Systematic review and evolution of the early Cytheruridae (Ostracoda)

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ABSTRACT – A review of the literature on the taxonomy of Triassic and Early Jurassic cytheracean Ostracoda reveals that the validity of many genera is questionable. A number of studies of the Triassic microfaunas from eastern European sequences have, in particular, obscured the true generic and suprageneric classification of many ostracod taxa. The present study concentrates on the diverse extant cytheracean family the Cytheruridae, whose origins are in the earliest Mesozoic–latest Palaeozoic, but it is clear that many contemporary cytheracean families present similar problems. This review clarifies the previous taxonomic confusion and obfuscation by demonstrating that many of these genera are spurious having been erected on specific rather than generic morphological criteria. Many of them are best accommodated within the extant genus *Eucytherura* Müller, 1894. Most of the cytherurid genera known from the Liassic deposits of NW Europe can be traced back to these Triassic assemblages. In considering the origin and earliest evolution of the Cytheruridae, we note that some Triassic taxa share characteristics typical of both the Cytheruridae and the Bythocytheridae and it is suggested that the former may have arisen from the latter family during the latest Permian or earliest Triassic. We also note that the palaeoenvironmental interpretation of many of the Triassic deposits is brackish-water, marginal marine. *J. Micropalaeontol.*, **19**:(2): 139–152, December 2000.

INTRODUCTION

The family Cytheruridae G. W. Müller, 1894 is one of the most diverse extant families of ostracods with a fossil record extending back to the Early Mesozoic or possibly the latest Permian. Today they are almost exclusively marine, although there are some euryhaline species. During the Cenozoic the family was almost equally diverse in shelf and deep-sea environments. Mesozoic cytherurids seem to have been largely confined to shelf depths but shallow, brackish-water taxa are also known. This paper is limited to a consideration of Permian, Triassic and earliest Jurassic taxa.

In an attempt to establish the phylogenetic origin of the cytherurids we have re-evaluated the available published descriptions of Triassic marine and marginal-marine cytheracean taxa in a literature search of global scope. In this study we have considered a large number of genera and species, many of which are discussed here. We have found it necessary to synonymize a number of genera and also entire families as Whatley & Moguilevsky (1998) did in a similar study of the Limnocytheridae. Within these Triassic assemblages we recognize some of the earliest representatives of the Cytheruridae. With some taxa we have experienced difficulties in determining their familial status. This is only to be expected early in the adaptive radiation of a superfamily and that of the Cytheracea is no exception (Whatley & Stephens, 1976; Whatley, 1988).

The first major evolutionary radiation within the Cytheruridae is recognized to have taken place during the latest Triassic to Early Jurassic (Whatley *et al.*, 1993), with some of these newly established genera surviving to the present day (e.g. *Cytheropteron*, *Eucytherura*). A large number of post-Palaeozoic cytheracean ostracod families can be traced back to the earliest Mesozoic, following the final extinction of many 'palaeocopid' ostracods by the close of the Permian (Whatley & Stephens, 1976). Some authors signally failed to recognize that many of these early Cytheracea belonged to pre-existing post-Triassic genera and placed them in a series of spurious new genera. This is particularly true of the marine and euryhaline assemblages of Central, East and SE Europe. One of the consequences is that these 'new' genera appear to be stratigraphically restricted to the Triassic. Furthermore, many of the new genera have been erected on the basis of what we regard as specific characteristics and this is supported by the observation that many of them are mono-specific and, in some cases, were erected on a single specimen. The true suprageneric position of these taxa has, therefore, been obscured and the phylogenetic significance of these assemblages has only recently become apparent. The problem is compounded by the fact that these new taxa were placed in new families that were also stratigraphically confined to the Triassic. Many Liassic species, as demonstrated below, were also placed in new genera restricted to the Early Jurassic and we have synonymized a number of them.

The Late Palaeozoic demise of the 'palaeocopids' and other ostracod groups resulted in the emergence of typical Mesozoic assemblages, many of which have not previously been recorded in pre-Jurassic sediments. It would appear that their 'absence' from Triassic sediments was an artefact caused by misidentification and mis-interpretation. We believe that it is now possible to establish the antiquity, if not necessarily the origin, of the Cytheruridae within these Triassic assemblages.

The taxonomic problems outlined above have been compounded further by the fact that fully marine Triassic sequences are rather rare in NW Europe, so that most attention has been directed towards marginal-marine or freshwater ostracod assemblages (e.g. Beutler & Gründel, 1963). Although most modern post-Liassic cytherurids (with notable exceptions) are marine, it now seems that some of their earliest representatives inhabited brackish-water marginal-marine environments. Marine sequences from the Early Mesozoic Tethys were largely unknown or ignored by European workers prior to the last 30 years. European studies in the epicontinental extension of Tethys, mainly by Kozur and colleagues (Kozur, 1968a,b, 1970a,b, 1971, 1972a, 1973; Kozur & Nicklas, 1970; Kozur *et* al., 1974) epitomised the problems outlined above with, what is in our opinion, unnecessary 'splitting' at generic level. Subsequently, Kristan-Tollmann (1972, 1983, 1986, 1989) Kristan-Tollmann & Hasibuan, (1990), Kristan-Tollmann & Gramann (1992), Kristan-Tollmann et al. (1991a,b) have extended our knowledge of Tethyan faunas through studies of Triassic marine deposits from the European Alps, Iran, Indonesia, China, Australia and New Zealand (see review in Kristan-Tollman, 1988). Most importantly she illustrated many Triassic taxa using scanning electron micrographs which are a significant improvement on the poorer quality reflected light microscope illustrations of earlier workers. Sohn (1968, 1970, 1987) has also added valuable information on Triassic ostracods from Israel, Pakistan and Alaska respectively. Basha (1982) reported Triassic ostracods from Jordan. A number of papers describe Triassic ostracodes from ODP Leg 122 of NW Australia (Crasquin-Soleau et al., 1990; Crasquin-Soleau & Dépêche, 1992; Dépêche & Crasquin-Soleau, 1992; Kristan-Tollmann & Gramann, 1992). Marine Triassic ostracods have also been described from China (Guan, 1985; Zheng, 1988).

The Cytheruridae belong to the Superfamily Cytheracea (Order Podocopina, Ordovician to Recent) which dominate most post-Palaeozoic marine assemblages. The Cytheracea are characterized, among other features, by a vertically aligned row of four (rarely three or five) adductor muscle scars. The majority of Palaeozoic ostracods are distinguished by the possession of a sub-circular, irregularly arranged group of between 10 and 100 individual muscle scars, the only known Palaeozoic cytheracean ostracods are the Permianidae, the Limnocytheridae (Whatley & Moguilevsky, 1998) which are non-marine, and the marine Bythocytheridae. The Permianidae are characterised by a vertically aligned row of three and the Bythocytheridae by five adductor muscle scars, while the Limnocytheridae like virtually all other Cytheracea have four vertically aligned adductors. It is our contention that the Bythocytheridae were the root stock which, during the Late Palaeozoic or Early Mesozoic interval, gave rise directly or indirectly to all other Cytheracea and that one of the earliest recognizable cytheracean families is the Cytheruridae.

