Early Cretaceous *Cypridea* Bosquet 1852 in North America and Europe

Benjamin Sames[1, 2]

[1]*Universität Wien, Institut für Paläontologie, Geozentrum, Althanstrasse 14, 1090 Wien, Austria*
[2]*Sam Noble Oklahoma Museum of Natural History (SNOMNH), 2401 Chautauqua Avenue,
Norman, Oklahoma 73072-7029, U.S.A.*
email: benjamin.sames@univie.ac.at

———————————

ABSTRACT: *Cypridea* Bosquet 1852 (Cypridoidea, Cyprideidae) is a Kimmeridgian to Lower Eocene nonmarine ostracod genus, the representatives of which are very common and stratigraphically useful in Late Tithonian to earliest Barremian "Purbeck/Wealden-like" nonmarine deposits of the world. The revision of particularly North American representatives led to progress in its taxonomy, and a breakthrough in its biostratigraphic supraregional biostratigraphic application. Key to their successful application is an upgraded taxonomic concept including new insights into the coherences of specific reproductive mechanisms (asexual and mixed reproduction) in the context with diversity and dispersal modes, combined with the understanding and evidence that these ostracods are not as endemic as erstwhile believed. This taxonomic concept resolves crucial problems resulting from an overestimation of the taxonomic significance of several carapace characters (particularly ornamentation elements and the outline), and facilitates improved stratigraphic and paleoecologic applications as well as providing the basis for further research. The revision includes an extensive historic overview of most relevant publications. Representatives of *Cypridea* have great utility in improving the biostratigraphic age determination for and correlation of Early Cretaceous formations of the Western Interior foreland basin.

With respect to suprageneric taxonomy, the family Cyprideidae Martin 1940 is partially revised as well. *Longispinella* Sohn 1979 is now considered a subgenus of *Cypridea* while *Cypridea (Guangdongia)* Guan 1978 is allocated to *Bisulcocypridea* Sohn 1969, and the genus *Praecypridea* Sames, Whatley and Schudack 2010(b) is included. The genus *Cypridea* is emended anew. As for the subgeneric taxonomy, the North American species *Cypridea (Pseudocypridina) inornata* (Peck 1951) is now considered a junior synonym of *Cypridea (P.) setina* (Anderson 1939), *Cypridea (P.) laeli* Sohn 1979 considered an ecophenotype of *Cypridea (P.) piedmonti* (Roth 1933), and *Cypridea (Longispinella) asymmetrica* Sohn 1979 designated synonymous (sexual dimorph) to *C. (L.) longispina* Peck 1941. Sexual dimorphism is presumed in several species of *Cypridea* and mixed reproduction corroborated as being the most likely reproductive mechanism among taxa of this genus. *Cypridea? minuta* (Peck 1951) most probably represents an early representative of the sulcate *Bisulcocypridea* Sohn.

Ostracod correlations mainly based on representatives of *Cypridea* strongly suggest a much higher maximum age for some Lower Cretaceous formations (Lakota Formation, South Dakota and Wyoming, and Cedar Mountain Formation, Utah) of the Western Interior foreland basin, i.e., Berriasian to Early Valanginian instead of Barremian or Aptian.

———————————

———————————

1. INTRODUCTION

Ostracods are among the most common fossils in late Mesozoic nonmarine deposits of the world. Because of their small size, good fossil record and preservation, as well as their ecology and dispersal strategies these ostracods have a high potential to be good index fossils. *Cypridea* Bosquet 1852 is a fossil (Kimmeridgian to Lower Eocene) nonmarine genus of the superfamily Cypridoidea, and the extinct family Cyprideidae Martin 1940 (not to confuse with the extant family Cyprididae Baird 1845). Representatives of *Cypridea* are common faunal elements of nonmarine late Mesozoic to early Cenozoic deposits virtually worldwide (except for Australia and Antarctica). In latest Jurassic to Cretaceous nonmarine sediments, taxa of this genus and its close relatives account for a large, if not dominant, proportion of the ostracod diversity. *Cypridea*-taxa have successfully been used for local biozonation in nonmarine deposits of upper-

most Jurassic (Late Tithonian) and Early Cretaceous age (Berriasian to Barremian, earliest Aptian) age, i.e., the so-called Purbeck/Wealden-like facies with particular good resolution in the "Boreal Cretaceous" of the NW European Purbeck/Wealden Basins: the Purbeck/Wealden facies of England, UK (type area), offshore Ireland, the Netherlands (subsurface), as well as the "German Wealden" of NW Germany.

Despite such excellent regional examples, it hitherto seemed barely possible to apply species of this genus to supraregional (i.e., inter-basinal and intercontinental) biostratigraphy. In contrast to other common contemporaneous taxa (e.g. representatives of the still extant subfamily Timiriaseviinae, like the extinct genus *Theriosynoecum*), *Cypridea* and its close relatives, that is the whole family Cyprideidae Martin 1940, are extinct. With exception of a few, mostly not very comprehensive publications, there have been almost no major revisions of the

taxonomy, relationships and phylogeny of the genus *Cypridea* or the family Cyprideidae, respectively, during about the past 50 to 60 years, but rather countless thematically confined publications describing new genera, subgenera, species, and subspecies thereby complicating the taxonomy and increasing the assumed factor of endemism. Furthermore, a biostratigraphic application was mostly not the main object of these revisions.

In the view of the author, the central issue inhibiting the harmonization of the taxonomy in *Cypridea* and the supraregional biostratigraphic application of its taxa has been the different usage, interpretation and evaluation of morphologic terms (notably "local ornamentation elements" as defined in Sames 2011c). This resulted in relatively restrictive or simply wrong taxonomic concepts of (sub-)species and (sub-)genera, i.e., taxa based on very few or even single characters. Therefore, to render a wider and global utilization possible, a new revision that places emphasis on specifying, redefining and harmonizing the morphologic terminology of *Cypridea* and its representatives became necessary, therewith integrating and discussing new discoveries in ostracod biology that were published in the last two decades (e.g. new insights into the influence of ecologic parameters on some ornamentation elements, reproduction and dispersal mechanisms and their consequences on population structure and intraspecific variation, such as the lateral outline).

Within the scope of a project carried out in cooperation with a research group from the Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma (lead by Richard L. Cifelli), dealing with early mammals, the taxonomy of *Cypridea* Bosquet 1852 and some of its representatives from the Lower Cretaceous of the U.S. Western Interior as well as other contemporaneous deposits of the world is revised. The main object of this project and cooperation was an examination of the ostracods retrieved from some Early Cretaceous non-marine formations of North-america where vertebrate remains (particularly early mammals) had been found, and to improve the age determination of such formations, if possible. During the project, it soon became clear that a comprehensive revision of the most important nonmarine ostracod index genera/species during Latest Jurassic-Early Cretaceous times (i.e. *Cypridea*, and *Theriosynoecum* Branson 1936; see Sames 2011a) was necessary to apply these to the biostratigraphy of North American Lower Cretaceous nonmarine formations. Many of these formations are poorly dated, often just known to lie above the Late Jurassic Morrison Formation and to be of Early Cretaceous (pre-middle Albian) age (Sames et al. 2010a). In addition, a lowermost Cretaceous age of some top parts of the Morrison Formation seems to be probable.

Consequently, this work focuses on selected *Cypridea* species of the Lower Cretaceous U.S. Western Interior, their comparison to the most adjacent faunas in Western Europe at that time (English Purbeck/Wealden, "German Wealden", "Spanish Wealden") as well as other continents in part, and their potential usability for supraregional and regional biostratigraphy, and paleoecology. The detailed implications and consequences of the taxonomic results for paleobiogeography of the North American taxa of *Cypridea* as well as the biostratigraphy and paleoecology of selected formations (top Morrison Formation and Lakota Formation, South Dakota; and Cedar Mountain Formation, Utah) of the U.S. Western Interior foreland basin and other areas will be published elsewhere, including the analysis of other ostracod taxa, and the charophytes. A detailed review

on the complex of stratigraphic problems in the nonmarine Early Cretaceous Western Interior basin has been published by Sames et al. (2010a).

Lacking own data from the Lakota and Cedar Mountain formations regarding the "Aptian-Albian fauna" of Peck (1956, 1959; mostly deriving from partially younger formations: Bear River Formation and upper Cloverly Formation, Wyoming; upper Gannett Group – Peterson, Bechler and Draney limestones, Wyoming and Idaho; Kootenai Formation, Montana; upper Cedar Mountain Formation, Utah), this ostracod fauna is mostly excluded here thus far. Some important taxa are discussed, however.

2. PREVIOUS WORK AND AIMS

2.1 Previous work regarding general taxonomy, biostratigraphy and paleogeography of *Cypridea*

Among the vast number of publications on *Cypridea*-taxa, there are relatively few publications giving either a) a comprehensive survey of the general taxonomy of the genus *Cypridea* and/or the family Cyprideidae Martin 1940 a wider context, or b) an approach to analyze the paleogeographic distribution of representatives of *Cypridea* and its close relatives in the global context, particularly with the aim of an application to supraregional biostratigraphy. Major taxonomic and systematic contributions include Martin (1940), Sylvester-Bradley (1949), Wolburg (1959), Szczechura (1981), and Horne and Colin (2005). With respect to the biostratigraphic application, the British micropaleontologist F. W. Anderson (1905-1982) is probable the most prominent pioneer regarding the successful biostratigraphic application of representatives of *Cypridea* and other ostracods to the the English Purbeck/Wealden. In fact, the extensive publications of F. W. Anderson on mostly nonmarine English Purbeck/Wealden ostracods and their biostratigraphic application (Anderson 1939, 1941, 1962, 1967, 1971, 1973, 1985; Anderson and Bazley 1971, Anderson et al. 1967) are regarded as classic examples of an application of ostracods to biostratigraphy in general (Horne 1995). Anderson's (1985) zonations are still applied and, as for the Berriasian to Barremian part, have been correlated to contemporaneous Boreal deposits of NW Europe as well as the marine Tethyan standard sections in SW Europe (see Hoedemaeker and Herngreen 2003 and references therein). Anderson's (1985) zonations have been critically revised by Horne (1995). A detailed historic overview of the taxonomically and stratigraphically important works is provided below (section 5.2.2).

