other than slight differences in outline, fit well in *Praecypridea* (Colin, pers. comm., 2008 and 2009). The assignment of *Cypridea suprajurassica* Mojon, Haddoumi & Charrière, 2009 to *Praecypridea* gen. nov. was confirmed by P.-O. Mojon (pers. comm., 2009).

**Repository of the type material:** Department of Geosciences, Palaeontology Branch, Micropalaeontological Collection, Freie Universität Berlin, Germany. The label refers to the material of Michael E. Schudack (MES) therein.

**Stratigraphical range.** Middle to Late Jurassic (Late Bajocian to Kimmeridgian), Early Cretaceous.

**Palaeoecology.** Non-marine, freshwater to oligohaline.

**Occurrence.** Middle Jurassic, Paris Basin, France. Upper Jurassic Morrison Formation, North America. Upper Jurassic, Democratic Republic of the Congo (formerly Zaire). Upper Jurassic (Oxfordian?–Kimmeridgian), Central High Atlas, Morocco. Lower Cretaceous, Bahia Supergroup, Itaparica Formation, Recôncavo Basin, NE Brazil.

**Remarks.** *Cypridea* and *Praecypridea* are distinguishable by the following features (as to *Cypridea* this applies to the type species and most other species, some variations do exist).

- *Cypridea*: Fully developed rostrum and alveolus, including the alveolar notch. Cyathus, developed in the larger valve only, mostly obtuse-angled and rounded. Hinge margin incised causing a distinct dorsal furrow.
- *Praecypridea*: Slightly obtuse-angled intersection of the anterior and ventral margins or barely to weakly developed rostrum. Generally no alveolus, occasional with faint alveolar furrow only. If rostrum developed, no alveolar notch present behind it but straight or slightly curved upwards ventral margin instead. Cyathus-like protrusion developed in both valves, although somewhat smaller and often somewhat more rounded in the smaller RV, and forms a straight or slightly downwards curved elongation of the ventral margin. Hinge margin not incised, no dorsal furrow.

Admittedly, the authors are well aware that some difficulties in establishing a robust and useful diagnosis for *Praecypridea* remain, especially to distinguish it from *Cypridea*. Nevertheless, we consider the given data easily sufficient to justify the establishment of this genus formally and to draw attention to the group of species assigned to it as ancestral stock for *Cypridea*. The mentioned difficulties particularly result from the lack of internal features of *Praecypridea* and presumed transitional stages between some taxa of *Praecypridea* and *Cypridea*, as well as problems in the taxonomy of *Cypridea* and its many, highly variable representatives. This also includes clarification of whether the cyathus-like protrusion in *Praecypridea* really comprises a ‘true’ cyathus in both valves and, thus, might be termed this way, or whether it is any different from a (cyprid) carapace with pointed posteroventral corner. With respect to *Cypridea* species, it has also to be taken into account that presumed juveniles of *Cypridea* show features that resemble the shape of *Praecypridea*, i.e. these may exhibit a weakly developed rostrum and alveolus, a strongly triangular shape with a narrow posterior margin, and a posteroventral prolongation. The taxonomical value of the hinge incisure and resulting dorsal furrow also has to be tested further, particularly concerning potential

transitional stages between representatives of both genera, but is here considered of some value in differentiating the two genera.

*Praecypridea* gen. nov. differs from the Early Triassic to Early Cretaceous non-marine cyprid genus *Clinocypris* Mandelstam in possessing a very steeply sloping or almost vertical posterior margin, the well-defined anterior cardinal angle and the cyathus. The marine genus *Paracypris* Sars, although showing an acute posteroventral end in both valves, has a concave ventral margin and its posterior margin is moderately sloping while its maximum height is clearly less than half carapace length.

*Praecypridea acuta* is considered a representative of this genus by its overall shape and the cyathus-like protrusion. It clearly shows a broad rostrum, a slightly upwards curved ventral margin behind it and a faint alveolar furrow but no alveolar notch. The cyathus-like protrusion is acute, similar to *Praecypridea acuticyatha* but less pointed. In other respects, *Praecypridea acuta* resembles *Praecypridea postelongata* except for the position of maximum height which is slightly in front of half length.

*Praecypridea suprajurassica* is very similar to the type species of *Praecypridea* gen. nov. in its overall shape, outline and development of the anteroventral area. This species is somewhat larger than *P. acuticyatha*, its cyathus-like protrusion is almost rectangular and not as acute as in the latter and, therefore, in these respects does not correspond to the type species. However, considering the possible intraspecific variability of representatives of cypridoidean genera that feature mixed reproduction (e.g. Horne & Martens, 1998; Martens *et al.*, 1998) – as presumed for species of *Cypridea* and, consequently, also possible in species of *Praecypridea* gen. nov. – this variation could well be within the range for a single species of *Praecypridea* featuring mixed reproduction. Such variation would particularly affect the lateral outline. So far, sexual dimorphism has not been observed in *Praecypridea*.

The gap in the stratigraphical record may be due to insufficient continuous documentation of taxa of *Praecypridea* gen. nov., as yet unrecognized representatives of this genus (e.g. *Cypridea aemulans* nom. nov. pro *C. acuta* Anderson, 1971) or that *P. acuta* does not belong to this genus.

*Praecypridea acuticyatha* (Schudack, 1998) comb. nov.  
(Pl. 1, figs 1–8)

? 1957 ‘Ostracode 12089’: Grekoff, p. 87, table 1.

\*1998 *Cypridea acuticyatha* sp. nov.: Schudack, p. 405, pl. 1, figs 4–6.

**Diagnosis.** A small to medium-sized (around 1 mm) species of *Praecypridea* with a strongly acute and pointed cyathus-like protrusion. Rostrum barely developed, only represented by a slightly obtuse-angled intersection of the anterior and ventral margins. Ventral margin straight. Anterior cardinal angle well defined, dorsal margin straight and long, with strong posterior slope. Posterior cardinal angle indistinct and rounded. Posterior margin truncate and almost vertical. Valve surface smooth.

**Holotype.** MES 356. Collection of Michael E. Schudack (MES), Department of Geosciences, Palaeontology Branch, Micropalaeontological Collection, Freie Universität Berlin, Germany.

**Material.** Sixty carapaces poorly to moderately well preserved and few valves (infilled and poorly preserved) from two samples. Most specimens more or less deformed by lateral compression, cyathus-like protrusion often broken off.