Conventionally, three subfamilies are recognized within the Cytheruridae: the Cytherurinae, the Cytheropterinae (Hanai, 1957) and the Paracytherideinae (Mandelstam, in Orlov, 1960) (although some authors accord the latter separate familial status while others would include additional subfamilies such as the Late Cretaceous to Recent Oculocytheropterinae Bate & Coleman, 1975 and the Jurassic to Recent Eucytherurinae Puri, 1974. The present authors contend that the majority of cytherurid species identified in the Triassic belong to the Cytherurinae while some are certainly, and others possibly, members of the Cytheropterinae. The family is known to be well established by the Early Jurassic. The Paracytherideinae are believed to have their earliest record in the Cretaceous and are not considered further in this study.

Unfortunately, many of the specimens figured in the literature on Triassic ostracods are often poorly illustrated and/or poorly preserved. As an additional complication, it is now clear that few of the types or specimens illustrated by Kozur and his colleagues were deposited in accessible collections and many are now certainly lost (Kozur, pers. comm.). Therefore, it is not possible to re-examine the majority of the type specimens and we are left with only the original illustrations, type descriptions and personal communications with the original authors. There are very few descriptions of taxonomically important internal features such as adductor muscle scars or hingement. Nevertheless, we believe that it is possible to draw important conclusions based on external features and gross carapace morphology. Hingement in Early Mesozoic cytheracean ostracods is generally lophodont, more rarely merodont. In the following sections we discuss the validity of many Permian to Early Jurassic genera. In many cases the type material is lost or was never curated. A complete taxonomic revision would warrant re-collection from all of the type localities combined with an exhaustive search of museum collections. We have chosen not to figure the few taxa that are available since they are already well illustrated in the literature. We have fully referenced the type description of each taxon discussed, since only through observing the original illustrations can the taxonomic problems be fully appreciated. We hope that this paper will stimulate further research on an important period in ostracod evolution

It is our opinion that many of the species recorded from the marginal-marine and marine Triassic deposits world-wide can easily be accommodated within already existing genera originally described from younger strata. Many previous taxonomic studies have obscured true evolutionary relationships by not distinguishing between generic and specific criteria. We have adopted the taxonomic philosophy outlined by Whatley & Ballent (1996) in which generic characters are of kind while specific characters are of degree. Clearly there is scope for future research into the Early Mesozoic development of cytheracean ostracods, a fundamentally important period in their evolution.

SYSTEMATIC DISCUSSION

What follows, in alphabetical order, is an evaluation of a number of Late Palaeozoic–Early Mesozoic genera that are possible candidates for inclusion within the Cytheruridae. Some are accepted as members of the family while others are rejected. Genera which we consider valid, whatever their family, are given *in titulo* underlined and are diagnosed, those that we consider valid but which only occur in sediments younger than Early Jurassic are not diagnosed. The family to which we believe the valid taxa belong is also given and modern diagnoses of the Cytheruridae and its two relevant subfamilies are also presented. LV, left valve; RV, right valve. The following convention is used to describe ostracod size (in adult specimens)

Very small < 0.4 mm Small 0.4–0.5 mm Medium 0.5–0.7 mm Large 0.7–1.0 mm Very large > 1.0 mm

Suprageneric classification

Class Ostracoda Latreille, 1802 Order Podocopida Müller, 1894 Suborder Podocopina Sars, 1866 Superfamily Cytheracea Baird, 1850 Family Cytheruridae Sars, 1925 Diagnosis. Small. Calcification ranging from thin to thickshelled. Subovate, subrhomboidal, subquadrate to subrectangular. Often with caudal process and many with flattened venter. Right valve only slightly larger than left. With or without subcentral tubercle. Ranging from non-alate to very strongly alate ventro-laterally or postero-ventrally. Blind or with eye spots or strong eye tubercles. Valves smooth, punctate, reticulate, costate to strongly carinate or combinations of these. Normal pore canals ranging from simple (the most common) to primitive sieve-type. Radial pore canals rather few, simple, often sinuous and with false canals. Mainly avestibulate but small vestibula may be developed at either end. Inner margin usually regular but may be very irregular. Frontal scar ovate, reniform to v-shaped and sometimes subdivided. Hinge lophodont or merodont, often strongly modified and sometimes secondarily adont, very rarely pentadont.

Subfamily Cytherurinae Sars, 1925

1968 Judahellidae Sohn: 12

1971 Kerocytheridae Kozur: 48

1972b Trachycytherinae Kozur: 13

1973 Mostlerellidae Kozur: 19

Diagnosis. Carapace generally subrectangular in lateral view and usually without strong alae. Caudal process often pronounced. Smooth to strongly ornamented with ribs, tubercles, etc. Vestibula small or absent. Hinge as for family but never adont. Inner margin parallel to widely divergent. Radial pore canals often long, sinuous with false canals. Eye tubercles frequently well developed in ornate taxa.

Subfamily Cytheropterinae Hanai, 1957

Diagnosis. Carapace subovate, with dorsal margin often rounded, to subquadrate and sub-rectangular. Feebly ornamented, smooth to punctate or reticulate. Usually strongly alate or tumid ventro-laterally. Small vestibula usually present. Hinge usually antimerodont but often modified. Without eye tubercles.

Generic classification

Genus Blomella Kozur, 1973

?1956 Speluncella Schneider; Mandelstam et al.: 120.

Type species. *Speluncella sulcata* Kozur, 1968b (p. 509, pl. 1, figs 3, 8, 23, 24, 27–29).

Diagnosis. Carapace small to medium size, smooth, LV > RV. Ventral margin straight; anterior, dorsal and posterior margins form a highly arched outline in lateral view. Ventral margin flat and extended laterally into distinct flanges. Hinge short, lophodont.

Remarks. The type species, *Blomella sulcata*, was originally assigned to *Speluncella* Schneider (in Mandelstam *et al.*, 1956) which Whatley & Moguilevsky (1998) place in the Limnocytheridae, Timiriaseviinae. *B. sulcata* is at least outwardly similar to members of the Timiriaseviinae. The type species is somewhat cytheropterine (reminiscent of Modern deep-sea taxa such as *Cytheropteron testudo*) but Kozur (pers. comm., 1997) states that the genus was recovered from brackish water sediments and it is very rare for fossil or Recent members of *Cytheropteron* or its allies to occur in environments of reduced salinity. Although Whatley & Moguilevsky (1998) did not include *Blomella* in their review of the Limnocytheridae, it is probably a valid member of that family and not a cytherurid. *Blomella* may be a junior synonym of *Speluncella* but for the time being we accept it as a valid taxon but not a member of the Cytheruridae.

Genus Citrella Oertli, 1959

Type species. *Citrella nitida* Oertli, 1959 (p. 118, pl. 2. figs 16–19, p.117, text-fig. 3).

Diagnosis. Carapace small, ovate in lateral view with short, sharp caudal process posteriorly, LV overlaps RV along dorsal and ventral margins. Lateral surface smooth. Ventro-lateral margin slightly extended. Anterior and posterior marginal pore canals few and straight. Four ovate adductor muscle scars and two frontal scars. Lophodont hinge.

Remarks. Citrella is a cytheropterine genus with smooth hinge elements which was originally described from Middle Jurassic sediments in France. It has superficial similarities with Cytheropterina Mandelstam (in Mandelstam et al., 1956) but the two genera are certainly not synonymous. Kozur & Bolz (in Kozur, 1971) described two species, Citrella? lata (p. 19, pl. 3, figs. 4-5) and Citrella? bairdiaformis (p. 18, pl. 3, figs 2-3) which they assigned, questionably, to this genus. Kozur (pers. comm., 1997) confirmed that these species were recovered from Triassic (Late Norian) marine sediments. A similar species, Cytheropteron? triassica Kozur (in Kozur, 1971) was described from what were 'probably marine sediments' (Kozur, pers. comm., 1997); the species has a lophodont hinge and cannot, therefore, belong to Cytheropteron sensu stricto although it is certainly cytheropterine and probably belongs to Citrella. Kozur (pers. comm., 1997) now concurs with this conclusion.