2.2 Previous work regarding nonmarine Late Jurassic to Early Cretaceous ostracods in North America

The scientific history of Late Jurassic - Early Cretaceous nonmarine Ostracoda of North America (U.S. Western Interior and Canada) began in 1886, when the well-known British paleontologist Thomas Rupert Jones (1819-1911) published a paper on "Some fossil Ostracoda from Colorado" (Jones 1886) he had received from the U.S. Geological Survey paleontologist C. A. White. The samples came from the "*Atlantosaurus* beds" (Upper Jurassic Morrison Formation near Cañon City, Colorado) and lacked any representatives of *Cypridea*. A few years later, Jones (1893) published another paper about (Early Cretaceous) ostracods from SW Wyoming and Utah, including representatives of *Cypridea*.
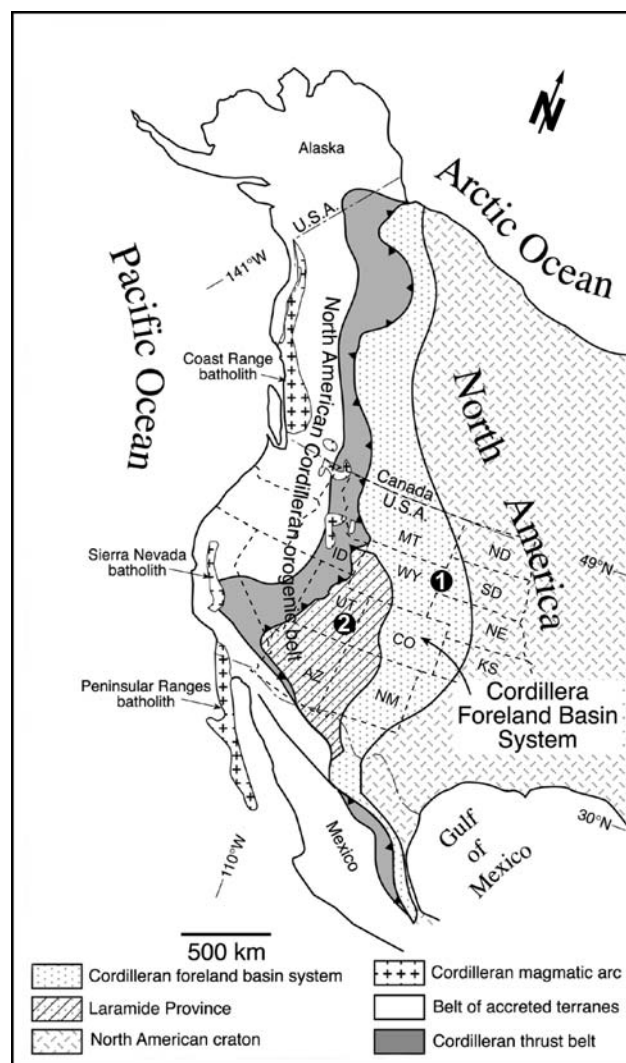
It was not until the late 1920s–early 1930s that this kind of work was continued. Besides other marine invertebrate taxa Vanderpool (1928) described some nonmarine ostracods from the Glen Rose and De Queen limestones of the Aptian-Albian Trinity Group in Arkansas and Texas, among them three representatives of *Cypridea*. Roth (1933) was the pioneer to describe ostracods from the (eastern) Black Hills area followed by Harper and Sutton (1935). At that time, the authors (Roth 1933, Harper and Sutton 1935) believed the ostracod-bearing beds in the Black Hills to be part of the Morrison Formation. Peck and Reker (1948) were committed to be able to distinguish Upper Jurassic Morrison deposits from Lower Cretaceous ones by means of microfossils (and/or molluscs), regarding the ostracods, mainly by the absence of typical Morrison taxa (op. cit.). As already stated by Sohn (1958), the deposits described by Roth (1933) and Harper and Sutton (1935) from the eastern Black Hills area (South Dakota) were part of the Lower Cretaceous Lakota Formation. Sohn (1958) based his conclusions on the presence of representatives of the Cyprideinae (recte Cyprideidae Martin 1940, see Sections 5.2.1 to 5.2.3 below for details), that is *Cypridea*-species, in the Lakota Formation, and their absence in the Morrison Formation, respectively.

During the middle of the 20th century, R. E. Peck was one of the main U.S. authors dealing with Mesozoic nonmarine charophytes and ostracods in the Rocky Mountain area, applying them to regional biostratigraphy (e.g. Peck 1937, 1941, 1951, 1956, 1959; Peck and Craig 1962). At the University of Missouri, Columbia, he had some Master's students working on ostracods (Looney 1948, Hoare 1953, Craig 1961) but, unfortunately, all the theses remained unpublished–though Peck and Craig (1962) published a general paper about ostracods and charophytes in Wyoming and adjacent areas. The new taxa erected in these theses therefore remain *nomina nuda*.

As for Canada, few papers have been published about Lower Cretaceous ostracods so far. The one by Loranger (1951; Loranger 1954 is a reprint of the 1951 paper with revisions) who described ostracods from the Ostracod/Calcareous Member of the Blairmore Formation of Alberta and southern British Columbia, is the most important as to *Cypridea*. Later publications from Finger (1983) as well as Tatman and Whatley (1996, 2001) again dealt with ostracods of this unit but focused on the whole fauna and the biostratigraphy and paleoecology (Finger 1983, Tatman and Whatley 1996) or on the taxonomy of ostracods other than *Cypridea* (Tatman and Whatley 2001).

Swain and Brown (1964, 1972) described Mesozoic nonmarine ostracods that include representatives of *Cypridea*, along with marine ostracods, from the southeastern United States and its Atlantic coastal region. These areas, however, are not part of the Western Interior foreland basin.

With respect to the Lower Cretaceous Lakota Formation, Black Hills area (South Dakota and Wyoming), I. G. Sohn was the main author in the second half of the 20th century. Sohn described the ostracods recovered by field parties mapping the southern and eastern Black Hills area between 1954 and 1958 (Sohn 1958, 1979). These field campaigns were carried out in collaboration of the U.S. Geological Survey and the U.S Atomic Energy Commission due to the discovery of detritic Uranium within the Mesozoic deposits of the Black Hills in 1951, and Sohn joined the field parties in 1957 to obtain additional collections (Gott et al. 1974, Sohn 1979). Sohn (1969)

TEXT-FIGURE 1
Generalized tectonic map of western North America (modified after De Celles 2004), showing the Cordilleran foreland basin system and the geographic position of the Black Hills uplift, South Dakota (1), as well as the distal position of the Lakota Formation within the foreland basin, and the position of the San Rafael Swell, Utah (2), with the more proximal position of the Cedar Mountain Formation within the foreland basin and in relation to the Cordilleran orogenic belt. Abbreviations for indicated states within the U.S.A.: ID–Idaho, ND–North Dakota, SD–South Dakota, MT–Montana, WY–Wyoming, UT–Utah, CO–Colorado, NE–Nebraska, KS–Kansas, AZ–Arizona, NM–New Mexico.

also described nonmarine Lower Cretaceous ostracods from NE Nevada.

The ostracods of the Cedar Mountain Formation (Utah) have never been described. Stokes (1952) only mentions ostracods (and charophytes) from the "Burro Canyon Formation" of eastern Utah (Salt Valley Anticline, Grand County)–now considered to be part of the Cedar Mountain Formation (see Kirkland et al. 1997)–which were determined by R. E. Peck (Stokes 1952).

For over 25 years, the nonmarine Early Cretaceous ostracods of the North American Western interior foreland basin, including

the representatives of *Cypridea* Bosquet, have not been subject to detailed research, and barely have been dealt with in a global context in the time before. One reason may be that these ostracod faunas were considered to be endemic traditionally and not well applicable to biostratigraphy. As Michael E. Schudack (1995, 1996, 1999, Schudack et al. 1998) has shown for the ostracods (and charophytes) of the nonmarine Upper Jurassic Morrison Formation that underlies many of the nonmarine Lower Cretaceous formations in the basin, the ostracod endemicity is not as strong as believed in the past. Quite the contrary, there are many close relations to the Iberian faunas (Spain) usable for biostratigraphy, biogeography and paleoecology/paleoclimate applications. Accordingly, there was a high probability that this is also true for the Lower Cretaceous faunas which was the starting point of the new research presented herein.

Sohn (1958) had already suggested and later confirmed (Sohn 1979) a Valanginian to Barremian age for the Lakota Formation of the Black Hills area (as can be confirmed here) based on comparison of the ostracod fauna to contemporaneous European and Asian faunas. Sohn (1979), though, only discussed similarities of representatives of these faunas, but retained established local taxon names and erected new ones. Sohn (1958, 1979) however, never went one step further and reevaluated his analyses of the taxa to make direct correlations.

As for the taxonomy and biostratigraphic application of *Cypridea* and its representatives, relevant publications including the North American works are listed and commented in Section 5.2.2.