**Type locality and horizon.** Kenton section, Cimarron County, Oklahoma, USA, Kenton 7.5' Quadrangle, C-SW1/4 Sec. 18, T. 5 N., R. 1 E. Upper part of Morrison Formation, biozone 4 (Kimmeridgian) of Schudack *et al.* (1998), 40 m above Bell Ranch Formation.

**Age.** Kimmeridgian.

**Description.** Oblique-trapezoidal in lateral outline. Maximum height at anterior cardinal angle, at about 2/5 of length; maximum length at ventral margin; maximum width at about half length. LV larger than RV, moderately overlapping it along the whole margin, also at hinge margin. Anterior margin broad and slightly infracurvate, almost equally rounded. Rostrum very poorly developed, only represented by a slightly obtuse-angled intersection of the anterior and ventral margins, very slight hint of alveolar furrow detectable in some specimens. Dorsal margin straight to slightly concave, considerably inclined (dipping 15–20°) to posterior. Posterior margin truncated, almost vertical. Cyathus-like protrusion long, extending far beyond posterior margin, and strongly acuminate in both valves, pointing in dorsoventral direction in an angle of about 45° from the ventral margin line. Anterior cardinal angle well defined (around 135°), moderately rounded, sometimes slightly less prominent in LV. Posterior cardinal angle indistinct, margin strongly rounded. Ventral margin straight. Dorsal view lenticular with pointed ends. Ventral view showing slight convex overlap of the left valve. Valve surface smooth. Internal features unknown. Sexual dimorphism not observed.

**Dimensions (mm).** Length 0.95–1.02, height 0.53–0.61, width 0.33–0.37.

**Occurrence.** North America: Morrison Formation, biozones 3 and 4 *sensu* Schudack *et al.* (1998), Kimmeridgian of the Front Range foothills in Oklahoma and Colorado, USA. Central Africa: Stanleyville Formation, Late Jurassic (probably Kimmeridgian), Democratic Republic of the Congo (pers. comm. Colin, January 2007).

**Remarks.** The cyathus-like protrusion is variable, being very distinct in typical specimens. Although there are specimens with an indistinct cyathus, this is due to bad preservation and/or processing.

'Ostracode 12089' of Grekoff (1957) is tentatively considered to be synonymous with *P. acuticyatha*. As stated above, there is only one, slightly damaged carapace and just a tiny line drawing. However, Colin (pers. comm., 2008) provided the authors with two SEM photographs of specimens that derive from the same horizon and locality as Grekoff's (1957) specimen. These are very similar to *P. acuticyatha* in general shape and clearly belong to *Praecypridea* gen. nov. but cannot be assigned to *P. acuticyatha* with certainty since they both show a strongly concave

ventral outline and are diagenetically deformed. The cyathus-like protrusion in these specimens, however, is as strongly acuminate as in *P. acuticyatha*. A closer relationship to *P. suprajurassica* seems to be less probable since the cyathus-like protrusion in the latter is almost rectangular.

*Praecypridea acuticyatha* differs from other species of the genus by its extremely acuminate cyathus-like protrusion, passing into the ventral and posterior margins with a clear concavity.

*Praecypridea postelongata* (Oertli, 1957) comb. nov.  
(Pl. 1, fig. 9)

\*1957 *Cypridea postelongata* sp. nov.: Oertli, p. 756, pl. 21, figs 5–7.

? 1981 *Cypridea postelongata*: Ware & Windle, p. 417.

1985 *Cypridea postelongata*: Dépêche, pl. 28, fig. 16.

non 1989 *Cypridea* cf. *postelongata*: Mojon, pl. 3, figs H, I, J.

non 2002 *Cypridea* cf. *postelongata*: Mojon, pl. 6, figs H, I, J.

**Diagnosis.** A relatively large (1.4 mm), elongate species of *Praecypridea* with a short and rounded rostrum, and a punctate surface. Cyathus-like protrusion well developed, slightly acuminate, almost right-angled. Dorsal margin straight. Posterior cardinal angle strongly rounded and barely recognizable.

**Holotype.** BBO 31, Collection of the Centre de Micropaléontologie Appliquée de l'Université de Paris, Paris, France. Specimen figured here is Paratype BE 195.

**Type locality and horizon.** Upper Bajocian (formerly considered to be Lower Bathonian, Colin & Carbonel, 1996, p. 188 – referring to Oertli, 1957), Vallée de la Vienne, Poitou, France.

**Age.** Upper Bajocian–Bathonian.

**Description.** Carapace elongated oblique-trapezoidal in lateral view. Maximum height at 1/3 of length, maximum length at ventral margin, maximum width at half length. LV larger than RV, overlapping the RV moderately along the entire margin except at hinge margin. Anterior margin slightly infracurvate, ventrally passing into a short and rounded rostrum. Posterior margin truncated, dipping about 80°. Cyathus-like protrusion almost right-angled to slightly acute, apex rounded. Dorsal margin straight, moderately inclined (10–15°) to posterior margin. Anterior cardinal angle indistinct but recognizable (obtuse angled, *c.* 140–145°). Posterior cardinal angle strongly rounded (obtuse angled, about 160–170°). Ventral margin straight to slightly concave. Carapace lenticular in dorsal view, slightly tapering towards both ends. Surface densely covered with small puncta. Internal characters not observed. Internal features unknown. Sexual dimorphism not observed.

**Dimensions (mm).** Length 1.4–1.6, height 0.7–0.8, width 0.5–0.6.

**Occurrence.** Upper Bajocian (formerly considered Lower Bathonian), Vallée de la Vienne, Paris Basin, France (Bernard *et al.*, 1957). Questionable: Bathonian, Forest Marble, Gloucestershire, England (Ware & Windle, 1981).

**Remarks.** ‘*Cypridea postelongata* Oertli in Timberlake (1982, pp. 209–211, pl. 7., figs T, U, V) does not possess a rostrum or angled intersection of the anterior and ventral margins, nor a cyathus-like protrusion and so does not belong to *Praecypridea* or *Cypridea*.

*Cypridea postelongata*, only mentioned by Ware & Windle (1981), has never been figured or described in a later publication. Its designation is very doubtful (see paragraph ‘Early evidence of the Cyprideidae’ above for details) as is, therefore, this English Middle Jurassic record of an early taxon of the Cyprideidae.