Speluncella? ampelsbachensis, from 'probable marine Late Norian sediments' (Kozur, pers. comm., 1997), was described by Kozur & Bolz in the same publication (Kozur, 1971, p. 46, pl. 3, figs 6–7) and is probably congeneric. A number of similar species are also present in the Early Jurassic sediments of the Mochras Borehole, Wales (Boomer, 1989 and unpublished data) and these almost certainly constitute a distinct group within the Cytheropterinae. It is our opinion, therefore, that the genus *Citrella* ranges from the Late Norian to the mid-Bathonian and possibly to the Tithonian (Pokorny, 1973).

Genus Cytheropteron Alexander, 1933

1964 Infracytheropteron Kaye: 105.

1974 Lobosocytheropteron Ishizaki & Gunther: 32

Diagnosis. Subcircular, subovate or subrhomboidal. With or without caudal process. Alate or, alternatively, very tumid ventro-laterally. Smooth, punctate, rarely reticulate or delicately ribbed. Blind. Median element of hinge sometimes strongly crenulate. Radial pores relatively few, well spaced, straight and simple.

Remarks. The genus *Cytheropteron* has been reported in Triassic assemblages as two distinct subgenera, *Cytheropteron (Cytheropteron), Cytheropteron (Stykella)*; the nominative subgenus has its oldest certain record in the Toarcian (*Cytheropteron alafastigatum* Fischer, 1962, *falciferum* Zone, Mochras Borehole, Great Britain; Boomer, 1989). The species *Cytheropteron? triassica* described by Kozur (1971) is almost certainly not a valid member of that genus. Bate & Coleman (1975) erected the subfamily Oculocytheropterinae to incorporate the eyed *Cyther-*

opteron-like species, i.e. the Late Cretaceous to Recent Oculocytheropteron Bate and they included the Liassic genera Rutlandella and Wellandia (see below). In the following sections we synonymize the latter two genera with Eucytherura which is accommodated within the Cytherurinae. The Oculocytheropterinae are not considered further here. Lobosocytheropteron is based solely on the fact that species such as C. alatum Sars, 1866 have a bend in the median element of the hinge. We do not consider this to be a generic characteristic.

Subgenus *Cytheropteron (Infracytheropteron)* Kaye, 1964 **Type species.** *Cytheropteron (Infracytheropteron) exquisita* Kaye, 1964 (p. 105, pl. 5, figs 9–10).

Remarks. The subgenus *Infracytheropteron* (originally erected as a monospecific Early Cretaceous taxon) was differentiated from *Cytheropteron* on the basis of hingement which was said to consist of a smooth bar in each valve, produced by the enlargement of the selvage and valve margins. This may have been erroneously described from a juvenile specimen, no internal views were figured in the type description although the duplicature was described as narrow. A number of Liassic species have subsequently been assigned to this subgenus (see Bate & Coleman, 1975; Knitter, 1983) an assessment which appears to be based largely on external characteristics, the status of this taxon is at best questionable and we consider it to be a junior synonym of *Cytheropteron*.

Subgenus Cytheropteron (Stykella) Kozur, 1971

Type species. *Cytheropteron (Stykella) sevatica* Kozur, 1971 (p. 20, pl. 3, fig. 8).

Remarks. This was erected as a subgenus of *Cytheropteron* to accommodate a single species. The straight hinge line precludes its inclusion in *Cytheropteron*. It is described as having a 'hemimerodont' hinge and from the type figures it clearly possesses an eye node, a caudal process and a ventro-lateral extension which terminates posteriorly in a small blunt spine. Its shape disqualifies it for inclusion within *Aversovalva* Hornibrook, 1952 or *Oculocytheropteron* Bate, 1972. In all characteristics it clearly belongs within *Eucytherura* Müller.

Genus Dettermania Sohn, 1987

Type species. Dettermania truncata Sohn, 1987 (p. 11, pl. 7, figs 4–15).

Remarks. Sohn (1987) described the type species of *Dettermania* together with two similar species which he assigned to *Covracythere* (Gramm, 1975) from the marine Triassic deposits of Alaska. All three species are morphologically similar and it is possible that they are congeneric. The genus *Covracythere* is, without doubt, a bythocytherid (possessing five adductor muscle scars) and was originally described along with two other bythocytherid genera, *Racevetina* and *Acvocaria*, from the Far East of the Former Soviet Union (Gramm, 1975). All three species figured by Sohn possess median sulcii and straight dorsal margins, indicating that they may belong within the Bythocytheridae. However, without supporting details of the muscle scars, any such assignments must remain uncertain.

No details of the muscle scars or hingement of *Dettermania* are available. The carapace shape and external morphology is distinct and strongly suggests that it is congeneric with *Mockella*

Bunza & Kozur, 1971, as is *Hasibuana* Kristan-Tollmann (in Kristan-Tollmann & Hasibuan, 1990; see below). *Dettermania* differs slightly from *Mockella* in that it lacks secondary intercostal ornament, however, we conclude that this is a specific character and therefore *Dettermania* is a junior synonym of *Mockella*.

Genus Eocythereis Anderson, 1964

Type species. *Eocythereis vertebralis* Anderson, 1964 (p. 145, pl. 13, figs 79–80).

Remarks. Anderson (1964) placed this genus in the Trachyleberididae which has its origins in the Early Cretaceous (Whatley *et al.*, 1993). Recent examination of the type material (originally erected on a single carapace), from the Rhaetian, Cotham Beds of Warwickshire, Great Britain (Anderson, 1964) reveals that it is congeneric with (and a junior synonym of) *Eucytherura*.

Genus Eucytherura Müller, 1894

1964 Eocythereis Anderson: 145.

- 1969 Nanacythere (Domeria) Herrig: 1085.
- 1969 Nanacythere (Nanacythere) Herrig: 1080.
- 1971 Gramella Kozur: 21.
- 1971 Movschovitschia Kozur: 29.
- 1971 Sohnetta Kozur: 42
- 1971 Cytheropteron (Stykella) Kozur: 20
- 1972a Grammicythere Kozur: 642 (nom. nov. for Gramella)
- 1975 Grammanicythere Gründel: 364
- 1975 Nanacythere (Goniocythere) Michelsen: 201
- 1975 Rutlandella, Bate & Coleman: 34.
- 1975 Wellandia Bate & Coleman: 32.
- 1987 Paratrachycythere Park: 63.

Type species. *Cythere complexa* Brady, 1867 (by subsequent designation: Alexander, 1936).

Diagnosis. See emended diagnosis in Ayress et al. (1995).

Remarks. A long-ranging genus originally described from Recent sediments in the Gulf of Naples (Müller, 1894) although the type species, Eucytherura complexa (Brady, 1867), was only later designated by Alexander (1936). The genus is distinguished from most other cytherurid taxa by its quadrate carapace in lateral view, which is only moderately inflated in dorsal view and the dominance of reticulate ornamentation. However, up to three longitudinal ribs (generally dorso-median or median and ventro-lateral in position) may also be present. Most species possess a strong tubercle or spine at the posterior apex of the ventro-lateral rib which itself may become quite inflated. Many species are characterized by the presence of a strong eye tubercle but Cenozoic and Recent species which live in deep water are blind. We prefer to include Eucytherura within the Cytherurinae, discussion of the status of the subfamily Eucytherurinae can be found in Maddocks & Steineck (1987).