2.3 Aims

Altogether, the reasons given might explain why no or only tentative attempts for supraregional comparison and correlation of Early Cretaceous nonmarine ostracods of the U.S. Western Interior were made in the second half of the 20th century. Hitherto, the supraregional nonmarine ostracod biostratigraphy of Lower Cretaceous rocks of North America is poorly developed (Sames et al. 2010a for overview), a gap to be partially filled with the results of this paper. A comprehensive review of the taxonomy shall provide the basis for a utilization of the nonmarine ostracods for applications like biostratigraphy, paleobiogeography and paleoecology.
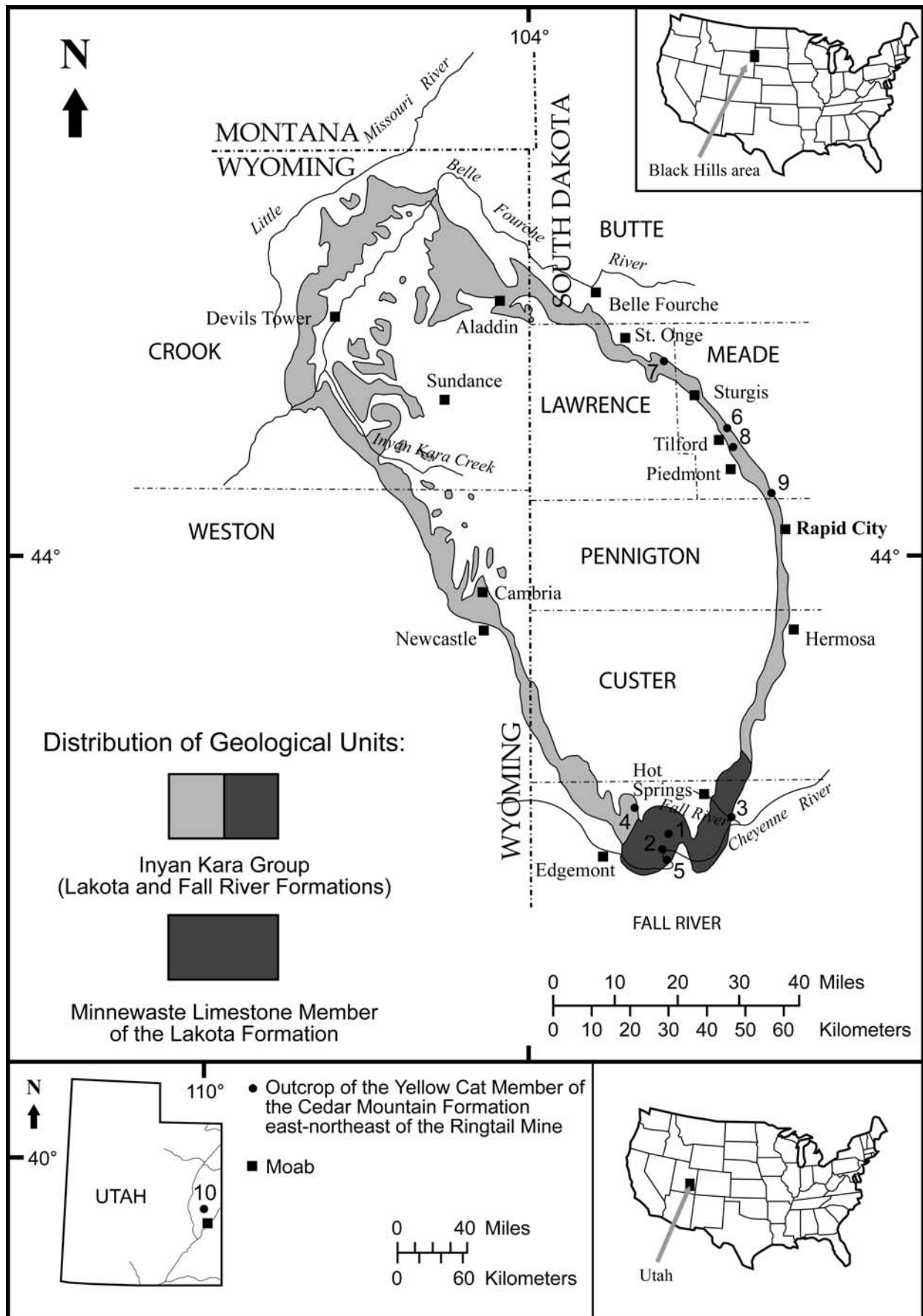
The comprehensive nature of this paper (necessarily including long synonymy lists, descriptions and discussions) derives–in the view of the author–from the need for:

A) compiling an enourmous amount of information scattered throughout hundreds of publications in many different languages, some difficult to obtain,

B) a detailed review, definition, and illustration of specific taxonomic terms in conjunction with progress in research of ostracod phylogeny, biology and ecology (this led to the detailed glossary, Sames 2011c),

C) describing and figuring as many carapace features as possible as well as discussing their taxonomic value,

D) a global approach as to the comparison of taxa and an integration of taxonomic and stratigraphic concepts.

TEXT-FIGURE 2

Locality Maps. Upper part: Black Hills area of South Dakota and Wyoming showing the distribution of the Inyan Kara Group (Lakota and Fall River formations) deposits (modified after Waagé 1959, and Sohn 1979), and the sample localities discussed herein (Nos. 1-9). Lower part: San Rafael Swell area of Utah with the sample locality in the Cedar Mountain Formation (No. 10). GPS coordinates in UTM projection (NAD 27):

1. Buck Canyon, section label BC (BCB, BCE; loc. 17 of Sohn, 1979), section of Bell and Post (1971, p. 530-531), northeastern Flint Hill Quadrangle, UTM: 13 T 611329E 4800660N.

2. Horse Sanctuary/Devil's Canyon, section label HSDC, section of Bell and Post (1971, p. 538-539), eastern Flint Hill Quadrangle. No GPS data.

3. Fall River Canyon, section label FRCA (close to loc. 12 of Sohn, 1979), SE of Hot Springs, southeastern Hot Springs Quadrangle. UTM: 13 T 625855E 4807594N.

4. Red Canyon, section label RCS (loc. 9? of Sohn, 1979), southeastern Edgemont NE Quadrangle, Fall River County, UTM: 13 T 598799E 4804793N.

5. Angell Ranch/Cheyenne River, section label ARCR, southeastern Flint Hill Quadrangle, Fall River County, UTM: 13 T 611226E 4792665N.

6. Little Elk Creek, section label LEC NE of Tilford, Meade County, UTM: 13 T 629259E 4901379N.

7. East of road to Belle Fourche, north of Whitewood, section label EBF (close to loc. 2 of Sohn, 1979), Hot Springs Quadrangle, Lawrence County, UTM: 13 T 608929E 4928509N.

8. Stage Barn Canyon Road, section label SBCR, SE of Tilford, Rapid City Quadrangle, Meade County, Roth's (1933) type locality (?), UTM: 13 T 633461E 4894622N (? value might be wrong).

9. Boxelder Creek east of Blackhawk, section label REKO 04, southeastern Black Hawk Quadrangle, Meade County, UTM: 13 T 638901E 4887800N.

10. Yellow Cat Member of the Cedar Mountain Formation, section label PS, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. UTM: 12 S 0634763E 4304116N.

One aim of this paper is to provide a synopsis within one publication that is hoped to be a good basis for future research regarding *Cypridea*–its taxonomy, phylogeny, and its stratigraphic and paleobiogeographic distribution worldwide. For the purpose of a better global approach, it is attempted to implicate as many references as possible in non-English languages and from continents other than North America and Europe, specifically South America (Spanish, Portugese, German) and Asia (Russian, Chinese), as well as Africa in part (French, German; altogether, the state of knowlegde about Upper Jurassic to Cretaceous nonmarine ostracods in Africa is not that good yet, except for central West Africa). As for the Central Asian ostracods, luckily there are some comprehensive newer publications, practically taxonomic atlases, summarizing and refiguring the so far published species: Hou et al. (2002), Nikolaeva and Neustrueva (1999) and Neustrueva et al. (2005).

For a revsion of the genus *Theriosynoecum* Branson, another important genus for biostratigraphy in nonmarine Lower Cretaceous deposits of Europe, and some North American representatives refer to Sames (2011a).

3. GEOLOGIC OVERVIEW, STRATIGRAPHY AND LOCALITIES

The North American Cordilleran foreland basin (U.S. Western Interior Basin) is the largest of its type known, reaching from northeast Canada to central Mexico and occupying an area of more than five million square kilometers (e.g. Kauffman and Caldwell 1993; see Text-fig. 1 herein). During Late Jurassic times, the basin began to develop between the North American Cordilleran orogenic belt to the west and the North American craton to the east in response to the subduction of oceanic plates of the pacific domain (Kauffman and Caldwell 1993, De Celles 2004). Contemporaneously, and in various types of process-response and feedback relationships, the orogenic belt and the foreland basin evolved together until Eocene times. Altogether, this evolution lasted for about 100myr, including two main orogenic phases: the Sevier orogeny ("Middle" to Late Cretaceous) and the Laramide orogeny (Late Cretaceous to Eocene). Basin subsidence was caused by flexural thrust-loading–a combination of the flexure of the lower crust due to overthrust, sediment load and longer wavelength (>400km) dynamic subsidence (e.g. De Celles and Giles 1996, De Celles 2004, Miall et al. 2008). Deposition during Late Jurassic to Early Creataceous times was strongly connected with the tectonic co-evolution of both the proto-Cordillera and its associated foreland basin, which affects source, supply rate and depozone of the nonmarine sediments (Kauffman and Caldwell 1993). De Celles and Giles (1996, p. 117) point out that in their expanded definition for foreland basin systems "… a depozone is defined in terms of its position during deposition, rather than its eventual position with respect to the thrust belt", which is important to understand the interaction of tectonics and syndepositional stratigraphic architecture, and its regional differences.

Stratigraphic correlation and refined dating of Late Jurassic to Early Cretaceous Western Interior nonmarine strata, having been problematic throughout the 20th century, improved since integrated stratigraphy was applied (e.g. Currie 1997, 1998, Way et al. 1998, Zaleha 2006). However, dating such formations is still a problem and especially the maximum age of the Lower Cretaceous formations or rather the hiatus between their base and the underlying Morrison Formation is controversially under discussion, a problem hoped to be solved by improving age estimations due to combined ostracod/charophyte biostratigraphy.

The Lakota Formation (Black Hills, South Dakota and Wyoming) was deposited in the distal part of the foreland basin, whereas the Cedar Mountain Formation (San Rafael Swell, Utah) represents its very proximal deposits (Text-fig. 1). The Laramide event led to fracturing of the craton and partitioned a part of the foreland basin ito a mosaic of smaller foreland basins and uplifts (e.g. De Celles 2004, Dickinson 2004), like the Black Hills uplift for example, the easternmost of the Laramide foreland uplifts.

The Inyan Kara Group, consisting of the Lakota Formation in its lower part and the overlying Fall River Formation, crops out along the flanks of the Black Hills uplift, South Dakota and Wyoming (Text-fig. 2). In most areas, the Morrison Formation unconformably underlies the Inyan Kara Group except for the southeastern area, where it is substituted by the locally occurring Unkpapa Sandstone. In his revision of the Lakota Formation, Waagé (1959) subdivided the Lakota Formation into "the Lakota formation below [the] Minnewaste limestone member" (op. cit., p. 86), the "Minnewaste limestone member" and the "Fuson member". Furthermore, Waagé (1959) restricted the term Inyan Kara Group and its formations to the Black Hills area, differentiated several sequences of the Lakota Formation in the Black Hills (the northwestern, the coal-bearing, the eastern, and the southern sequence, whereas the southern is the stratigraphic most complex and probably most complete) to illustrate some of its principal variations, and also defined a new reference section for it in the Fall River Canyon (Text-fig. 2, No. 3). Post and Bell (1961) designated the lower part of the Lakota Formation as Chilson Member, particularly in the southern Black Hills.

Way et al. (1998) subdivided the Lakota Formation in the northern Black Hills into three informal intervals (L1, L2 and L3), L1 corresponding to the Chilson Member including the Minnewaste Limestone Member restricted to the southern Black Hills (Zaleha 2006, see Text-fig. 2 herein also), L2 correlating with the lower part of the Fuson Member as defined for the western Black Hills by Post and Bell (1961), and L3 with the upper part of the Fuson Member of workers like Post and Bell (1961) or Dahlstrom and Fox (1995). Zaleha (2006) correlated these informal intervals with Lower Cretaceous rocks of central and western Wyoming, thereby giving an Barremian to Aptian (112.2 Ma), age for the Lakota Formation, possibly Hauterivian and even Valanginian for some deposits of the L1 interval.