*Cypridea cf. postelongata* of Mojon (1989, 2002, plates identical) does not belong to *Praecypridea postelongata*. Regardless of the bad preservation, the specimens possess a different outline. There is no sign of a rostrum, and the maximum height is slightly in front of half length, and not at about 1/3 of length. In addition, the posterior margin is far from being almost vertical and does not show a cyathus-like protrusion, and the ventral part of the posterior margin is curved upwards. However, Mojon (1989, p. 9) states that, along with a fine punctuation and a longitudinal striation, the adult specimen also possesses ‘... un ébauche à peine perceptible de rostre antéro-ventral ...’ (translation: a hint of a scarcely noticeable anteroventral rostrum), and notes that J.W. Neale told him about the occurrence of similar forms in the Upper Jurassic of Syria. Since it comes from the same locality, Mojon’s species may be the one that Oertli & Ziegler (1958, p. 390) described as *Paracypria*. Given the morphological differences, we do not consider the presence of a faint rostrum-like structure alone as adequate evidence to refer *Cypridea cf. postelongata* of Mojon (1989, 2002) to *Praecypridea* gen. nov. Nevertheless, *Cypridea cf. postelongata* of Mojon should be included in forthcoming studies of possible ancestors of the *Praecypridea–Cypridea* lineage.

*Praecypridea acuta* (Moos in Wicher, 1959) comb. nov.  
(Pl. 1, figs 14–15)

\*1959 *Cypridea acuta* sp. nov.: Moos in Wicher, p. 46, pl. 9, figs 3 a, b.

non 1971 *Cypridea acuta* sp. nov.: Anderson, p. 50, pl. 16, fig. 5  
non 1985 *Cypridea aemulans* nom. nov. pro *C. acuta* Anderson, 1971: Anderson, p. 25, pl.4, fig. 2.

**Emended diagnosis.** A relatively large (1.4 mm) species of *Praecypridea* with a moderately acute cyathus-like protrusion. Posterior margin nearly straight, dipping with about 55° and passing smoothly into the cyathus-like protrusion. Anterior margin moderately infracurvate with weakly developed but broad rostrum not overreaching the ventral margin. Ventral margin slightly curved upwards behind rostrum, faint alveolar furrow. Dorsal margin short. Maximum height slightly anterior of mid-height. Posterior cardinal angle more distinct than anterior one. Surface smooth.

**Holotype.** B.f.B., T.-K.-Nr. 3179. Geoscientific collections of the former ‘Bundesanstalt für Bodenforschung’ (B.f.B.), today ‘Bundesanstalt für Geowissenschaften und Rohstoffe’ (BGR) and ‘Landesamt für Bergbau, Energie und Geologie’ (LBEG), Micropalaeontology, Hanover, Germany.

**Type locality and horizon.** Lower Cretaceous, Itaparica Formation (or Group/Series of some authors), Bahia Supergroup (Recôncavo Series), Dom João-Oilfield, Recôncavo Basin, NE Brazil.

**Age.** Early Cretaceous, ‘Neocomian’, pre-Late Barremian.

**Description.** Carapace relatively large and stretched-trapezoidal in lateral view. Maximum height slightly anterior of half length, maximum length at ventral margin, maximum width at half length. LV larger than RV, moderately overlapping the latter along the entire margin except at hinge margin. Anterior margin infracurvate, ventrally passing into a rostrum. Faint alveolar furrow, only developed in the right valve according to Moos (*in Wicher, 1959*). Ventral margin straight, slightly curved upwards behind the rostrum. Posterior margin almost straight, dipping about 55° and passing smoothly into a moderately acute cyathus-like protrusion. Dorsal margin short and straight, moderately inclined (10–15°) to posterior margin. Anterior cardinal angle indistinct, strongly rounded and strongly obtuse (160°). Posterior cardinal angle rounded, more distinctly marked than the anterior one but less obtuse (135°). Carapace lenticular in dorsal view, slightly tapering towards both ends. Valve surface smooth. Internal features unknown. Sexual dimorphism not observed.

**Dimensions (mm).** Length 1.4, height 0.7–0.8, width 0.5–0.6.

**Occurrence.** Lower Cretaceous, Itaparica Formation (or Group/Series of some authors), Bahia Supergroup (Recôncavo Series), Recôncavo Basin, Brazil (Moos *in Wicher, 1959*). Pre-Late Barremian Lower Cretaceous, ‘Neocomian’, Pre-Salt Section of West Africa, Gabon, Republic of the Congo, Democratic Republic of the Congo, Angola including Cabinda (Bate, 1999).

**Remarks.** Since the name was preoccupied, *Cypridea acuta* Anderson, 1971 has been renamed *Cypridea aemulans* by Anderson (1985). Its specimens are inverse (RV > LV). This species is very different from *Praecypridea acuta* (Moos *in Wicher*) in outline, has a fully developed rostrum and a distinct alveolar furrow. However, since *C. aemulans* does not exhibit an alveolar notch it might be taken into consideration for being a different species of *Praecypridea*.

Except for the first description, *P. acuta* has not yet been well studied and needs revision. As far as known, it seems to have a limited chronological and geographical distribution (Pre-Salt rift basins of West Africa and NE Brazil).

*Praecypridea suprajurassica* (Mojon, Haddoumi & Charrière, 2009) comb. nov.  
(Pl. 1, figs 10–13)

\*2009 *Cypridea suprajurassica* sp. nov.: Mojon *et al.*, p. 14, pl. 2, figs G1–G6, pl. 3, fig. E

**Emended diagnosis.** A medium sized (1.25 mm) species of *Praecypridea* with a weakly developed, almost rectangular cyathus-like protrusion. Ventral margin straight but curved upwards anteriorly at 1/4 of length. Rostrum barely recognizable.

**Holotype.** MHNG 60562. Collection of P.-O. Mojon at the 'Muséum d'Histoire Naturelle de Genève'. Refigured herein.

**Type locality and horizon.** Red Marls forming the base of the Iouaridéne Formation, shore of (barrier lake) Bin el Oidane, Ouaouizagth Syncline, Moroccan Atlas, Morocco.

**Age.** Oxfordian? and Kimmeridgian.

**Description.** For details, see Mojon *et al.* (2009). Amendment: Weak cyathus-like protrusion. Sexual dimorphism not observed.