We consider *Eucytherura* to be a senior synonym of the following Early Mesozoic taxa (with the family they were originally assigned to, if available): *Eocythereis* (Trachyleberididae), *Gramannicythere*, *Grammella*, *Grammicythere*, *Movschovitschia*, *Nanacythere* (*Domeria*) (Cytheridae), *Nanacythere* (*Goniocythere*), *Paratrachycythere*, *Rutlandella* (Oculocytheropterinae), *Wellandia* (Oculocytheropterinae) and a number of Early Jurassic species assigned by some workers to Acrocythere (e.g. Michelsen, 1975). All the above spurious taxa, and others erected in the subsequent Mesozoic and Cenozoic are, in our opinion, the product of confusing generic and specific criteria. Gründel (1975) claimed that all Mesozoic *Eucytherura* are vestibulate, however, our own observations do not support this statement. We consider the subgenus *Eucytherura (Vesticytherura)* (Gründel, 1964) to be an unnecessary taxon.

Genus Falloticythere Kozur et al. 1974.

Type species. *Falloticythere mulderae* Kozur *et al.* 1974 (p. 36, text figs 19a,b,d; pl. 2, figs 9–13).

Remarks. This genus was placed in the Cytherissinellidae by Kozur *et al.* (1974) and this family has now been subsumed within the Limnocytheridae (Whatley & Moguilevsky, 1998). Kozur *et al.* commented on the presence in the type species, *Falloticythere mulderae*, of an antero-ventral node and an antero-median to mid-anterior node, these features produce a mid-valve sulcus which is found in most bythocytherid and many limnocytherid taxa. The hinge was described as lophodont with weak terminal teeth. The type species occurs in salinities ranging from marine to continental hyposaline (Kozur, pers. comm.).

Although possibly a cytherurid, and without internal details it is impossible to be sure, we believe that the weak hingement and carapace shape are best accommodated within the Bythocytheridae, and *Falloticythere* may be a junior synonym of *Monoceratina* Roth, 1928. As with *Covracythere* a number of Triassic cytheracean taxa appear to share common bythocytherid and cytherurid characteristics, indicating the possible origin of the Cytheruridae from bythocytherid stock in the Late Permian or earliest Triassic.

Genus Gramannicythere Gründel, 1975.

Type species. *Lophodentina? bachi* Gramann, 1962 (p. 195, fig. 2; pl. 2, fig. 5a–c).

Remarks. This is synonymous with *Nanacythere (Goniocythere)* Michelsen, 1975 which was published a few months later. The genus comprises a few, mainly Pliensbachian, cytherurid species with a strongly angular development in the lateral primary ribbing. The taxonomic status of both *Nanacythere (Domeria)* Herrig, 1969 and *Nanacythere (Nanacythere)* are discussed below. We consider *Gramannicythere* and, therefore, *Nanacythere (Goniocythere)* to be junior synonyms of *Eucytherura*. Although possibly a valid taxon (and we consider it as such in the summary table), the lack of descriptive and illustrative material makes it impossible to provide a meaningful diagnosis at this time.

Genus Grammicythere Kozur, 1972a nom. nov.

Type species. *Gramella hungaric*a Kozur, 1971 (p. 22, pl. 1. fig. 1; pl. 4, fig. 3).

Remarks. Grammicythere replaced Grammella Kozur, a junior objective homonym of a bryozoan. The original publication also mis-spelt the name as Gramella. The type species possesses a straight to slightly convex dorsal margin and reticulate lateral surfaces with a ventro-lateral rib, it clearly belongs within the Cytherurinae and seems best accommodated within Eucytherura, although no eye-spots were recorded (many modern species of Eucytherura lack eyes, especially those which occur in deep

water). Kozur (1971) states that it is closely related to *Lutkevichinella* Schneider (in Mandelstam *et al.*, 1956) a genus which Whatley & Moguilevsky (1998) have shown to be a limnocytherid. However, on the basis of the very poor illustrations of the type species of *Grammicythere* it is difficult to observe any points of similarity with *Lutkevichinella*. Notwithstanding this, we believe the genus to be another junior synonym of *Eucytherura*.

Genus Gruendelicythere Kozur, 1971

Type species. *Gruendelicythere ampelsbachensis* Kozur & Bolz n. sp. in Kozur, 1971 (p. 24, pl. 6, figs 6–10).

Diagnosis. Carapace small, rather elongate, dorsal and ventral margins straight converging slightly posteriorly. Posterior and anterior margins rounded in lateral view, compressed in dorsal view. Lateral surface bears marked reticulate nodes and sulcii, the largest of which are in the mid- to postero-ventral region. They do not extend beyond the dorsal margin in lateral view. Ventral surface flat and broad. Hinge probably lophodont.

Remarks. The type species is a very small cytherurid and, although it resembles Eucytherura, it differs from most species of that genus in possessing particularly large nodes and tubercles for such a small ostracod. It has a slightly produced posterior with compressed anterior and posterior margins. Kozur (1971) refers to the similarity of its noding to Judahella Sohn, 1968 but the distribution and nature of the noding in the two genera is quite different, as is the carapace outline (most species of Judahella have well developed nodes which extend beyond the dorsal margin) and the similarity is probably convergence. In the shape of the carapace and the distribution of nodes it differs significantly from the nodose Liassic cytherurid Trachycythere Triebel & Klingler, 1959. There are superficial similarities with Cretaceous and Cenozoic genera, such as Chapmanicytherura Weaver, 1982, Hemingwavella Neale, 1975 and Parahemingwayella Dingle, 1984 but Gruendelicythere differs sufficiently from all the above comparitors for us to consider it valid. A species assigned to this genus has been described from the Late Permian of northern Hungary (Kozur, 1985).

Genus Hasibuana Kristan-Tollmann (in Kristan-Tollmann & Hasibuan, 1990)

Type species. *Hasibuana asiatica* Kristan-Tollmann (in Kristan-Tollmann & Hasibuan, 1990) (p. 176, pl. 1, figs 1–5).

Remarks. The type species possesses a well-developed pair of diagonal, lunate ribs with weak intercostal reticulation; a poorly developed eye-spot is also present. The carapace has a straight dorsal and highly convex ventral margin and in this respect is very similar to *Dettermania* in lateral outline. However, it lacks the median sulcus of that genus. Kristan-Tollmann (in Kristan-Tollmann & Hasibuan, 1990) noted that *Hasibuana* differs from *Dettermania* in possessing an eye-spot, and antero and posteromarginal ribs. We consider these differences to be of specific rank only and, therefore, that *Hasibuana*, like *Dettermania*, is a junior synonym of *Mockella* based on carapace shape, size and distribution of major ribs.

Genus Judahella Sohn, 1968

1968 Ophthalmonodella Knüpfer & Kozur: 322 1971 Judahella (Costahella) Kozur: 42 1971 Mostlerella Kozur: 37

1985 Buekkella Kozur: 31

Type species. Judahella tsorfatia Sohn, 1968 (p. 15, pl. 3. figs 20–21).