The Cedar Mountain Formation has been defined by Stokes (1952) based on a type section at the northern San Rafael Swell, Emery County, Utah. He (op. cit.) included the Buckhorn Conglomerate as its basal member and the shale below the Dakota Formation. Kirkland et al. (1997, 1999) defined four additional members based on the distribution of four distinct dinosaur faunas (in ascending order): the Yellow Cat Member, the Poison Strip Sandstone (cf. Text-fig. 11 herein), the Ruby Ranch Member, and the Mussentuchit Member.

The ostracod samples dealt with in this paper derive from the Lakota Formation in its eastern and southern sequence of South Dakota (Text-fig. 1, No. 1; Text-fig. 2, localities), and the Yellow Cat Member of the Cedar Mountain Formation in the San Rafael Swell area of Utah (Text-fig. 1, No. 2; Text-fig. 2, No. 10), below the Poison Strip Sandstone.

As mentioned before, detailed implications and consequences of the taxonomic results for biogeography, biostratigraphy, and paleoecology will be analyzed and discussed elsewhere. An overview with reference to the stratigraphy of the Western Interior foreland basin and some implications of new biostratigraphic results from ostracod correlations (with emphasis on higher maximum ages of Lower Cretaceous formations) on the basin's geology and paleontology is given in Sames et al. (2010).

4. MATERIAL AND METHODS

Surface bulk samples from promising lithologies (calcareous claystones, marls and calcareous silt- and sandstones) were taken from several sections of the Lakota Formation in the southern and eastern Black Hills (South Dakota, Text-figs. 1 and 2) and a locality from the Cedar Mountain Formation (Utah, Text-figs. 1 and 2). Processing followed using standard methods, treating the samples with warm water, and 2-8% hydrogen peroxide (0.5-3 hours), if necessary (i.e. if samples did not disperse in warm water only). The samples were then washed through sieves (500, 250, and 125m), picked and scanned uncoated with a LEO 1450 VP Scanning Electron Microscope at the Sam Noble Oklahoma Museum of Natural History (Norman, Oklahoma) in variable pressure mode using the four-quadrant backscatter detector. Some type and reference material from the collection of The National Museum of Natural History, Smithsonian Institution, Washington was scanned there, also using backscatter mode. The backscatter mode proved to be ideal for displaying and analyzing ornamentation and surface characters.

The specimens were mounted using needle and wax, which, without coating, may appear as small black grains on the specimens, because without coating the contrast between organic (dark, very low conductivity) and anorganic (bright, stronger conductivity) matter is very strong.

For purposes of clarity, the taxonomic descriptions follow a consistant scheme as far as possible, maintaining the same succession of terms within paragraphs. To enable the reader of a better evaluation of the hypotheses and results presented herein, the discussion section of each species reviewed herein is detailed and sucessively deals with nearly all species as listed in the synonymy that required further comments.

Specific morphologic terms that the author considers in need of clarification in the context of their usage and interpretation, particularly as to *Cypridea*, are elucidated and discussed in the glossary (Sames 2011c). Considered of particular importance is the newly proposed definition of ornamentation (ornamentation elements), and the differentiation of "local ornamentation elements" and "area-wide ornamentation elements/surface characters" (op. cit.).

The size parameters used are as follows: Very small: 0.20-0.60mm; Small: 0.60-1.00mm; Medium: 1.00-1.50mm; Large: 1.5-5mm (in relation to maximum length parallel to basic line). For purpose of better readability and intelligibility, abbreviations are avoided mostly. The few common abbreviations used are: LV for left valve, RV for right valve, L/H for length/height-coefficient, L/W for length/width-coefficient, L for length, H for height and W for width. For better accuracy, measurements were obtained digitally from the SEM pictures by using the CANVAS (ACD Systems) program.

The measured parameters in order to describe the carapace are illustrated in Text-figure 4. In lateral view, the carapace is oriented in relation to the base line. Maximum length, height, and width include all protrusions that overreach the outline but not the very variable and environmentally influenced local ornamentation elements (*sensu* Sames 2011c) such as tubercles and spines. Thus, the carapace outline is significant prior to the outer margins where applicable (e.g. ventral overreach due to ventral ridge which is a genetically fixed character).

The abbreviations for "plate(s)" and "(text-)figure(s)" are given in upper case (Pl. and Text-fig.,) when referring to those in this publication whereas lower case (pl. and fig.) indicates those of cited references.

For the reason to give a comprehensive revision that shall provide a fundamental basis for future taxonomic and stratigraphic research, the synonymy lists are as complete as possible, depending on the references available and accessible. As for the discussion of synonymy, this has been done as comprehensively as necessary. However, to avoid an exorbitant dimension of the already comprehensive manuscript, only ambiguous taxa (with question mark in synonymy), taxa with different names and/or rank, taxa that needed discussion for particular reasons (terminologically, taxonomically etc.) as well as those of actual or potential stratigraphic significance were particularly addressed. Others, like those having repeatedly used by the same author(s) in the same context or taxonomic name and rank as well as those conform with the present author's view not having to be auxiliary commented, are just listed and cited.

Owing to the impossibility to fully accomplish the comprehensiveness of a global approach, the data given under the item "stratigraphic and geographic distribution" of the respective taxa must inevitably remain a selection, which was conducted appropriate to facilitate biostratigraphic application. Therefore, most data derive from Europe, from where the best data with good resolution are available, particularly the English Purbeck/Wealden (Anderson 1939 et seq.). Information from other continents and areas have been implemented to the best extend possible (i.e., available data and publications). For more information, the reader be kindly referred to the references in respective publications, stratigraphic atlases or databases, such as that of Kempf (1980 et. seq.).

The classification of brackish waters follows the Venice System according to Oertli (1964).

With respect to salinity (*sensu lato)* tolerances and paleoecology, the classification of brackish waters is based on the Venice System according to Oertli (1964).

The item "faunal association" in the taxonomic description refers to North American assemblages only. Regarding species belonging to other genera than *Cypridea*, these will be dealt with in other papers, concerning *Theriosynoecum* refer to Sames (2011a).

The correlation and age determination of NW European Purbeck/Wealden deposits follows the local zonation schemes, particularly the revised ostracod biozonation scheme for the English Purbeck/Wealden after Horne (1995), and the extensive integrated and supraregional correlation-chart of Hoedemaeker and Herngreen (2003). Although there are still a few details to be discussed, the latter is the most recent and comprehensible

dataset available, which is also very useful dataset in a practical format because of the detailed information given therein.

Abbreviations and symbols used in the synonymy list follows the established biologic nomenclature (cf. Granzow 2000, for example) and are explained at the beginning of taxonomic section (section 5.2).

As for those species reported from material of the collection of R. E. Peck at the University of Missouri, Columbia (Missouri, U.S.A.), no data of faunal associations is available at all, neither from the records in the collection (visit of BS in 2005) nor from his publications (Peck 1941, 1951, 1956, 1959; Peck and Craig 1962; Peck and Reker 1948). The tables in the publications only list species of the same sample localities, but there is no information if they derive from the same samples/sample horizons. Since the whereabouts of Peck's type material at his collection at the University of Missouri (see item 5.1 below) are unknown, some Master's theses of students of Peck (Looney 1948, Craig 1961) are cited here, because these particularly Craig (1961) provide much valuable additional information that are not available from Peck's (1941, 1951, 1956, 1959; Peck and Craig 1962; Peck and Reker 1948) publications and his location catalog. Unfortunately, the whereabouts of "type" material of the theses (Looney 1948, Craig 1961) are unknown as well.

For practical purposes, the "International Code of Zoological Nomenclature" (International Commision on Zoological Nomenclature 1999, online) is abbreviated and cited ICZN (1999) in the text.

5. SYSTEMATIC SECTION

5.1 Repositories and their abbreviations

The specimens figured herein and the image files will be deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. (USNM) under the numbers given. Abbreviations for repositories cited are as follows:

• BMNH – The Natural History Museum (formerly the British Museum, Natural History), London, UK.

• BGS – British Geological Survey Palaeontological Collections, BGS Headquarters Keyworth, Nottingham: Mik (M) xxxx.001 (.001 suffix of earlier citations)

• U.M. – University of Missouri Collection, Columbia, Missouri, U.S.A. Unfortunately, the disposition of the ostracod type material and many of the figured specimens is unknown, although it is listed in the catalog (visit of the author May, 2005; pers. comm., R.L. Ethington, University of Missouri).

• USNM – The National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

5.2 Taxonomy

Abbreviations (combined in part) used in synonymy lists (cf. Granzow 2000, for example):

* (star) indicates the type species

• (dot) The author of this (critical) synonymy list indicates that he or she takes responsibility for this assignment.

? (question mark) indicates questionable synonymy

non (Latin for "not") Indicates that, in the opinion of the author, the respective taxon given in the synonymy list does *not* belong to the taxon discussed.

pars (Latin for part) The author of this (critical) synonymy list has the opinion that only a part of the specimens discussed or figured in the respective publication belong to the discussed taxon.

v (from Latin "*vidi*" = I have seen) The author indicates that he or she has personally inspected the respective type specimen, or respective reference specimens of the given reference (other types, figured specimens).

[] Squared brackets in synonymy lists enclose information not really belonging to the list but that contribute towards a better understanding (comments for example).

5.2.1 *Suprageneric taxonomy*

Class OSTRACODA Latreille 1802
Order PODOCOPIDA Müller 1894
Suborder CYPRIDOCOPINA Jones 1901

Superfamily **CYPRIDOIDEA** Baird 1845

Remarks: According to the International Code for Zoological Nomenclature (ICZN 1999) the ending "-oidea" is used for superfamily level (i.e. Cypridoidea instead of Cypridacea), thereby avoiding confusion with plant taxa.

Family **CYPRIDEIDAE** Martin 1940 emend.

Diagnosis: (Author's translation of Martin's diagnosis 1958, p. 313): "Ostracods of the suborder Podocopa [order Podocopida, suborder Cypridocopina according to Horne et al. 2002] with the following particularities: Both valves bear a more or less well pronounced rostrum (hook, beak) at the anterior half of the ventral margin that is an integrating, non-decorative element of the valve. Situated directly behind is a sligthly to deeper incised recess (rostral groove [i.e., alveolar furrow, see Sames 2011c]). Beak or groove may be only allusively present in some cases but are never missing. The central muscle scar field consists of 6 adductor muscle scars approximately in the center of the valve, as well as anterior of and transversely below it two small scars of the mandibles, and transversely above it two small scars of the antennae, respectively. Four large scars lie in the central field, three of which lie transversely above each other in a semi-circle whereas the fourth is situated behind them; one very small roundish scar each lies so close to the two lowermost main scars that they are often hardly ever or not at all to distinguish from the latter. – The marginal pore canals are bulbous inflated close to their [outer] aperture. – Simple notched hinge without teeth. – Strong ventral overlap of either the left or the right valve."