**Dimensions (mm).** Length 1.05–1.25, height 0.55–0.80, width 0.42–0.46.

**Occurrence.** Upper Jurassic (Oxfordian?–Kimmeridgian), continental 'Red Beds' of the Ouaouizagth Syncline and Iouaridéne Syncline, Moroccan Atlas, Morocco.

**Remarks.** in a preliminary report (Mojon *et al.*, 2005, *Cypridea suprajurassica* Mojon & Haddoumi), on which the later article (Mojon *et al.*, 2009) is based. Unlike the description in Mojon *et al.* (2009), we consider the valve-size relation to be normal ( $LV > RV$ ), not inverse, since the LV is larger than the RV in the type species and the majority of species in *Cypridea* as well as in all species of *Praecypridea*.

*P. suprajurassica* is easy distinguishable from the otherwise similar *P. acuticyatha* by its weakly developed, almost rectangular cyathus – this also applies for 'Ostracode 12089' of Grekoff (1957) – and the anteriorly upwards curved ventral margin.

## DISCUSSION

As to the other possible species of *Praecypridea*, *Cypridea modica* Lyubimova, 1956 matches the diagnosis of *Praecypridea* gen. nov., except for the inverse ( $RV > LV$ ) valve overlap. Whether or not such inverse overlap is taxonomically significant and, if significant, at what taxonomic level, remains somewhat unclear and to be tested (in general we do not believe this character significant at the generic or specific level). The cyathus-like protrusion is well defined and acute, but only weakly pointed, while the rostrum is hardly developed.

*Paracypris* sp. *sensu* Schudack & Schudack (2002) is included here with considerable uncertainty because of its outline and acute cyathus-like posteroventral area. Since there is only one carapace and no internal features are available, the arguments for its designation as *Paracypris* sp. are also weak.

*Daurina mongolica* Sinitsa, 1986 (as figured in Nikolaeva & Neustrueva, 1999, pl. 12, fig. 4) is similar to *Praecypridea acuticyatha* in outline and shape of the posteroventral end of carapace, yet strongly rectangular in general shape and lacking an anteroventral angle or rostrum. More data and material are needed to clarify its taxonomic position in relation to *Praecypridea*.

The South American species *Salvadoriella? acuta* Krömmelbein & Weber, 1971 from the São Sebastião Beds ('NE Brazilian Wealden', Early Cretaceous, Brazil) is included in *Praecypridea* gen. nov. with reservations. At first view this species seems to be very similar to the type species *P. acuticyatha* in outline, especially regarding the development of the (strongly

acute) cyathus-like protrusion(?) and matches overall the generic diagnosis. However, it differs from *P. acuticyatha* in that its maximum height is more posterior and the otherwise straight ventral margin is curved downwards anteriorly at about 1/4 of carapace length, and somewhat more strongly developed in the larger left valve. Krömmelbein & Weber (1971, p. 46) had questionably assigned this species to *Salvadoriella* Krömmelbein because of its greater size (about 1.4 mm) in comparison to all other representatives of this genus, plus its different outline. They also (1971, p. 46) indicated its similarity to *Cypridea acuta* Moos in Wicher (1959), which is included in *Praecypridea* here, except for the missing rostrum in their *Salvadoriella? acuta*. Colin (written comm., 2009) examined topotypes of both species (PETROBRAS ostracod collections, Rio de Janeiro, Brazil) and confirmed their very close relationship, except for slight differences in outline and the large size of Krömmelbein & Weber's (1971) species. In the case that both taxa belong to *Praecypridea* gen. nov. but are different species *Salvadoriella? acuta* would have to receive a new species name.

*Cypridea aemulans* nom. nov. pro *Cypridea acuta* Anderson, 1971 (*non* Moos) is an inverse ( $RV > LV$ ) species, which mostly matches the diagnoses of *Praecypridea* in outline, development of the rostrum, absence of the alveolar notch, slight punctation and a faint alveolar furrow. However, from Anderson's (1971) descriptions and figures it is unclear whether this species exhibits a cyathus or a cyathus-like protrusion, and the anteroventral end is obtuse-angled ( $>90^\circ$ ) and overreached by the posterior margin. With respect to the latter features, this species more probably belongs to *Cypridea*. Yet, original material has to be restudied to test whether the species should better be assigned to *Praecypridea* or not.

There are a couple of known Late Jurassic or Early Cretaceous non-marine ostracod species showing similarity to *Praecypridea* at first view, such as *Cypridea blackbushensis* Anderson, 1967 (*in* Anderson *et al.*, 1967) and *Eoparacypris abbreviata* Anderson, 1971 from the English Purbeck and Wealden, for example. However, owing to the rather dated publications and insufficient descriptions and figures in many cases, these require detailed revision and study of the original material regarding their assignment to either *Praecypridea* or *Cypridea*. With respect to the given examples, *Eoparacypris abbreviata* is very thin-shelled, very small ( $< 0.7$  mm) and most probably represents juveniles of a species of *Cypridea*, which would also explain the narrow posterior margin. The type material has been inspected by BS, is pyritized with almost steinkern preservation (true for the holotype figured in Anderson, 1985, pl. 11, fig. 6) and the shell mostly dissolved. *Cypridea blackbushensis* is very small and thin shelled as well and exhibits a very acute spine-like ventrolateral protrusion. Nevertheless, it is also considered to represent (juvenile specimens of) a species of *Cypridea* due to its fully developed rostrum and distinct alveolar furrow. The taxa given are just a few examples from NW Europe. Other potential candidates from Middle Jurassic to Early Cretaceous non-marine deposits world-wide will be discussed elsewhere.

Thus far, it is unclear whether the North American *Praecypridea acuticyatha*, the northwest African species *P. suprajurassica* and 'Ostracode 12089' of Grekoff (1957) belong to the same species or not. *P. acuticyatha* and 'Ostracode 12089' are very similar in outline, size and the strongly acute cyathus-like

protrusion. *P. suprajurassica*, in contrast, is somewhat larger than the latter two species, its outline is more rounded and the cyathus-like protrusion nearly right-angled. However, some specimens of *P. acuticyatha* (see Pl. 1, figs 5 and 7) also exhibit such an overall shape and a much less acute to right-angled cyathus-like protrusion. Considering the possible morphological variation within species of *Cypridea*, the conclusion is that this may also apply to species of *Praecypridea*. That would mean the differences between *P. acuticyatha* and *P. suprajurassica* might be ontogenetic (juveniles of *Cypridea* generally show a narrower posterior margin that causes a more acute-angled cyathus than that developed in adults) and/or conceal a sexual dimorphism.