Diagnosis. Small, oval to triangular in lateral view. Dorsal margin straight, ventral margin convex, strongly so in some species. Anterior margin flat to broadly rounded. Greatest length near dorsal margin, greatest height near anterior margin. The valves are sometimes smooth but more commonly reticulate and bear a number of distinct swellings or nodes which are consistently developed within species. In many species these nodes extend beyond the dorsal margin in lateral view. There may also be a longitudinal rib present ventro-laterally. Hinge merodont. Muscle scars a vertically aligned row of four.

Remarks. Sohn (1968) originally placed this genus in the Palaeocopida (Superfamily unknown) and in a new family, the Judahellidae. Sohn discussed its possible relationship to a number of genera such as *Cornigella* Warthin, 1930 and *Trachycythere*. We consider *Judahella* to be a cytheracean, and almost certainly a cytherurid, characterized by a small, straighthinged carapace with 3–4 large dorsal tubercles extending beyond the dorsal margin.

Kozur (1968b, p. 502) noted that *Casachstanella scungayica* Schleifer, 1966, the type species of that genus, is a brackishwater form related to *Judahella*. Kozur (1970a) later considered *Judahella* to be a junior synonym of *Triassinella* Schneider (in Mandelstam *et al.*, 1956), however, Whatley & Moguilevsky (1998) placed *Triassinella* in the Limnocytheridae which precludes synonymy with the present genus. Confusingly, in the same paper Kozur (1970a) also established *Judahella* as a subgenus of *Triassinella*. The species illustrated by Kristan-Tollmann *et al.* (1991b, pl. 8, fig. 1) as *Triceratina fortenodosa* (Urlichs, 1972) is a species of *Judahella*.

Sohn (1968) discussed the possible relationship between Judahella and Liasssic species of Trachycythere Triebel & Klingler (1959) which also bear large tuberculae. However, the disposition of tuberculae in the two genera is quite different and we believe that this similarity is merely homeomorphic (see further discussion on Trachycythere below). Judahella andrussovi Kozur & Bolz, 1971 of Kristan-Tollmann et al., 1991a,b resembles another Liassic genus, Paratrachycythere Park, 1987. That genus was named for its superficial similarity to the younger Trachycythere (Triebel & Klingler), which is unfortunate because the two Liassic taxa are quite different, particularly in hingement, size and lateral outline. Neither genus can be confidently related to Judahella which we consider to be a valid cytherurid taxon. There is evidence that Judahella ranges back to at least the Late Permian of northern Hungary (Kozur, 1985). In the same publication a new genus was erected, Buekkella Kozur, which may be a junior synonym of Judahella.

Subgenus Judahella (Costahella) Kozur, 1971

Type species. Judahella (Costahella) hungarica Kozur, 1971 (p. 28, pl. 2. fig. 6).

Remarks. Erected as a subgenus of *Judahella* Sohn, based on the presence of a rib below the four main dorsal tubercles. In our opinion this is at best a specific character, or common to a group of *Judahella* species, and the diagnosis of *Judahella* has been

emended above accordingly. We consider the subgenus to be a junior synonym of *Judahella*.

Genus Kerocythere Kozur & Nicklas, 1970

1972 Rekocythere Kristan-Tollmann: 46

Type species. *Cythere raibliana* Gümbel, 1869 (p. 184, pl. 6, fig. 36a).

Diagnosis. Carapace elongate, triangular in lateral view, greatest height near anterior margin. Dorsal margin straight, ventral margin convex, greatest length above mid-height. Carapace outline triangular in end view with greatest width across ventral surface. Surface of valves smooth or reticulate. Valves bear distinct circum-marginal ribs or flanges (which may be perforate, see Kristan-Tollmann *et al.*, 1991a, pl. 2, figs 1,2), cardinal angles well marked and may bear projections. One species, *Kerocythere bulbosa* (Kristan-Tollmann, 1972), also possess large bulbous inflations anteriorly. Eye spots weak or absent. The hinge is very characteristic. The terminal elements in the LV are single smooth loculi, while the median element, a possibly denticulate bar, is extended distally (both anteriorly and posteriorly) into a large hemispherical boss.

Remarks. The genus was originally placed in the Trachyleberididae. In the type description Kozur & Nicklas (1970) designated *Cythere raibliana* Gümbel, 1869 as the type species but did not figure any new specimens of that species. They figured three species, two of which were referred to *Kerocythere* n. sp.1 Bolz and *Kerocythere* n. sp.2 Bolz and the third to *Kerocythere* n. sp. The reason for reference to Bolz on this publication is unclear.

Kerocythere sp.1 Bolz (Kozur & Nicklas, 1970, pl. 2, fig. 1) possesses three distinct longitudinal ribs (dorsal, mid- and ventral), a denticulate anterior margin and a weak eye spot. *Kerocythere* sp. 2 Bolz (Kozur & Nicklas, 1970, pl. 2, fig. 2) possesses a dorsal, ventral and antero-marginal rib. The dorsal part of the ventral rib displays a series of short vertical riblets. The antero-cardinal angle terminates in a small boss while the postero-dorsal cardinal angle possesses a short, dorso-ventrally projecting spine (an extension of the dorsal rib). Kozur & Nicklas (1970) also figured material assigned to *Kerocythere* n. sp. which is probably a juvenile of one of the aforementioned species.

According to Kozur & Nicklas (1970), the genus possesses an amphidont hinge, this is both phylogenetically unlikely and entirely unsubstantiated by the illustrations. Indeed, the hingement appears to be peratodont (sensu Bate, 1972), whereby the median element is inflated terminally. Indeed, from the available illustrations it appears that the terminal teeth (in the right valve and terminal inflations of the median element in the left valve) are very strongly developed, although this may be an artefact of the illustration process (possibly retouched). The hingement is better illustrated in Kozur, 1971 (pls 7 & 8), indeed pl. 7, fig. 5b shows a crenulate median element although this too may have been manually retouched. The hingement closely resembles that of certain Campanian to Recent taxa belonging to the Pectocytheridae, an essentially Southern Hemisphere and mostly Pacific family whose hinge is termed pentadont (Hanai, 1957), which seems to be synonymous with holoperatodont, the former having priority. We consider Kerocythere to be a valid

cytherurid genus with a distinctive carapace outline, ornament and hingement.

Subgenus Kerocythere (Rekocythere) Kristan-Tollmann, 1972 **Type species.** Kerocythere (Rekocythere) bulbosa Kristan-Tollmann, 1972 (p. 46, pl. 2, figs 6,7).

Remarks. A subgenus which was originally distinguished from *Kerocythere sensu stricto* by the presence of a median rib, which we consider to be a differentiating character at species level only. Furthermore, the type species is almost certainly a junior synonym of *Kerocythere veghae* Kozur, 1971 (in Bunza & Kozur, 1971). Kristan-Tollmann (1972) made no reference to this species when erecting the subgenus nor did she reference the publication and it is probable that she did not see it before publishing her work. We do not accept the validity of this subgenus and have emended the diagnosis of *Kerocythere* to accommodate it.

Genus Lophodentina Apostolescu, 1959

Type species. Lophodentina lacunosa Apostolescu, 1959 (p. 814, pl. 3, figs 56,57).

Diagnosis. Carapace medium sized, well calcified, ovate to subrectangular in lateral view. Anterior and posterior margins broadly rounded, dorsum straight, venter sinuous to weakly concave. Carapace uniformly inflated without distinct marginal compression. External ornament variable but usually well developed as reticulae and a combination of longitudinal, transverse or marginal ribbing. Hinge straight, weakly merodont. Inner lamella of medium width.