Addition to diagnosis: Internal view showing local widening of inner lamella (where rostrum and/or alveolar notch occur), marginal pore canals missing in the area above the alveolar notch (=attached area). Interrupted selvage along the posterior part of the rostrum, or a similar anteroventral structure. Posteroventral area generally developed as 'true' cyathus, in some cases indistinct or with transition to cyathus-like protrusion. Valve size re-

lation generally inequivalve, normal or inverse. Inner lamella usually well developed–broad anteriorly, moderate posteriorly, and widest anteroventrally and posteroventrally. Dorsal furrow or hinge incisure of variable intensity, but usually well developed (see Text-figs. 7 and 8).

Remark: Sexual dimorphism may not be apparent in (fossil) valves of representatives of the Cypridoidea (e.g. Horne and Martens 1998). However, some taxa of the Cyprideidae Martin 1940 including representatives of *Cypridea* are presumed to clearly show sexual dimorphism (see paragraph 'sexual dimorphism' under genus *Cypridea* below for details).

Discussion: With reference to the systematics above family level, this article follows Horne et al. (2002) who place the extant nonmarine Cypridoidea under the infraorder Cypridocopina. As for the assignment to a family/subfamily, this has been under discussion for a long time and different authors subsequently placed *Cypridea* and closely related genera in different Cypridoidean families (see Szczechura 1981, p. 262 et seqq.).

Recapitulatory, Martin (1940) established the Cyprideinae as subfamily of the 'Cypridae' (recte Cyprididae Baird 1845) because the subfamily Rostrocyprinae erected by Anderson (1939) was not consistent with the International Code of Zoological Nomenclature since it did not comprise the nominate genus (*Cypridea*) and had, thus, to be considered invalid. This systematic position of *Cypridea* (Cyprididae–Cyprideinae) was maintained by many authors. However, Sylvester-Bradley and Harding (1953), when reviewing the nomenclature of the genus *Cytherideis*, proposed the family Cyprideidae Martin 1940 while also keeping the subfamily Cyprideinae Martin with *Cypridea* as type genus.

Not mentioning Sylvester-Bradley and Harding (1953), Martin (1958) emended his subfamily (Cyprideinae) to family status, the Cyprideidae Martin 1940, thereby making the subfamily superfluous. He (op. cit., p. 313 et seqq.) argued and discussed at length that there would be no reason anymore to assign the forms deriving from, or related to, *Cypridea* to the 'Cypridae' (recte Cyprididae Baird 1845) due to diagnostic carapace features differing from any other fossil and recent ostracod family. Many subsequent authors cited Hartmann and Puri (1974, p. 57) as reference for the emendation of the Cyprideinae to family level, but this is neither correct nor do Hartmann and Puri explain or comment their decision at all. Therefore, the correct author and date of the family name Cyprideidae is Martin (1940).

The closer relations of the Cyprideidae to extant families are controversial and not satisfactory resolved to date. Depending on the view how the extinct genus *Cypridea* is related to extant representatives of the Cypridoidea there are several possibilities:

1) We can keep *Cypridea* in the separate family of the Cypridoidea, the Cyprideidae Martin 1940 (based on a separate *Cypridea-Bisulcocypridea* lineage, then to be considered extinct), the view adopted here.

2) We regard the group as more closely related and belonging to the extant Cyprididae Baird 1845, which would result in its designation as subfamily Cyprideinae Martin 1940 (extinct) under the latter family. Horne and Colin (2005) showed that the mod-

ern cypridoidean with closest affinities to *Cypridea* is *Bennelongia* De Deckker and McKenzie 1981, a genus, however, being restricted to New Zealand and Australia, a continent which has failed to reveal any *Cypridea* taxa to date as well as other pre-Pliocene nonmarine ostracods. Based on soft parts, *Bennelongia* belongs to the extant family Cyprididae Baird 1845, subfamily Cyprinae, but since the soft-parts of *Cypridea* are unknown, no further arguments supporting a closer relation of both genera are available so far.

3) We retain the "classic" view of putting *Cypridea* under the subfamily Cyprideinae into the family Ilyocyprididae Kaufmann 1900(a). Based on Swain's (1949) account on "early Tertiary" Ostracoda from the U.S. Western Interior, particularly his *Cypridea bisulcata* (recte *Bisulcocypridea bisulcata*). Sylvester-Bradley (1976; title of Swain 1949 wrongly cited therein) already discussed a possible lineage from *Cypridea* to the modern *Ilyocypris* (*Cypridea-Bisulcocypridea-Ilyocypris* lineage), i.e., from the Cyprideidae Martin 1940 to the Ilyocyprididae Kaufmann 1900(a). The latter is, in turn, based on the similarities of *Bisulcocypridea* Sohn 1969 to *Cypridea* by, amongst other characters, presence of a rostrum; and to *Ilyocypris* by possessing two dorsolateral sulci.

Although the view given under item 1 right above is followed herein, either concept cannot be ruled out thus far.

Horne and Colin (2005) had analyzed and discussed possible relations of *Cypridea* s.l. that is the Cyprideidae to fossil to recent representatives of the cypridoidean families Ilyocyprididae, Cyprididae and Notodromadidae by emphasizing the adductor muscle scar patterns and the marginal zone structures (see Section 5.2.2 "Historic overview" below also). While not ruling out a *Cypridea-Bisulcocypridea-Ilyocypris* lineage, these authors (op. cit.) point out that the fossil record can as well be interpreted as "… indicating two parallel lineages: the [extant] Ilyocyprididae (*Rhinocypris-Ilyocypris*) and the [extinct] Cyprideidae (*Cypridea-Bisulcopridea*)" (op. cit., p. 27).

When phylogeny is interpreted, chronologic or stratigraphic aspects must also be taken into account alongside morphology. For example, if the view of a *Cypridea-Bisulcocypridea* lineage that belongs to the Ilyocyprididae (see No. 3 above) would be accepted, this would pose several questions as to the phylogeny of *Bisulcocypridea* Sohn 1969 in context with the Ilyocyprididae. Undoubted representatives of the Ilyocyprididae (i.e., representatives of the genus *Rhinocypris* Anderson 1941, Late Jurassic – Kimmeridgian, Schudack and Schudack 2002) occur much earlier than any representatives of *Bisulcocypridea* Sohn (Late Cretaceous?-Paleogene). It is much unlikely that the *Cypridea*-lineage (Kimmeridgian-Eocene) totally lost the (one or two) pair(s) of median dorsolateral sulci (as always present in the Ilyocyprididae) before these reappeared in *Bisulcocypridea* tens of million years later. The herein described species *Cypridea? minuta* (Peck 1951) shows one weak pair of dorsolateral sulci and could come into consideration as ancestor of an *Cypridea-Bisulcocypridea (-Ilyocypris?)* lineage. This would support Swain's (1949) arguments that *Bisulcocypridea* was a *Cypridea* that had become bisulcate and Sylvester-Bradley's (1976) tentative suggestion of *Bisulcocypridea* as being the intermediate form (in time and morphology) between *Cypridea* and *Ilyocypris*. Based on this and the fact that the oldest known representatives of both, *Rhinocypris* and *Cypridea*, are of Kimmeridgian age (e.g. Schudack and Schudack 2002,

Sames 2008), it is not clear how *Rhinocypris* would fit into such hypothesis.

Whichever argumentation is followed: there is still not enough data available yet to make either of these considerably more credible than the others. Many concepts are based on sparse information (stratigraphic record) and few arguments (number of carapace characters). As stated by Horne and Colin (2005), the adductor muscle scar patterns are no sufficient indicators to clarify the affinities of the Cyprideidae to other cypridoidean families. Whereas the presence or absence of the *Cypridea*-type rostrum and alveolus, for example, seems to be a strong argument in consequence of these character's complexity (see Sames 2011c), ornamentation elements occurring in the taxa involved are, in contrast, often not diagnostic. Moreover, there are many transitions in the development of several characters in the Cyprideidae, e.g. the cyathus and cyathus-like protrusion (see Text-fig. 5/C), or the development of the alveolar notch (see Text-fig. 5/B and Sames 2011c), in part having been a terminologic problem.

In summary, this article follows the most convincing data and line of argument available which is the carapace-based taxonomy in Martin (1958, see diagnosis above), Szczechura (1981) as well as Horne and Colin (2005), thus placing *Cypridea* in the family Cyprideidae Martin 1940, along with *Paracypridea* Swain 1946, *Bisulcocypridea* Sohn 1969, and *Mongolocypris* Szczechura 1978. Unlike given in Horne and Colin (2005, table 1 therein), the genus *Longispinella* Sohn 1979 is regarded and justified as being a representative (subgenus) of *Cypridea* herein, instead of considering it a discrete genus within the Cyprideidae (see Table 1 herein). In addition, the new genus *Praecypridea* Sames, Whatley and Schudack 2010 is integrated (Sames et al. 2010b) as well as the proposed genus *Kegelina* (Queiroz Neto et al. 2010, in prep.).

Additional remarks concerning usage of the Family/Subfamily Cyprideidae/Cyprideinae: Several authors (e.g. Mandelstam and Schneider 1963) also used the family/subfamily Cyprideidae/Cyprideinae in a wider sense by including genera without a beak, that is: *Latonia* Mandelstam, *Limnocypridea* Ljubimova, *Zejaina* Mandelstam, *Cyprideamorphella* Mandelstam, *Mongolianella* Mandelstam, *Hourcqia* Krömmelbein (pars, Do Carmo et al. 2008, see under description of the genus *Cypridea* below for comments), and *Ilyocyprimorpha* Mandelstam–a view not followed herein.

Other taxa bearing homeomorphic beak-like structures (also called rostrum-like processes) on the valves have been included in the Cyprididae Baird 1845 (see for example Khand 2000: *Bogdocypris*, *Talicypridea*; or Szczechura 1978: *Altanicypris*, *Khandia*) for the reason of their different internal valve structure (i.e., their beak-like structure is formed by the outer lamella only, not by the fused outer lamella and selvage as in *Cypridea*, cf. fig. 4 in Horne and Colin 2005, and Text-fig. 8 herein). We owe it to Szczechura (1981), who demonstrated that it is essential to analyze internal and external valve morphology to distinguish between *Cypridea* and these superficially similar genera with beak/rostrum-like processes. This provided the basis and data to exclude such taxa from the Cyprideidae Martin and to relate them to other families, e.g. the Cyprididae Baird.