The widely assumed strong endemism of Mesozoic non-marine ostracod faunas in general, and that of the Jurassic–Cretaceous Gondwanan rifts of Brazil and West Africa in particular, has become doubtful due to progress in the worldwide documentation of these faunas and new insights into the taxonomy, distribution (e.g. passive transport of living ostracods or their eggs by animals or wind) and reproductive mechanisms (mixed sexual and asexual reproduction) of the cyprid taxa. Therefore, a Late Jurassic faunal exchange between West Africa and North America does not seem to have been impossible and should be taken into consideration during taxonomic analyses.

Provided that the postulated ancestorship of at least some taxa of *Praecypridea* to *Cypridea* is correct, the evolution from *Praecypridea* (with weakly developed or no rostrum, missing alveolar notch and rarely occurring alveolar furrow, cyathus-like protrusion in both valves) to the ‘true’ *Cypridea* (with distinct rostrum and fully developed alveolus with alveolar notch, ‘true’ cyathus, dorsal furrow due to incised hinge margin) remains unclear. Some species of *Cypridea* might have (partially) reduced(?) rostrum and alveolus and possibly even the pointed cyathus. Based on the available data, the transition between the genera appears to be continuous and the fossil record of representatives of *Praecypridea* remains geographically sporadic and stratigraphically fragmentary to date. The so far oldest taxon *P. postelongata*, for example, seems to be relatively advanced for the time in the development of its rostrum, but lacks the alveolar notch. The Kimmeridgian taxa *P. acuticyatha* and *P. suprajurassica*, in contrast, have no alveolus, barely show a rostrum and co-existed with representatives of *Cypridea* (see Schudack & Schudack, 2002; Schudack & Sames, 2003; Sames, 2008). Younger forms of *Praecypridea* that co-existed with many taxa of *Cypridea*, such as *P. acuta*, show a combination of plesiomorphic (cyathus-like protrusion, no alveolar notch, very weak alveolar furrow) and apomorphic (strong rostrum, weak dorsal furrow) features. The problem is further complicated by the fact that the functional morphology of some most important features of the Cypridoidea, i.e. rostrum, alveolus and cyathus as well as cyathus-like protrusion, is as yet unknown. *P. postelongata*, on the one hand, and *P. acuticyatha* and *P. suprajurassica*, on the other hand, may belong to two different lineages that had already separated as early as the Bathonian. Because of its relatively well-developed rostrum, *P. postelongata* would then come into consideration for the most probable ancestor to a *Cypridea* lineage, and this would also explain the occurrence of taxa of ‘true’ *Cypridea* as early as Kimmeridgian (as known to date, probably even older). Conse-

quently, *P. acuta* would be a late representative of that lineage and morphologically represent a transitional stage in the evolution from *Praecypridea* to *Cypridea*. In contrast, *P. acuticyatha* and *P. suprajurassica* may represent a more primordial sideline, lacking a true rostrum and alveolus, that might have become extinct by the end of the Kimmeridgian.

Admittedly, since the Middle to Upper Jurassic fossil record of the Cypridoidea is still very sparse and fragmentary and the internal carapace features are unknown, the above remarks remain speculative for the moment and other scenarios are conceivable.

## CONCLUSIONS

The details of the origin and early evolution of the non-marine Cypridoidea remain poorly understood. The resting egg has certainly been a key factor for the success of the early non-marine Cypridoidea with respect to adaptation to temporary water bodies and passive dispersal. The time of its origin within this superfamily, however, remains to be clarified. It is likely that the first sustained cypridoidean colonization of continental environments took place in the Middle Jurassic. Representatives of the extinct Family Cypridoidea Martin, 1940 were part of this event. The taxa of *Praecypridea* gen. nov. are presumed to be the earliest representatives of this family. Based on the concept of a *Praecypridea*–*Cypridea*–*Bisulcocypridea* lineage, the oldest taxon of the Cypridoidea is the Bathonian *Praecypridea postelongata* (Oertli), the youngest taxon is the Eocene *Cypridea (Cypridea) pingyiensis* Guan. Accordingly, the Cypridoidea are considerably older than has been previously assumed. During the Kimmeridgian, the more conservative morphotypes of *Praecypridea* taxa co-existed with ‘true’ *Cypridea*, suggesting a pre-Kimmeridgian to early Kimmeridgian origin of one or more *Cypridea*-lineages.

The reasons for the differential success of the Cypridoidea during the latest Jurassic to Early Cretaceous, as compared to other lineages of the Cypridoidea, are as yet unresolved. Further studies will be needed to find out if one factor could have been their swimming ability in combination with a possible change in the plankton association of their habitats (the resting egg is not considered a factor in this context because it also occurs in other cyprids and within the Cytheroidea, see also Horne & Martens, 1998). Possibly, the trophic system in the water bodies changed so much that representatives of the Cypridoidea were able to radiate (dramatically?). Yet, whether rostrum and alveolus are features related to feeding, swimming or something else is unknown. Another possibility could have been the acquisition of mixed reproduction, which can strongly raise the genetic and morphological variability, thereby feigning a higher diversity in the fossil record, or a combination of several factors.

However, the immense diversity of this group, particularly during the Early Cretaceous, has been challenged recently (Horne in Nye *et al.*, 2008; BS, research in progress) and is considered to have been highly overestimated. Therefore, it also becomes questionable whether the Cypridoidea – the representatives of *Cypridea* in particular – really dominated the ostracod faunas in non-marine habitats of that time in terms of diversity.

Based upon the current state of research, it seems apparent that the latest Jurassic/Early Cretaceous radiation of the now-extinct family Cypridoidea (i.e. *Cypridea* and its close relatives)

in non-marine deposits of the Lower Cretaceous virtually worldwide may have started earlier (Middle instead of latest Jurassic). The faunal importance of (early) Cyprideidae in Middle to Late Jurassic times has certainly been underestimated due to the difficulties in identifying the representatives of this family, while the latest Jurassic to Early Cretaceous diversity of the Cyprideidae (particularly within *Cypridea*) has been strongly overestimated at the species level. Nevertheless, species diversity within *Praecypridea* seems to be much lower than in *Cypridea*. The differentiation of the Cyprideidae had begun earlier and the species diversity and geographical distribution was already fairly high by the Kimmeridgian. A detailed synopsis of the many problems in the context of the early (pre-Bathonian) evolution of non-marine Cypridoidea will be given elsewhere. We hope that the new data and ideas presented here will help to clarify the situation with respect to the given problems, and encourage further studies.