Remarks. The genus was originally described from Liassic sediments in the Paris Basin and was placed within the Cytherinae. This medium-sized genus was named for its lophodont hingement which, in fact, now seems to be merodont with a weakly crenulate median element. Subsequently, Gramann (1962) assigned one new species (*Lophodentina? bachi*) and one undescribed Liassic species to this genus. Those latter two species we consider to belong to *Eucytherura*. The taxonomic status of *Lophodentina* remains in question but may be a valid genus. The earliest representatives of the genus are probably Liassic. Given its large size, carapace shape and lateral outline we do not consider this to be a cytherurid.

Genus Metacytheropteron Oertli, 1957

Type species. *Metacytheropteron elegans* Oertli, 1957 (p. 8, pl. 1, fig. 12).

Remarks. Metacytheropteron is a Middle Jurassic to Cretaceous member of the Cytheropterinae and, as such, is outside the scope of this study. However, Anderson (1964) assigned a Rhaetian species (*Metacytheropteron nannodes*) to this genus. We have now examined the type specimen of *Metacytheropteron nannodes* and consider that it belongs to the genus *Procytherura* Whatley, 1970. Since the genus does not occur in Permian or Triassic sediments a diagnosis is not included.

Genus Mockella Bunza & Kozur, 1971

1981 Renicytherura Gründel: 543

1987 Dettermania Sohn: C11.

1990 Hasibuana Kristan-Tollmann; Kristan-Tollmann & Hasibuan: 175.

Type species. *Mockella meulleri* Bunza & Kozur, 1971 (by subsequent designation; Kozur, 1973) (p. 8, pl. 1, fig. 12).

Diagnosis. Medium-sized carapace, dorsal margin slightly convex and sinuous, ventral margin strongly convex, LV > RV. Medianly sulcate, may have antero-central node in front of sulcus. Lateral surfaces smooth or finely punctate with median and ventro-lateral longitudinal ribs present, the latter parallels ventral margin. Eye spot may be well developed. Hingement lophodont, small vestibulum both anteriorly and posteriorly.

Remarks. The authors assigned a taxon as type species which was due to be published shortly afterwards (*Mockella marinae*), however, that publication never appeared (Kozur, pers. comm.). In 1973, Kozur subsequently designated *Mockella meulleri* Bunza & Kozur, 1971 as the type.

The type species described and figured by Bunza & Kozur (*Mockella muelleri*, p. 8, pl. 1, fig. 12) was originally assigned to the Glorianellidae which is now considered to be a junior synonym of the Limnocytheridae (Whatley & Moguilevsky, 1998). From published illustrations and the original generic diagnosis, we infer that *Mockella* is a senior synonym of both *Dettermania* Sohn, 1987 and *Hasibuana* Kristan-Tollmann (in Kristan-Tollmann & Hasibuan, 1990). Lord *et al.* (1993) figured a *nomina aperta* species of *Renicytherura* Gründel, 1981 from the Early Jurassic off Western Australia which may be congeneric. We therefore consider *Mockella* to be a senior synonym of *Dettermania* and *Hasibuana* and to be a valid genus of the Cytheruridae, Cytherurinae.

Genus Mostlerella Kozur, 1971

Type species. *Mostlerella nodosa nodosa* Kozur, 1971 (p. 38, pl. 4, figs 10, 12, 14, 16).

Remarks. Kozur assigned two new species to this genus. Both possess a very straight dorsal margin, bulbous swellings along the dorsal margin and a ventro-lateral rib. These features accord well with the emended diagnosis of *Judahella* (see above). Kozur originally described the genus as possessing a lophodont hinge, however, Kristan-Tollmann (1982) illustrated a number of *Mostlerella* species and emended the diagnosis to include a noridont hinge. We regard this genus as a junior synonym of *Judahella*.

Genus Movschovitschia Kozur, 1971

Type species. *Movschovitschia norica* Kozur & Bolz, in Kozur, 1971 (p. 33 pl. 3, figs 9–14).

Remarks. Originally erected as a subgenus of *Lophodentina*, illustrations of the type species clearly show great similarity with the type species of *Rutlandella* (*Rutlandella transversiplicata* Bate & Coleman, 1975) which is a junior synonym of *Eucytherura* (see below). All of the species assigned to this genus are congeneric and we regard *Movschovitschia* as a junior synonym of *Eucytherura*.

Genus Nanacythere Herrig, 1969

1969 Nanacythere (Domeria) Herrig: 1085.

1975 Nanacythere (Goniocythere) Michelsen: 201.

Type species. Nanacythere simplex Herrig, 1969 (p. 1081, pl. 1, figs 3–4, text figs 6,7).

Remarks. *Nanacythere* was originally described from mid- and Upper Liassic deposits in northern Germany (Herrig, 1969), it

has not been recorded from the Triassic or the Lower Liassic and it appears to be restricted to the Pliensbachian and Toarcian. Three subgenera have been described to date and we consider all three to be junior synonyms of *Eucytherura*.

Genus Noricythere Bolz & Kozur (in Kozur, 1971)

Type species. Noricythere hartmanni Bolz & Kozur, in Kozur, 1971 (p. 54, pl. 7, figs 1,4,5; pl. 8, figs 4,7).

Remarks. Noricythere is a junior synonym of Kerocythere Kozur & Nicklas, 1970. The type species bears regular punctation and small nodes on the lateral surfaces with slight inflation of the circum-marginal rib at the cardinal angles. However, some species assigned to this genus, such as Noricythere mostleri Bolz & Kozur, 1971 are best assigned to Eucytherura.

Genus Ophthalmonodella Knüpfer & Kozur, 1968

Type species. Ophthalmonodella reticulata Knüpfer & Kozur, 1968 (p. 323, pl. 1, figs 3a-c, 10, 13-24).

Remarks. The type description was published just a few months after *Judahella* Sohn of which it is acknowledged to be a junior synonym (Kozur, 1970a, p. 404). The type illustrations show details of the adductor muscle pattern with four elongate oval scars.

Genus Paratrachycythere Park, 1987

Type species. *Paratrachycythere pseudotubulosa* Park, 1987 (p. 63, pl. 3, figs 19–22).

Remarks. This taxon was originally named for its alleged similarity to *Trachycythere tubulosa* Triebel & Klingler, 1959. The lateral tubercles which are the main feature linking the two genera can also be found, albeit weakly developed, in *Eucytherura* species from the Liassic of the Danish Embayment (Michelsen, 1975 as *Acrocythere*). We believe this feature is homeomorphic and that the two genera (*Eucytherura* and *Trachycythere*) are distinct and probably unrelated. We consider this genus to be a junior synonym of *Eucytherura*.

The suprageneric position of genera such as *Trachycythere* remains in question. It was originally assigned to the Trachy-leberididae, however, that family is now considered to range from the Early Cretaceous.

Genus Procytherura Whatley, 1970

Type species. Procytherura tenuicostata Whatley, 1970 (p. 323, pl. 6, figs 1-8).

Diagnosis. Carapace small, rounded, ovate elongate outline in lateral view. Dorsal and ventral margins weakly convex. Ornament variable but usually dominated by longitudinal ribs with secondary reticulation. Lateral projections rare. Hinge lophodont. Vestibulate.