Some authors, e.g. Peck 1951, also used the subfamily name Cyprideinae Martin 1940 in the meaning of *Cypridea sensu lato* as resulting from the view to integrate *Cypridea* and its relatives

in either the cypridoid families Cyprididae Baird 1845 or Ilyocyprididae Kaufmann 1900(a), either of which not being followed herein.

Horne and Colin (2005) pointed out that earlier concepts of the Cyprididae Baird 1845 i.e., those of Triebel (1960) and Sczechura (1981) "… were approximately equivalent to our [i.e., Horne et al. 2002] concept of the Suborder Cypridocopina and Superfamily Cypridoidea, respectively …" (Horne and Colin 2005, p. 27).

A particular case is the Pliocene nonmarine genus *Karshicypridea* Gramm and Burkharina 1967, which shows a rostrum very similar to that of *Cypridea*, separated from the ventral margin by a broad incision, but lacking an alveolar, furrow-like structure. Also, the anteroventral part of the zone of concrescence in *Karshicypridea* is homogeneous in internal view, without an attached area being devoid of marginal pore canals as occurring in *Cypridea* (Text-fig. 8). Since the anteroventral characters in *Karshicypridea* are only outwardly similar to *Cypridea* and the adductor muscle scar pattern of the former does more resemble that one of the Candonidae Kaufmann 1900(b) rather than that of the Cyprideidae Martin 1940, a closer relation of the two seems improbable. However, a modern revision of *Karshicypridea* based on more material is wanting and no substantiated hypothesis as to its closer relationships can be given at the moment.

Genera of the family Cyprideidae Martin 1940: This includes representatives of the genus *Cypridea sensu stricto*–i.e., *Cypridea (Cypridea)*–and *Cypridea sensu lato* (see Section 5.2.2: Historic overview below as well as the synonymy list regarding the genus *Cypridea*, and Table 1), as well as: *Bisulcocypridea* Sohn 1969, *Mongolocypris* Szczechura 1978, and *Paracypridea* Swain 1946. In addition, the genus *Longispinella* Sohn 1979 is herein considered and defined as subgenus of *Cypridea*, and the genera *Praecypridea* Sames, Whatley and Schudack 2010 (Sames et al. 2010b) and *Kegelina* (Queiroz Neto et al. 2010; in prep.) are newly included.

Cypridea (Sebastianites) Krömmelbein 1962 will probably have to be separated from *Cypridea* and raised to genus rank (see Table 1 and discussion of synonymy of the genus *Cypridea* below) but remain in the Cyprideidae Martin 1940.

The genus *Cultella* Lyubimova 1959, as wrongly included into the Cyprideidae Martin 1940 in the Ostracod Treatise (Moore and Pitrat 1961), questionably belongs to the family Trapezoidellidae Sohn 1979 following Nikolaeva and Neustrueva (1999, p. 34).

Cypridea (Yumenia) Hou 1958 is excluded from being a representative of *Cypridea* Bosquet 1852 and the Family Cyprideidae Martin 1940 here for the reasons of lacking many diagnostic characters: rostrum, alveolus and cyathus. *Yumenia* has been placed into the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34).

5.2.2. Historic overview – Chronology of the genus Cypridea Bosquet 1852

The literature about the overwhelming amount of representatives of *Cypridea* (refer to Kempf 1980-2002, for example) is vast and nearly impractical to capture, to compile, and to summarize. Hence, it seemed appropriate and essential to include a (partially commented) synopsis of relevant publications. In the

TABLE 1
Emended overview of genera included in (or excluded from) the family Cyprideidae Martin 1940, Late Jurassic to Paleogene (Kimmeridgian to early Eocene) as discussed herein (Section 5.2.1; see Table 1 of Horne and Colin 2005 also).

Family **Cyprideidae** Martin 1940	
Valid representatives:	**Questionable and invalid representatives:**

Genus ***Bisulcocypridea*** Sohn 1969
Genus ***Cypridea*** Bosquet 1852
   Cypridea (Cyamocypris) (Anderson 1939)
   Cypridea (Cypridea) Bosquet 1852
   Cypridea (Longispinella) (Sohn 1979) **stat. nov.**
   Cypridea (Morinina) (Anderson 1939)
   Cypridea (Morininoides) Krömmelbein 1962
   Cypridea (Pseudocypridina) (Roth 1933) syn.
   Langtonia Anderson 1939
Genus ***Kegelina*** Queiroz Neto, Sames and Colin 201X
Genus ***Mongolocypris*** Szczechura 1978
Genus ***Paracypridea*** Swain 1946
Genus ***Praecypridea*** Sames, Whatley and Schudack 2010
	Genus ***Cultella*** Lyubimova 1959 [a]
	Genus ***Cypridea*** Bosquet 1852
	   Cypridea (Guangdongia) Guan 1978 [b]
	   Cypridea (Ulwellia) Anderson 1939 [c]
	   Cypridea (Sebastianites) Krömmelbein 1962 [d]
	   Cypridea (Yumenia) Hou 1958 [e]

a) wrongly included into the Cyprideidae Martin 1940 in the Ostracod Treatise (Moore and Pitrat 1960, p. Q243-Q245, fig. 179A); questionably belonging to the family Trapezoidellidae Sohn 1979 following Nikolaeva and Neustrueva (1999, p. 34)
b) allocated to *Bisculcocypridea* herein
c) rejected (see text for explanation)
d) to be revised, questionably belonging to the Cyprideidae Martin, will probably have to be raised to genus rank; tentatively placed in the subfamily Ilyocyprimorphinae Sinitsa 1999 of the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 35)
e) different genus most probably not belonging to the Cyprideidae Martin due to the lack of many diagnostic characters (rostrum, alveolus, cyathus, incised hinge margin/dorsal furrow); placed into the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34)

following chronologic overview, however, only a confined selection is given. On the one hand, that concerns the taxonomic and application-oriented relevant publications, on the other hand that concerns taxa from the areas this research mainly focuses on: the European Purbeck/Wealden and the North American Western Interior foreland basin as well as relevant Purbeck/Wealden-like deposits in other parts of the world.

In 1852, Bosquet proposed the new genus *Cypridea* from the Wealden of England and Germany for some species not mentioned by name and referred them to have been described by Sowerby, Roemer and Dunker as *Cypris* Müller 1776, but did not give a reference (he most certainly referred to Sowerby 1836, Roemer 1839, and Dunker 1846). Bosquet (1852) noticed the difference of these species from the living *Cypris* in possessing "... a small hook or prolongation in the form of a beak. That difference to me appears being of sufficient importance to establish a new genus, and I propose to name this genus *Cypridea*" (translated from Bosquet 1852, p. 47: "... un petit crochet ou prolongement en forme de bec. Cette différence me semble être d'une importance suffisante pour l'etablissement d'un nouveau genre, et je propose de donner à ce genre le nom de *Cypridea* ..."). Sylvester-Bradley (1949, p. 125) noted: "In a footnote he [Bosquet] mentions that a considerable number of new species were soon to be described by 'M. le professeur E. Forbes, de Londres.' Actually Forbes never lived to describe

these species, though in 1855 Sir Charles Lyell published woodcuts of some of them in the fifth edition of his Manual of Elementary Geology, with Forbes' name attached (Forbes 1855). One, designated '*Cypris punctata* E. Forbes', was quoted from the Lower Purbeck." However, the designation of this species as genotype by Anderson (1939) is invalid, because "*Cypris punctata* Forbes was not published until three years after Bosquet's proposal for *Cypridea*" (Sylvester-Bradley 1949, p. 126). Therefore, Sylvester-Bradley (1949) designated *Cypris granulosa* Sowerby 1836 as lectotype ("genolectotype" in Sylvester-Bradley 1949) of *Cypridea* (Sylvester-Bradley 1949, see p. 125-126, firstly having [uncommented] been designated by Sylvester-Bradley 1947 in a short note).

As for the genus *Cypridea* Bosquet 1852, name and author are valid because they meet the requirements of the International Code of Zoological Nomenclature (ICZN, 4th Edition 1999) for a genus erected at that time, as given in article 11 and 12 therein.

Important to note is the fact that *Cypris granulosa* (Sowerby 1936) as given by Dunker (1846) is not identical to the type species of *Cypridea* Bosquet 1852 as designated by Sylvester-Bradley (1949). In his invaluable "Index and Bibliography of Nonmarine Ostracoda" Kempf (1980a) gave this case as example for man-made complex taxonomic problems occurring casually: "The story of this case reveals that Dunker, 1946,

described a species under the name of *Cypris granulosa* Sowerby. This was regarded by Jones, 1978, as a wrong identification and for that reason newly combined in the form of *Cypridea granulosa* (Dunker), not *Cythere* ? *granulosa* (Sowerby). In 1885, however, Jones introduced the new combination *Cypridea granulosa* (Sowerby, 1836), which even became the type species of the genus *Cypridea* [as designated by Sylvester-Bradley 1949]. Instead of the earlier combination *Cypridea granulosa* (Dunker, 1846) the new name *Cypridea dunkeri* was introduced by Jones in the same paper" (Kempf 1980a, p. 17).

More than thirty years later, T.R. Jones (1885, p. 336) described the genus *Cypridea* Bosquet 1852 in greater detail as follows: "Carapace-valves subtriangular, obovate, or ovate-oblong; convex in the middle; broad (high) at the anterior third; narrower behind, one or both ends obliquely rounded; somewhat compressed anteriorly; notched at the antero-ventral angle, behind a small beak-like process; sometimes having only a slight indentation below and behind a thickening of the antero-ventral angle; sometimes this is traceable only by a curvature of the edge inside. Edge-view more or less narrow-ovate. End-view subovate. Surface punctate; sometimes almost smooth; often tuberculate; tubercles small or large, variously disposed. The hinge-margin is definitely straight along the middle third or more of the dorsal edge, with the hinge-angles more or less defined, and is oblique to the main axis of the valve. The left valve is the largest, and receives the dorsal edge and a straight ridge of the other valve in grooves on its dorsal and ventral contact-margins, the outer edge of the ventral margin of the left valve overlapping that of the right valve. The ridges and furrows or ledges of contact vary in intensity in different individuals." Remarkably, although partially described with other terms, Jones (1885, p. 336) already gave most of the valid diagnostic characters: rostrum ("beak-like process"), alveolar notch, interrupted selvage ("curvature of the edge inside"), carapace surface mostly punctate, rarely smooth, often tuberculate, LV>RV, hinge margin straight and so forth.

A year later, Jones (1886) published a short article about some ostracods from Colorado (U.S.A.) that derived from a sample he had received from U.S. Geological Survey Geologist C. A. White. However, this sample from the Morrison Formation did not contain representatives of *Cypridea*.