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#### REFERENCES

- Anderson, F.W. 1971. Part II – The ostracods. In: Anderson, F.W. & Bazley, R.A.B. The Purbeck Beds of the Weald. *Bulletin of the Geological Survey of Great Britain*, **34**: 1–174.
- Anderson, F.W. 1985. Ostracod faunas of the Purbeck and Wealden of England. *Journal of Micropaleontology*, **4**: 1–68.
- Anderson, F.W., Bazley, R.A.B. & Shephard-Thorn, E.R. 1967. The sedimentary and faunal sequence of the Wadhurst Clay (Wealden) in boreholes at Wadhurst Park, Sussex. *Bulletin of the Geological Survey of Great Britain*, **27**: 171–269.
- Bate, R.H. 1999. Non-marine ostracod assemblages of the Pre-Salt rift basins of West Africa and their role in sequence stratigraphy. In: Cameron, N.R. & Clure, V.S. (Eds), *The Oil and Gas Habitats of the South Atlantic*. Geological Society, London, Special Publications, **153**: 283–292.
- Bernard, F., Bizon, J.-J. & Oertli, H.J. 1957. Ostracodes lacustres du Bathonien du Poitou (Bassin de Paris). *Bulletin de la Société Géologique de France*, **6**(6): 753–770.
- Branson, C.C. 1935. Freshwater invertebrates from the Morrison (Jurassic?) of Wyoming. *Journal of Paleontology*, **9**: 514–522.
- Bussert, R., Heinrich, W.-D. & Aberhan, M. 2009. The Tendaguru Formation (Late Jurassic to Early Cretaceous, southern Tanzania): definition, palaeoenvironments, and sequence stratigraphy. *Fossil Record*, **12**: 141–174.
- Colin, J.-P. & Carbonel, P. 1996. Middle Jurassic record of the limnic ostracode genus *Rosacythere* (Limnocytheridae, Timiriaseviinae): Implications on the origin and evolution of the *Kovalevskiella* group. *Journal of Micropaleontology*, **15**: 187–191.
- Dépêche, F. 1985. Lias supérieur, Dogger, Malm. In: Oertli, H.J. (Ed.), *Atlas des Ostracodes de France (Paléozoïque – Actuel)*. *Bulletin des Centres des Recherches Exploration-Production Elf-Aquitaine*, Mémoire **9**, Société Nationale Elf Aquitaine (Production), Pau, 119–145.
- Gou, Y.-S. & Cao, M.-Z. 1983. Stratigraphic and biogeographic distribution of the *Cypridea*-bearing faunas in China. In: Maddocks, R.F. (Ed.) *Applications of Ostracoda. Proceedings of the 8th International Symposium on Ostracoda, July 26–29, 1982*, Department of Geosciences, University of Houston, Houston, 381–393.
- Gradstein, F.M., Ogg, J.G. & Smith, A.G. (Eds). 2004. *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge, 610pp.
- Grekoff, N. 1957. Ostracodes du Bassin du Congo. 1. Jurassique supérieur et Crétacé inférieur du nord du bassin. *Annales du Musée Royal du Congo Belge, Tervuren, Série in-8°, Sciences géologiques*, **19**: 1–97.
- Guan, S.-Z., Pang, Q.-Q. & Xiao, Z.-Z. 1997. The early Eocene non-marine ostracods from Pingyi Basin, Shandong. *Acta Micropaleontologica Sinica*, **14**: 321–340.
- Hahn, G. & Hahn, R. 1999. Pinheirodontidae n. fam. (Multituberculata) (Mammalia) aus der tiefen Unter-Kreide Portugals. *Palaeontographica*, **A253**: 77–222.
- Harper, F. & Sutton, A.H. 1935. Ostracodes of the Morrison Formation from the Black Hills, South Dakota. *Journal of Paleontology*, **9**: 623–628.
- Helmdach, F.-F. 1971. Zur Gliederung limnisch-brackischer Sedimente des portugiesischen Oberjura (ob. Callovien–Kimmeridge) mit Hilfe von Ostrakoden. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, Jahrgang **1971**: 645–662.
- Helmdach, F.-F. 1974. A contribution to the stratigraphical subdivision of nonmarine sediments of the Portuguese Upper Jurassic. *Comunicações dos Serviços Geológicos de Portugal*, **57**: 5–21.
- Horne, D.J. 1995. A revised ostracod biostratigraphy for the Purbeck–Wealden of England. *Cretaceous Research*, **16**: 639–663.
- Horne, D.J. 2002. Ostracod biostratigraphy and palaeoecology of the Purbeck Limestone Group in southern England. *Special Papers in Palaeontology*, **68**: 53–70.
- Horne, D.J. & Colin, J.-P. 2005. The affinities of the ostracod genus *Cypridea* Bosquet, 1852, and its allies, with consideration of implications for the phylogeny of nonmarine cypridoidean ostracods. *Revue de Micropaléontologie*, **48**: 25–35.
- Horne, D.J. & Martens, K. 1998. An assessment of the importance of resting eggs for the evolutionary success of Mesozoic non-marine cypridoidean Ostracoda (Crustacea). *Archives Hydrobiologica Special Issues on Advanced Limnology*, **52**: 549–561.
- Hünicken, M.A. & Chaia, A.A. 1992. Registro de ictiolitos y fósiles asociados en la Formación Las Cabras (Triásico medio) del noreste de Mendoza. *Revista Asociación Geológica Argentina*, **47**: 266.
- Kietzke, K.K. & Lucas, S.G. 1995. Ostracoda and Gastropoda from the Kayenta Formation (Lower Jurassic) of Arizona, U.S.A. *Journal of Arizona–Nevada Academy of Science*, **28**: 23–32.
- Krömmelbein, K. & Weber, R. 1971. Ostracoden des 'Nordost-Brasilianischen Wealden'. *Beihefte zum Geologischen Jahrbuch*, **115**: 1–93.
- Lyubimova, P.S. 1956. Ostracody Melovykh Otlozheniy Vostochnoy Chasti Mongolskoy Narodnoy Respubliki i ikh Znachenie dlya Stratiografii [Ostracoda from Cretaceous deposits of the eastern part of the