Remarks. This valid cytherurid genus, which extends from the latest Triassic through to the Cretaceous and possibly into the Early Cenozoic, lacks the distinct eye tubercle and posteroventral projection of *Eucytherura*. It can also be distinguished by its more elongate, lanceolate carapace lateral outline. It differs from *Cytherura* Sars in the presence of vestibula. Ornament is dominantly of ribbing rather than reticulation, although some species are smooth or very weakly ornamented. Recent examination of Anderson's (1964) Rhaetian material has revealed that *Metacytheropteron nannodes* Anderson belongs

to *Procytherura*, thus extending the range of this genus back to the Late Triassic.

Genus Rutlandella Bate & Coleman, 1975

Type species. *Rutlandella transversiplicata* Bate & Coleman, 1975 (p. 34, pls 13.7–13.10, 13.12, text figs 14a,b, 15, 16).

Remarks. This genus was erected on characteristics which are essentially specific. Within the literature there are a number of closely related species which have been assigned to genera such as *Rutlandella*, *Movschovitschia* and *Eocythereis*. We do not consider that these species warrant separate generic status and, therefore, *Rutlandella* is placed in synonymy with *Eucytherura*.

Genus Simeonella Sohn, 1968

Type species. Simeonella brotzenorum Sohn, 1968 (p. 23, pl. 2, figs 1–4, 6–8, 12–22).

Remarks. Simeonella Sohn, 1968 was described from the Triassic of Israel. The carapace is sub-rectangular in lateral view, inflated laterally with a reticulate external surface and an antimerodont hinge. Sohn (1968) placed it questionably in the Cytheruridae, while Bunza & Kozur (1971) placed it in the Progonocytheridae. Sohn suggested that Scabriculocypris Anderson, 1940 and Tchunguania Zhong, 1964 may be synonymous with Simeonella. Tchunguania, however, is a non-marine genus belonging to the Permianidae, which is characterized by the possession of 3 adductor muscle scars (Whatley & Moguilevsky, 1998). Sohn also placed some Chinese species of Gomphocythere described by Zhong (1964) into Simeonella. We disagree with Sohn on these possible synonymies. We follow Whatley & Moguilevsky (1998) who placed Simeonella in the Cytherissinellidae in possible synonymy with Lutkevichinella Schneider (in Mandelstam et al., 1956). They also subsumed the Cytherissinellidae within the Limnocytheridae, Limnocytherinae. The adductor muscle scar pattern clearly precludes the inclusion of this genus within the Cytheracea and therefore the Cytheruridae.

Genus Sohnetta Kozur, 1971

Subgenus Sohnetta (Sohnetta) Kozur, 1971

Type species. Sohnetta (Sohnetta) meulleri Kozur, 1971 (p. 42, pl. 2, fig. 8).

Remarks. From the type figure and description, the genus possesses a very small, sub-triangular carapace and the hinge is probably lophodont. In our opinion this taxon certainly belongs to the Cytherurinae (Cytherurinae). Only one figure was given of the holotype which is sub-triangular in lateral outline, has a slightly convex dorsal margin and two dominant longitudinal ribs extending from postero-dorsal to antero-ventral. The type species is easily accommodated within *Eucytherura*. Kristan-Tollmann (1983, p. 153) placed the type species into *Judahella (Costahella)*, however, the lack of tubercles and convex dorsal margin distinguish this species from *Judahella*. We consider *Sohnetta* to be a junior synonym of *Eucytherura*.

Genus Boogaardella Kozur, 1971

Type species. Sohnetta (Boogaardella) triassica Kozur & Bolz n.sp. in Kozur, 1971 (p. 45, pl. 5, figs 1, 3-5).

Diagnosis. Carapace small, triangular to sub-rectangular in lateral view, dorsum and venter straight and convergent

posteriorly, anterior and posterior margins broadly rounded. Carapace only weakly inflated, trapezoidal in dorsal view, broadest in posterior ¹/₄. Lateral surfaces reticulate and bear strong ribs and minor tubercles. Strong ventro-lateral rib extends along anterior margin. Smaller transverse ribs originate at postero-dorsal tubercle. Internal features unknown.

Remarks. The subgenus *Sohnetta* (*Boogaardella*) Kozur was erected in the same publication as *Sohnetta* (*Sohnetta*). However, the poor quality of the illustrations precludes a complete review of the relationship between these taxa. In our opinion the type species, *Sohnetta* (*Boogardella*) triassica Kozur, is clearly a cytherurid characterized by its small carapace size and ornamentation. Although external ornament is similar to that of other taxa discussed herein we have retained this as a valid genus due to the distinctly different carapace shape which is much more angular in lateral view that that of *Judahella*. More importantly the outline in dorsal/ventral view (Kozur, 1971, pl. 5, fig.1c) is distinctly unlike that of any other contemporaneous species.

We conclude that *Sohnetta (Boogardella)* is a valid genus while *Sohnetta (Sohnetta)* is a junior synonym of *Eucytherura. Boogardella* is therefore raised to generic status.

Genus <u>Speluncella</u> Schneider (in Mandelstam *et al.*, 1956) **Type species** Speluncella spinosa Schneider (in Mandelstam *et al.*, 1956, p. 120, pl. 19, fig. 3).

Diagnosis. Egg-shaped, very rounded anteriorly, almost pointed posteriorly, smooth apart from ventro-lateral and ventral ribs (after Whatley & Moguilevsky, 1998).

Remarks. Whatley & Moguilevsky (1998) retained this genus in the family Spelluncellidae which they subsumed within the Limnocytheridae, Timiriasevinae. Bunza & Kozur (1971) tentatively assigned a new species (*Speluncella? karnica*) to this genus but provided only two unremarkable line drawings to illustrate it (pl.1, fig. 2a,b). These drawings are similar to some species of Cytheropterinae. However, without examination of the type material or clearer illustrations it is not possible to confirm its taxonomic position. We consider the genus to be a valid taxon but not a cytherurid. *Speluncella* may be a senior synonym of *Blomella*.

Genus Telocythere Kozur, 1970b.

1973 Veghicythere Kozur: 14.

Type species. *Glorianella? fischeri* Kozur, 1968a (p. 860, pl. 2, fig. 12a–c).

Remarks. The type species is elongate sub-rectangular in lateral view, laterally compressed with longitudinal ribs. It was described from brackish-water deposits in association with *Darwinula* and *Chara*. The genus includes a number of species assigned by Kozur (1970a) to *Lutkevichinella (Cytherissinella)* which Whatley & Moguilevsky (1998) included within the Limnocytheridae. Although the type species is somewhat similar in its external morphology to some Liassic cytheruridae. Based on the limited illustrations and descriptions available it is difficult to reconcile the inclusion of species such as *T. tollmanni* Kozur (1970b) in the same genus as the type species and there are major inconsistencies in that particular study. *Pajanites*, also

described by Kozur (1970b), may be congeneric with *Telocythere*. Whatley & Moguilevsky (1998) suggested that *Pajanites* may belong within the Limnocytheridae, Timiriaseviinae, the brackish-water ecology of the type species supports the inclusion *Telocythere* within the Limnocytheridae. *Telocythere* may be a valid genus but is not a cytherurid.

Genus Trammerella Kozur, 1973

Type species. *Timiriasevia of entalensis* Urlichs, 1972 (p. 686, pl. 2, figs 1–4).

Remarks. Although the familial assignment of this genus is uncertain, it is clearly not a cytherurid. The poor quality of the type illustrations render it impossible to establish its true familial status. The ornament resembles that of *Timiriasevia*, a Triassic to Early Cenozoic, fresh-brackish-water genus, but the carapace shape is distinctly different. Indeed, the carapace shape is similar to the exclusively Triassic, brackish-water genus *Rhombocythere* (Anderson, 1964) which Whatley & Moguilevsky (1998) placed within the Loxoconchidae, Mandelstaminae. Until further material is made available we consider the genus valid, but not a member of the Cytheruridae.