In 1893, Jones again described ostracods from the U.S.A. from samples he had received from C. A. White, this time from Wyoming and Utah. A sample from the Bear River Formation near Cokeville (WY) revealed a species of *Cypridea*, Jones designated as *Cypridea tuberculata* var. *wyomingensis* nov.

Vanderpool (1928) described and figured three species of *Cypridea* from the southern U.S.A. (Trinity Group of Arkansas, Oklahoma, Texas and Louisiana).

Roth (1933) erected the genus *Pseudocypridina* based on (smaller) size and position of the beak (rostrum) and absent alveolar notch, one of the taxa now considered being a subgenus of *Cypridea* from North American nonmarine deposits (actually from the Lakota Formation, not the Morrison Formation as Roth believed).

Harper and Sutton (1935) pointed out that Roth (1933) had failed to demonstrate the absence of a notch [i.e., the absence of the alveolar furrow according to concepts herein, the alveolar notch is present] in the description of his new genus *Pseudocypridina* as well as in the illustrations and suggested to better refer it to *Cypridea*.

Anderson (1939), established the new subfamily 'Rostrocyprinae' (a name not according to the International Code of Zoological Nomenclature and thus changed to Cyprideinae by Martin 1940; see discussion of the family Cyprideidae Martin 1940 above) and subdivided the genus *Cypridea* Bosquet 1852 into five genera (*Cypridea*, *Cyamocypris*, *Langtonia*, *Morinina*, *Ulwellia*), only to be lumped together soon (Martin 1940) and later defined as *Cypridea* s.l. (Sylvester-Bradley 1949, see below).

In his extensive monograph of the North-German "Purbeck/Wealden" ostracods, Martin (1940, p. 281-284) described the genus *Cypridea* in detail, particularly treating the characters of the valve margin and the pore canals (marginal and normal pores). He (Martin 1940) already noted the strong ventral overlap of the larger valve. Martin (op. cit.) also revised the genus *Cypridea* and combined Anderson's (1939) new genera with rostrum (beak) and alveolar notch (*Cypridea*, *Cyamocypris*, *Langtonia*, *Morinina*, *Ulwellia*) plus *Pseudocypridina* Roth 1933 together under *Cypridea*, as well as shortly discussed the stratigraphic distribution and the potential of the taxa for biostratigraphic application.

One of the classic substantial works about Lower Cretaceous nonmarine microfossils of the U.S.A. (ostracods and charophytes) is that of Peck (1941). Peck (op. cit.) described many new species from Lower Cretaceous deposits of Colorado, Utah, Idaho, Wyoming and Montana, among them eight species of *Cypridea*, six of these which were new. Peck (op. cit.) denoted the similarities of his faunas and floras to the Purbeck and Wealden of England and the potential stratigraphic value of these.

Swain (1946), in his work about nonmarine ostracods of Brazil and New Mexico, did establish a new subgenus of *Cypridea*: *Paracypridea*, which few years later was challenged and raised to generic rank by Sylvester-Bradley (1949; see right below). Swain (op. cit., p. 548) also proposed the redefinition of *Pseudocypridina* Roth 1933 as subgenus of *Cypridea*.

In a short note, Sylvester-Bradley (1947) did uncommented designate *Cypris granulosa* Sowerby 1836 as new type species of *Cypridea* Bosquet 1852, which he later (Sylvester-Bradley 1949, p. 125-126) constituted and elaborated.

In the year 1948, Hugh Marvin Looney, a student of Raymond E. Peck at the University of Missouri, presented his Master's thesis (Looney 1948) about ostracods from the Lower Cretaceous Bear River Formation of Wyoming (U.S.A.) which, unfortunately, remained unpublished (as well as the thesis of Craig 1961, see below). The thesis is cited here because it contains valuable information about the concerning ostracod fauna (thesis available upon request from the Library of the University of Missouri). Since Looney's (1948) thesis remained unpublished, however, several new species therein are *nomina nuda*, and concerning species of of *Cypridea*, these are: *Cypridea laevicula*, *Cypridea nodulata*, *Cypridea pyriformis*, as well as *Cypridea sulcata*. However, *Cypridea laevicula* has been published as *Pseudocypridina laevicula* sp. nov. [recte *Cypridea (Pseudocypridina) laevicula*] by Peck (1951), and *Cypridea sulcata* has been used by Mandelstam (1955) to newly describe

a species from Mongolia (Kempf 1980d). Unfortunately, the specimens are indeed registered in the catalog of the University of Missouri Collection, Columbia (Missouri, U.S.A.), but are not in the collection anymore (their whereabouts are unknown, R. L. Ethington, pers. comm., BS visit 2005).

Taxonomically most important is the work of Sylvester-Bradley (1949), who emended and clarified the taxonomy of *Cypridea* and designated a valid lectotype for the type species (*Cypris granulosa* Sowerby 1836, see above for details). Sylvester-Bradley (1949, p. 130) was the the first to point out the beak/rostrum and alveolar notch as most important diagnostic characters as well as the typical central muscle scar field, and comprehensively described the genus including many internal features, e.g. the marginal pore canals plus cross-sections of the margin, the duplicature, a detailed description of the hinge as well as that he discussed related (North) American species. Sylvester-Bradley (1949) changed the rank of Anderson's (1939) genera with rostrum (beak) and alveolar notch (*Cypridea, Cyamocypris, Langtonia, Morinina, Ulwellia*) to subgenera of *Cypridea*, also including *Pseudocypridina* Roth 1933 (as proposed by Swain 1946), which he (Sylvester-Bradley 1949) synonymized with *Langtonia* Anderson 1939 (Sylvester-Bradley 1949, p. 126-127), the latter thus being a junior synonym of the former. As for *Cypridea (Paracypridea)* Swain 1946, Sylvester-Bradley (1949) raised this subgenus to generic rank, for the reasons of its different shape and muscle scar field. Sylvester-Bradley (op. cit.) as well defined *Cypridea (Cypridea)* Bosquet 1852 as (subgenus) *Cypridea sensu stricto* (*Cypridea* s.s.), and therefore, the other included subgenera were later subsequently combined under *Cypridea sensu lato* (*Cypridea* s.l.) by many authors (see this paragraph below, particularly Horne and Colin 2005; and Table 1 herein).

Peck (1951, p. 318-319) supported Roth's (1933) view in keeping *Pseudocypridina* Roth 1933 a from *Cypridea* separate genus with weak beaks and notches, and weak ornamentation (punctation, a category of surface ornamentation *sensu* Sames 2011c), a view that was refused by authors of subsequent publications.

Hanai (1951) described some ostracods from the "Sungari Group" in Manchuria (today NE China and SE Russia comprising the Quantou [spelled Chuantou in Hanai 1951], Qingshankou, Yaojia, and Nenjiang [spelled Nengkiang in Hanai 1951] formations, Albian to Campanian, see table 1 in Sha 2007, for example), including four new species of *Cypridea*. Hanai (1951) also was the first author to concretely consider, describe and figure sexual dimorphism in a species of *Cypridea* that is *Cypridea subvaldensis* Hanai 1951.

One of the early pioneer works in attempting relatively precise nonmarine ostracod-based biostratigraphy at the Jurassic-Cretaceous transition and possible correlations over long distances is that of Grekoff (1953). He (op. cit.) analyzed and compared representatives of Late Jurassic to Early Cretaceous (Purbeck/Wealden-like) nonmarine ostracod faunas known at that time (southern England, France, Switzerland, NW Germany, North Cameroon [then northern "French Cameroun"], Gabon [then "French Equatorial Africa"], Canada [Alberta], U.S.A., and Brazil) as well as that he gave some perspectives for possible circum-Atlantic correlations of the Purbeck/Wealden-like deposits, and an alphabetic list of index taxa.

One of the few reports about Early Cretaceous nonmarine ostracods from Canada (including a few charophytes) is Loranger (1951, 1954), whereas the 1954 publication is merely a reprint of that of 1951 with revisions. Loranger analyzed subsurface samples of the Blairmore Group from drillings in Alberta (geochronologic age of the Blairmore Group is 115-103 Ma following Ross et al. 2005). Amongst others, Loranger (op. cit.) described two species of *Cypridea*: *Cypridea tilleyi* sp. nov. and *Cypridea wyomingensis*.

Oertli (in Bernard et al. 1957) described *Cypridea postelongata* from the upper Bajocian (believed to be lower Bathonian at the time of publication, op. cit.) of the Paris Basin. This species has recently been integrated into the new genus *Praecypridea* Sames, Whatley and Schudack 2010 (Sames et al., 2010b).

Martin (1958) confirmed his opinion (Martin 1940) to include many thus far established separate genera into *Cypridea* (*Cyamocypris, Langtonia, Morinina, Ulwellia*) for the reason that differences in valve size [and differences in valve size relation and inverse forms, see Sames 2011c], ornamentation, development of the rostrum and the alveolus are not sufficient for a generic separation. Martin (1958) as well confirmed his perception of *Pseudocypridina* Roth 1933 being a subtaxon of *Cypridea* (also followed by Sylvester-Bradley 1949 but challenged by Peck 1951, see right above) and established the new family Cyprideidae Martin 1940 (not to confuse with the Cyprididae Baird 1845, for details refer to the discussion of the family above).

Sohn (1958) published his first (short) account about the ostracods of the Upper Jurassic Morrison Formation and Lower Cretaceous Lakota Formation in the Black Hills. He (op. cit.) developed some ideas to differentiate between the ostracods of these formations and pointed out that the ostracods described by Roth (1933) as well as Harper and Sutton (1935) from the Black Hills area derived from the Lakota Formation rather than the Morrison Formation. In addition, Sohn (1958) made first estimations as to the age of the Lakota Formation and suggested: "… that the basal part of the Lakota formation will probably prove to be older than is indicated on the chart [Aptian] …" (op. cit., p. 122).

One of the comprehensive early Chinese works about nonmarine Jurassic-Cretaceous nonmarine Cyprideidae is that of Hou (1958). Hou (op. cit.) published his complete article bilingually (Chinese/English). He (op. cit.) also established the subgenus *Cypridea (Yumenia)* which is, however, excluded from being a representative of *Cypridea* as well as the Cyprideidae Martin 1940 herein for the reasons of lacking many diagnostic characters of *Cypridea* (see Table 1 and discussion of synonymy under genus *Cypridea*, Section 5.2.3 below), following Nikolaeva and Neustrueva (1999).