- People's Republic of Mongolia and their significance for stratigraphy]. *Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo – Razvedochnogo Instituta (VNIGRI), Novaya Seriya*, **93**: 1–174.
- Lüttig, G. 1962. Zoologische und paläontologische Ostracoden-Systematik. *Paläontologische Zeitschrift*, **H. Schmidt-Festband**: 154–184.
- Martens, K., Horne, D.J. & Griffiths, H.I. 1998. Age and diversity of non-marine ostracods. In: Martens, K. (Ed.), *Sex and Parthenogenesis – Evolutionary Ecology of Reproductive Modes in Non-marine Ostracods*. Backhuys Publishers, Leiden, 37–55.
- Martin, G.P.R. 1940. Ostracoden des norddeutschen Purbeck und Wealden. *Senckenbergiana*, **22**: 275–361.
- Martin, G.P.R. 1958. *Cetacella* – eine neue Ostracoden-Gattung aus dem Kimmeridge Nordwestdeutschlands. *Paläontologische Zeitschrift*, **32**: 190–196.
- Martin, T. 1999. Dryolestidae (Dryolestidea, Mammalia) aus dem Oberen Jura von Portugal. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, **550**: 1–119.
- Mohr, B.A.R. 1989. New palynological information on the age and environment of Late Jurassic and Early Jurassic vertebrate localities of the Iberian Peninsula (eastern Spain and Portugal). *Berliner Geowissenschaftliche Abhandlungen, Reihe A*, **106**: 291–301.
- Mojon, P.-O. 1989. Charophytes et ostracodes laguno-lacustres du Jurassique de la Bourgogne (Bathonien) et du Jura Septentrional Franco-Suisse (Oxfordien). Remarques sur les discontinuités émersives du Kimméridgien du Jura. *Revue de Paléobiologie, Volume spécial*, **3**: 1–18.
- Mojon, P.-O. 2002. Les Formations Mésozoïques à Charophytes (Jurassique Moyen – Crétacé Inférieur) de la Marge Téthysienne Nord-Occidentale (SE de la France, Suisse occidentale, NE de l'Espagne). Sédimentologie, micropaléontologie, biostratigraphie. *Géologie Alpine, Mémoire H.S.*, **41**: 1–386.
- Mojon, P.-O., Haddoumi, H. & Charrière, A. 2005. Nouvelles données sur les Charophytes et Ostracodes du Jurassique-Crétacé de l'Atlas marocain. In: Mojon, P.O. (Ed.), *Recherches sur la Pangée mésozoïque*. Digit Presse Sàrl, Lausanne, Suisse, Neocomiana.com, **1**: 1–43.
- Mojon, P.-O., Haddoumi, H. & Charrière, A. 2009. Nouvelles données sur les Charophytes et Ostracodes du Jurassique moyen-supérieur – Crétacé inférieur de l'Atlas marocain. *Carnets de Géologie/Notebooks on Geology, Brest, Memoire 2009/3*: 1–39.
- Nikolaeva, I. & Neustrueva, I.Y. (Eds). 1999. *Prakticheskoye Rukovodstvo po Mikrofaunje, Tom 7. Ostracody Mesosoya (Practical Manual on Microfauna, Vol. 7. Mesozoic Ostracoda)*, VSEGEI Press, St Petersburg, 244pp.
- Nye, E., Feist-Burkhardt, S., Horne, D.J., Ross, A.J. & Whittaker, J.E. 2008. The palaeoenvironment associated with a partial *Iguanodon* skeleton from the Upper Weald Clay (Barremian, Early Cretaceous) at Smokejacks Brickworks (Ockley, Surrey, UK), based on palynomorphs and ostracods. *Cretaceous Research*, **29**: 417–444.
- Oertli, H.-J. 1957. In: Bernard, F., Bizon, J.-J. & Oertli, H.-J. Ostracodes lacustres du Bathonien du poutou Bassin de Paris. *Extrait du Bulletin de la Société Géologique de France*, **6**: 753–770.
- Oertli, H.-J. (Ed.). 1985. Atlas des Ostracodes de France (Paléozoïque–Actuel). *Bulletin des Centres des Recherches Exploration-Production Elf-Aquitaine, Memoir*, **9**, Société Nationale Elf Aquitaine (Production), Pau, 11–396.
- Oertli, H.-J. & Ziegler, M. 1958. Présence d'un Séquanien lacustre dans la région de Pontarlier (Département Doubs, France). *Eclogae Geologicae Helvetiae*, **51**: 385–390.
- Pang, Q.-Q. & Whatley, R.C. 1990. The biostratigraphical sequence of Mesozoic non-marine ostracod assemblages in northern China. In: Whatley, R.C. & Maybury, C. (Eds), *Ostracoda and Global Events. Proceedings of the 10th International Symposium on Ostracods, Aberystwyth*, 1988. Chapman & Hall, London, 239–250.
- Retrum, J.B. & Kaesler, R.L. 2005. Early Permian Carbonitidae (Ostracoda): ontogeny, affinity, environment and systematics. *Journal of Micropalaeontology*, **24**: 179–190.
- Roth, R.I. 1933. Some Morrison Ostracoda. *Journal of Paleontology*, **7**: 398–405.
- Sames, B. 2008. Application of Ostracoda and Charophyta from the Late Jurassic to Early Cretaceous Tendaguru Formation at Tendaguru, Tanzania (East Africa) – Biostratigraphy, Palaeobiogeography and Palaeoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **264**: 213–229.
- Sames, B. 2010. To correlate or not to correlate – That is not the question anymore! Continental Late Jurassic to Early Cretaceous supraregional correlation based on freshwater to brackish-water ostracods. *Palaaios*, **25**: 3–5.
- Sames, B., Cifelli, R.L. & Schudack, M.E. 2010. The nonmarine Lower Cretaceous of the North American Western Interior foreland basin: new biostratigraphic results from ostracod correlations and its implications for paleontology and geology of the basin – an overview. *Earth Science Reviews*, **101**: 207–224.
- Schleifer, A.G. 1966. Ostracody Baskunchakskoy Serii Nizhnego Triasa Prikaspiyskoy Vpadiny i ikh stratigraficheskoe znachenie [Ostracoda of the lower Triassic Baskunchak Series from the Precaspian Depression and their stratigraphical importance]. In: Gubkina, I.M. (Ed.), *Geology of the Russian Platform. The Pricaspian and Ohrenberg regions*. Trudy Moscow Institut, 111–129.
- Schudack, M.E. 1998. Appendix: The ostracodes and charophytes of the Morrison Formation. In: Schudack, M.E., Turner, C.E. & Peterson, F. Biostratigraphy, paleoecology and biogeography of charophytes and ostracodes from the Upper Jurassic Morrison Formation, Western Interior, USA. *Modern Geology*, **22**: 402–414.
- Schudack, M.E. 2006. Basal Jurassic nonmarine ostracods from the Moenave Formation of St. George, Utah. In: Harris, J.D., Lucas, S.G., Spielmann, J.A., Lockley, M.G., Milner, A.R.C. & Kirkland, J.I. (Eds), *The Triassic–Jurassic Terrestrial Transition. New Mexico Museum of Natural History and Science Bulletin*, **37**, 427–431.
- Schudack, M.E. & Sames, B. 2003. Probable Kimmeridgian (mid Late Jurassic) first appearance of *Cypridea* on the Gondwana continent and its relation to plate tectonics and paleoclimates. In: Rodríguez-Lázaro, J. & Baltanás, Á. (Eds), *Fifth European Ostracodologists Meeting Cuenca 2003, Abstracts & Guidebook of Excursions*, p.44.
- Schudack, M.E. & Schudack, U. 2002. Ostracods from the Middle Dinosaur Member of the Tendaguru Formation (Upper Jurassic of Tanzania). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **6**: 321–336.
- Schudack, M.E., Turner, C.E. & Peterson, F. 1998. Biostratigraphy, paleoecology and biogeography of charophytes and ostracods from the Upper Jurassic Morrison Formation, Western Interior, USA. *Modern Geology*, **22**: 379–414.
- Sinitas, S.M. 1986. Rakoobraznye: Ostracody. *Trudy Sovmestnaya Sovetsko-Mongolskaya Paleontologicheskaya Ekspeditsiya*, **28**: 174–178.
- Sohn, I.G. 1958. Middle Mesozoic non-marine ostracodes of the Black Hills. *Wyoming Geological Association Guidebook, 13th Annual Field Conference*, Wyoming Geological Association, Casper, 120–126.
- Sohn, I.G. 1979. Nonmarine ostracodes in the Lakota Formation (Lower Cretaceous) from South Dakota and Wyoming. *Geological Survey Professional Paper*, **1069**: 1–24.
- Strand, E. 1928 (for 1926). *Miscellanea Nomenclatorica Zoologica et Palaeontologica. Archiv für Naturgeschichte, Abteilung A*, **92**: 30–75.
- Szczuchura, J. 1981. The taxonomy of *Cypridea* Bosquet, 1852, and similar ostracods. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **161**: 254–269.
- Timberlake, S. 1982. *A taxonomic and population study of the Limnocytheridae Ostracoda from the Forest Marble of Tarlton, Gloucestershire*. Magister thesis, University College of Wales, Aberystwyth, 395pp. (Thesis and material are available from the Palaeontology Department of The Natural History Museum, London, former Aberystwyth University Microfossil Collection.)
- Ware, M. & Windle, T.M.F. 1981. Micropalaeontological evidence for land near Cirencester, England in Forest Marble (Bathonian) times: a preliminary account. *Geological Magazine*, **118**: 415–420.
- Whatley, R.C. 1986. Biological events in the evolution of Mesozoic Ostracoda. In: Walliser, O. (Ed.), *Global Bio-Events. Lecture Notes in Earth Sciences*, **8**: 257–265.
- Whatley, R.C. 1988. Patterns and rates of evolution in Mesozoic Ostracoda. In: Hanai, T., Ikeya, N. & Ishizaki, K. (Eds), *Evolutionary*