Genus Trodocythere Kozur, 1971

Type species. *Trodocythere anisica* Kozur, 1971 (p. 47, pl. 2, fig. 7).

Remarks. The carapace is triangular in lateral outline with noding along the dorsal margin. There may be a lateral spine, but the type figure is unclear. There is at least one strong anteriorly produced spine (others may be missing). According to Kozur (pers. comm.), this is a marine deep water taxon. It has similarities to some deep-sea species of *Eucytherura* (such as *Eucytherura parabatalaria* Ayress *et al.*, 1995) from the Cenozoic of the Pacific, if a little larger. Many aspects of this species suggest that it may well belong to the Bythocytheridae (straight dorsal margin, lateral spine and nodes), possibly related to genera such as *Nagyella* (Kozur, 1970a). This can only be resolved through studies of the adductor muscle scars; until then it is not possible to determine the validity or the familial status of this genus.

Genus Veghicythere Kozur, 1973

Type species. Lutkevichinella (Cytherissinella) multistriata Kozur, 1970a (p. 402, pl. 2, figs 6–7).

Remarks. Externally the type species is very similar to *Telocythere fischeri*, the type species of that genus, which we consider to belong within the Limnocytheridae. The external ornament of longitudinal ribs is also similar to that of some Liassic species of *Procytherura* but we do not believe this to be taxonomically significant. The genus is probably a junior synonym of *Telocythere* and, therefore, not a cytherurid.

Genus Wellandia Bate & Coleman, 1975

Type species. Wellandia ornata Bate & Coleman, 1975 (p. 32, figs 11.10–11.17).

Remarks. As with *Rutlandella*, which was erected in the same publication, we consider this genus, originally classified within the Oculocytheropterinae, to be a junior synonym of *Eucytherura* (see comments for *Rutlandella* above).

FAMILY	SUBFAMILY	VALID GENERA	SYNONYMS
Cytheruridae	Cytheropterinae	Citrella Oertli, 1959	
		Cytheropteron Alexander, 1933	Infracytheropteron Kaye, 1964
		Metacytheropteron Oertli, 1957	
	Cytherurinae	<i>Eucytherura</i> Müller, 1894	Cytheropteron (Stykella) Kozur, 1971 Eocythereis Anderson, 1964 Gramannicythere Grundel, 1975 Gramella Kozur, 1971 Grammicythere Kozur, 1972 Movschovitschia Kozur, 1971 Nanacythere (Domeria) Herrig, 1969 Nanacythere (Goniocythere) Herrig, 1969 Nanacythere (Nanacythere) Herrig, 1969 Paratrachycythere Park, 1987 Rutlandella Bate & Coleman, 1975 Sohnetta Kozur, 1971
		Gruppdelieuthara Kazur, 1971	Wellandia Bate & Coleman, 1975
			Buddalla Karus 10050
		Judahella (Judahella) Sohn, 1968	Judahella (Costahella) Kozur, 1957 Judahella (Costahella) Kozur, 1971 Mostlerella Kozur, 1971 Ophthalmonodella Knüpfer & Kozur 1968
		Kerocythere Kozur & Nicklas, 1970	Kerocythere (Rekocythere) Kristan-Tollmann, 1972 Noricythere Bolz & Kozur, 1971
		Mockella Bunza & Kozur, 1971	Dettermania Sohn, 1987 Hasibuana Kristan-Tollmann, 1990 Renicytherura Gründel, 1981
		Procytherura Whatley, 1970	
		Boogardella Kozur, 1971	
Limnocytheridae	Limnocytherinae	Simeonella Sohn, 1968	
	Timiriaseviinae	Blomella Kozur, 1973	
		Speluncella Schneider, 1956	
		Telocythere Kozur, 1970	Pajanites Kozur, 1970b? Veghicythere Kozur, 1973
Loxoconchidae	Mandelstaminae	Trammerella Kozur, 1973	
Bythocytheridae?	Subfamily uncertain	Falloticythere Kozur et al, 1974	
		Trodocythere Kozur, 1971	
Cytherideidae?	Subfamily uncertain	Lophodentina Apostolescu, 1959	

Table 1. A taxonomic, hierarchical revision of the Early Mesozoic Cytheruridae with a list of valid genera and synonymies.

SUMMARY

A summary of our taxonomic review is given in Table 1 and the stratigraphical distribution of valid genera is presented in Fig. 1.

It is well documented that many faunal and floral lineages did not survive the mass extinction at the close of the Permian and the Ostracoda are no exception (Whatley *et al.*, 1993). Many of the major post-Palaeozoic ostracod families were established by the mid- to Late Jurassic and we are now in a position to outline the rise of one family in particular, the Cytheruridae.

- 1. It is clear that certain members of this family already existed during the Permian (namely *Judahella* and *Gruen-delicythere*, recorded by Kozur (1985) from northern Hungary).
- 2. The great similarity between some early Cytheruridae (Triassic–Early Jurassic) and Early Mesozoic Bythocytheridae (which are distinguished by the possession of five rather than four adductor muscle scars) suggests that certain elements of this polyphyletic family may have arisen from the Bythocytheridae. Indeed, this may also have been the origin of genera such as *Judahella* during the Late Palaeozoic. The Bythocytheridae are the oldest and longest-ranging Podocopida (Ordovician to Recent).
- 3. External characteristics and gross carapace morphology

also support the suggestion of Gründel & Kozur (1975) that some post-Palaeozoic Cytheracea may also have derived from the Palaeocopid Kirkbyacea (Devonian-Triassic).

4. Finally, it is significant to note that many of the Triassic assemblages referred to above are recorded from shallow shelf and marginal marine (even brackish-water) environments. The opening up of new environments consequent upon the global rise of Triassic sea-level clearly played an important role in increasing marine biodiversity at this time.

There are a number of papers describing Permian ostracod assemblages which may provide evidence of links between Palaeozoic and post-Palaeozoic ostracod lineages (Kozur, 1981, 1985, 1991a, 1991b; Gerry *et al.*, 1987; Knüpfer, 1967). Gerry *et al.* (1987) included a new genus, *Arqoviella*, which may be ancestral to Triassic-Early Jurassic genera such as *Ektyphocythere* Bate, 1963.

Although this review deals essentially with the Cytheruridae, other podocopid lineages which first appeared in the Early Mesozoic also had their origins in Late Permian and Triassic times. A particular problem surrounds a number of genera recorded from Liassic sediments in NW Europe (e.g. *Kinkeli*-



Fig. 1. Stratigraphical occurrence of valid Cytheruridae from the Early Mesozoic.

nella, Ektyphocythere, Pleurifera) which may have evolved from, or even belong to, the Cytheruridae given their merodont hingement, simple marginal pore canals and muscle scar patterns. While a study of these taxa is beyond the scope of this review, it is important to realize that such taxa may also be ancestral to other families which, with evolution, become readily separable during the Middle Jurassic. Such families include the Cytherideidae, Schulerideidae, Progonocytheridae and Protocytheridea.

The physical and biological pressures which acted upon Early Mesozoic faunas to bring about relatively rapid diversification were not confined to the early Cytheruridae; they also caused other families to become abundant and diverse.

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