- biology of Ostracoda, its fundamentals and applications*. Developments in Palaeontology and Stratigraphy, **11**: 739–758. Kodansha/Elsevier, Tokyo.
- Whatley, R.C. 1990a. Ostracoda and Global Events. In: Whatley, R.C. & Maybury, C.A. (Eds), *Ostracoda and Global Events. Proceedings of the 10th International Symposium on Ostracods, Aberystwyth, 1998*. Chapman & Hall, London, 3–24.
- Whatley, R.C. 1990b. The relationship between extrinsic and intrinsic events in the evolution of Mesozoic nonmarine Ostracoda. In: Kaufmann, E.G. & Walliser, O.H. (Eds), *Extinction events in Earth History*. Lecture Notes in Earth Sciences, **30**: 253–263.
- Whatley, R.C. 1992. The reproductive and dispersal strategies of Cretaceous nonmarine Ostracoda: the key to pandemism. In: Mather, N.J. & Chen, Pei-ji (Eds), *Aspects of nonmarine Cretaceous Geology*. China Ocean Press, Beijing, 177–192.
- Whatley, R.C. & Ballent, S.C. 1996. In search of the earliest nonmarine cypridacean ostracods: New discoveries from the early Mesozoic of Western Argentina. In: Riccardi, A.C. (Ed.), *Advances in Jurassic Research*. GeoResearch Forum, **1**(2): 111–118.
- Whatley, R.C., Ayress, M., Downing, S., Harlow, C. & Kesler, K. 1985. *Aratrocypris*, an enigmatic new cyprid ostracod from the Tertiary of D.S.D.P. sites in the S.W. Pacific. *Journal of Micropalaeontology*, **4**: 69–79.
- Whatley, R., Witte, L. & Coles, G. 1989. New data on the ostracod genus *Aratrocypris* Whatley *et al.* 1985, with description of species from the Upper Cretaceous of Europe and the Cainozoic of the North Atlantic. *Journal of Micropalaeontology*, **8**: 207–214.
- Wicher, C.A. (with appendix by B. Moos). 1959. Ein Beitrag zur Altersdeutung des Reconcavo, Bahia (Brasilien). *Geologisches Jahrbuch*, **77**: 35–58.
- Xu, M.-Y. 1983. Ostracods from the Mesozoic coal-bearing strata of South China. In: Maddocks, R.F. (Ed.), *Applications of Ostracoda. Proceedings of the 8th International Symposium on Ostracoda, July 26–29, 1982*. Department of Geosciences, University of Houston, Houston, 352–371.
- Ye, C. 1994. Succession of Cypridacea (Ostracoda) and nonmarine Cretaceous stratigraphy of China. *Cretaceous Research*, **15**: 285–303.