With regards to the biostratigraphic application of *Cypridea*, one eminent early work and introducing a remarkable method is that of Wolburg (1959, in German), who taxonomically dealt with the representatives of *Cypridea* from the "NW-German Wealden" in greater detail, with emphasis on their application. The highly remarkable advantage in Wolburg's (op. cit.) approach is that it renders an (successful!) application of long-lasting taxa possible, and he furthermore attributed the same stratigraphic value to these taxa as to the "… so-called index taxa that are confined to a particular horizon" (present author's translation, op. cit., p. 228). Based on the ample amount

of data from the British Purbeck and Wealden as well as contemporaneous deposits in NW Germany already available at that time, Wolburg (op. cit.) established species groups which he considered as phylogenetic lineages, and successfully applied these to improve the biostratigraphic subdivision of the "NW German Wealden". The fundamental point of Wolburg's (1959) successful approach was and is his methodology: his taxonomy is based on carapace shape (outline, L/H-coefficients, position of maximum height, shape differences between the valves) rather than ornamentation, thereby diminishing the taxonomic significance of ornamentation (particularly local ornamentation elements *sensu* Sames 2011c). This is conform with the concept on the ecophenotypic or ontogenetic character of many of these ornamentation elements (nodes, tubercles and spines) as revised and elaborated herein, based on new insights in the coherences of reproductive modes and genetic and morphologic diversity in cypridoid ostracods (see Sames 2011c for terminologic details and Sections 5.4.1, 6.1, and 6.3 herein for elucidation). Wolburg's results, as published in several articles (Wolburg 1949, 1950, 1959, 1962b), later flew into the comprehensive book "Leitfossilien der Mikropaläontologie" (Micropaleontologic Index Fossils) for Central Europe with emphasis on Germany (Wolburg 1962a).

As to the early publications in Russian, the late 1950s and 1960s saw many comprehensive fundamental publications about, or including, Early Cretaceous ostracods from the former Soviet Union and The People's Republic of Mongolia mainly, just to give a few: Lyubimova (1956, 1965), Lyubimova et al. (1960; that is the chapter about Cypridoidea in the "Russian Ostracod Treatise"), Mandelstam (1955), and Mandelstam and Schneider (1963).

Major contributions to our knowledge about Late Jurassic to Cretaceous nonmarine ostracods of West Africa were provided by Nicolas Grekoff (1957, 1960a), who published several monographies about Late Jurassic to Neogene (only Jurassic to Cretaceous cited here) nonmarine ostracods of the Congo Basin, today Democratic Republic of the Congo and Republic of the Congo, from surface samples and drillings. The ostracods described by Grekoff (1957, 1960a) include several representatives of *Cypridea* of different subgenera. Based on this research, Grekoff (1960b) again discussed the possibility of correlations of circum-Atlantic nonmarine deposits of Early Cretaceous age (from Europe, and North and South America) with the ostracods from in Equatorial (West) Africa, mainly representatives of *Cypridea (Cypridea)*. He (op. cit.) furthermore considered their possible distribution by migrating dinosaurs and came to the conclusion that long-distance correlations are possible with nonmarine late Mesozoic ostracods.

William W. Craig, another student of Raymond E. Peck at the University of Missouri, presented a Master's thesis about "Aptian nonmarine ostracods of the subfamily Cyprideinae from the Northern Rocky Mountain area" (Craig 1961) which, like the thesis of Looney (1948, see above), remained unpublished (thesis available upon request from the Library of the University of Missouri). The thesis is likewise cited here because it contains valuable information about the concerning ostracod fauna. Craig (op. cit.) as well erected, amongst others, some new species of *Cypridea* from the Cloverly Formation, Wyoming, which are *nomina nuda*: *Cypridea grandis*, *Cypridea hudsoni*, *Cypridea ovata* [having been erected as *Cypridea (Yumenia) ovata* sp. nov. Qi 1988 (according to

Kempf 1997b, 1997d); *Yumenia*, however, is considered neither to belong to *Cypridea* nor to the Cyprideidae at all (see synonymy and discussion of genus *Cypridea* below)], *Cypridea trispinosa* [used by Zhang (1985), who erected *Cypridea (Cypridea) trispinosa* sp. nov. Zhang], and *Ulwellia crescenti* [recte *Cypridea crescenti*]. As for most of Peck's type material, the specimens are indeed registered in the catalog of the University of Missouri Collection, Columbia (Missouri, U.S.A.), but, unfortunately, are not in the collection anymore (its whereabouts are unknown, R.L. Ethington, pers. comm., BS visit 2005).

One year later, however, Peck and Craig (1962) published a stratigraphic synopsis of their results regarding "Lower Cretaceous nonmarine ostracods and charophytes of Wyoming and adjacent area", giving an overview of the stratigraphically important taxa and their distribution. Unfortunately, this was the last of Peck's as well as Craig's publications on the topic, and the taxonomy remained unpublished. Like in all of Peck's publications (as well as Peck's locality catalog, present author's visit 2005), the exact position or coordinates of the collecting localities, and particularly the stratigraphic position of the samples, are imprecise and hardly traceable, and if at all to relocate, this must be done in the field.

Within the scope of ostracod studies in Lebanon, Bischoff (1963) described seven new taxa of *Cypridea* he partially related to those having been described from Brazil by Krömmelbein (1962).

Major early contributions to the Early Cretaceous nonmarine ostracods of Brazil (and West Africa to a minor part) were published by Karl Krömmelbein during the 1960s and early 1970s, regarding *Cypridea* and close relatives these are: Krömmelbein 1961, 1962, 1964, 1966, and Krömmelbein and Weber 1971. Krömmelbein established two new subgenera of *Cypridea*, *Cypridea (Morininoides)* Krömmelbein 1962 and *Cypridea (Sebastianites)*, the latter questioned to be a representative of *Cypridea* here (see discussion of synonymy of the genus *Cypridea* below, and Table 1).

In his frequently cited compendium about post-Paleozoic Ostracoda, van Morkhoven (1963, p. 93, fig. 128) incorrectly refigured a drawing (having-been as well frequently reproduced and cited) of the internal view of the LV of *Cypridea propunctata* from Sylvester-Bradley (1949, p. 131, fig. 17a). The former figure shows marginal pore canals in the attached area, where they do not occur *per definitionem*.

Bielecka and Sztejn (1966) described the Jurassic-Cretaceous transition beds of northern Poland from 16 boreholes, and distinguished six local ostracod horizons with slightly different assemblages, including many typical representatives of *Cypridea*.

In the late 1960s, Grekoff and Krömmelbein (1967) combined their data and published a comprehensive comparison of the Early Cretaceous nonmarine ostracods assemblages from South America (Brazil) and West Africa (Gabon), comprising taxa of *Cypridea* and listing the deposits where these occur.

Based on Wolburg's (1959) and his own data, Anderson (1962) published a first attempt to correlate the English Purbeck with the "German Wealden" using the *Cypridea setina*-group and the *C. propunctata*-group.

With reference to the documentation of the ostracod stratigraphy and subdivision of the NW-German Upper Jurassic and the "German Wealden", two important publications are included in the reference book "Leitfossilien der Mikropaläontologie" (Micropaleontologic Index Fossils): Klingler et al. (1962) and Wolburg (1962a), in which the stratigraphically important ostracods are described and figured, and their stratigraphic distribution is given and documented in detailed stratigraphic charts.

Wolburg (1962b) published an innovative paper in which he documented the morphologic transition from *Cypridea fasciculata* (Forbes 1855) and *Cypridea altissima* Martin 1940, two taxa formerly believed to be entirely separate. Although Wolburg (1962b) mainly put emphasis on the L/H-coefficient and minor tubercles/node-like tubercles and his interpretation regarding the taxonomic significance of the latter is outdated (see Sames 2011c), his conclusions were groundbreaking because he deduced a phylogenetic relationship from a continuous development from one form to the other over time, documented by many specimens from different localities and supported by morphometric analysis (L/H-coefficient), and he tried to utilize these for biostratigraphic application.

Oertli (1963) gave an account of the "Purbeck" ostracods of the Paris Basin comprising several species of *Cypridea*.

As for the Iberian Peninsula, an importat work is that of Kneuper-Haack (1966), who described nonmarine ostracods from the "Spanish Wealden" (NW Iberian Chains), including many new species of *Cypridea*. The author (op. cit.) noted that the research had already been done and finished between 1954 and 1957, and that due to the work of Wolburg (1959) some of the newly described species and subspecies of *Cypridea* in Kneuper-Haack (1966) are to be assigned to the groups described and already published by Wolburg (1959). This needs to be revised. The research on nonmarine Early Cretaceous ostracods of North Spain is recently continued by U. Schudack and M. E. Schudack (Schudack and Schudack 2009a). Owing to its paleogeographic position between Europe, North America and Africa during Late Jurassic to Cretaceous times, the Iberian Peninsula certainly played an important role as a bridge for the longitudinal distribution of nonmarine ostracods on the one hand, and for the latitudinal distribution and faunal exchange between Boreal and Tethyan faunas.

Viana (1966) published a detailed account on the stratigraphic distribution of ostracods in the Upper Jurassic? to Lower Cretaceous Bahia supergroup of Brazil. This includes several species of *Cypridea*, six of which were new.

Gramm and Burkharina (1967) described the new Pliocene genus *Karshicypridea* (extinct) from Uzbekistan, showing a rostrum similar to that of *Cypridea*. *Karshicypridea*, however, is not closer related to *Cypridea* and is only outwardly similar to the latter (name!; see also end of discussion of the family Cyprideidae under Section 5.2.1 herein for details).

Other taxonomically and stratigraphically important works are that of Anderson et al. (1967) about the Wadhurst Clay (regarded Wadhurst Formation of the Hastings Group in modern terminology) ostracods, and that about the Weald Clay (regarded Weald Clay Group of the Wealden Series Supergroup in modern terminology) ostracods (Anderson 1967) of southern England, UK, both including numerous new species and sub-

species (most of these considered variants here) of *Cypridea* and their stratigraphic distribution. In the former (Anderson et al. 1967), Anderson introduced his famous, and frequently misinterpreted, "faunicycles" (critically reviewed by Horne 1995), and defined some new terms for characters mostly diagnostic to *Cypridea*: alveolus, cyathus, and rostrum (see Sames 2011c for discussion). Anderson (in Anderson et al. 1967, p. 202-204) as well classified the carapace ornamentation elements into "surface sculpture" (redefined area wide ornamentation elements/surface characters, Sames 2011c) and "surface ornament" (redefined local ornamentation elements in Sames 2011c). He (Anderson in Anderson et al. 1967) also developed a labeled grid for the identification of individual tubercles or spines in *Cypridea* (op. cit., p. 203, figs. 1 and 2), which was applied for several taxa in the latter publication (Anderson 1967, p. 239, Text-fig. 1). However, since local ornamentation elements are considered of low taxonomic relevance (see remarks/discussion of ornamentation in Sames 2011c), Anderson's complex model is taxonomically relatively useless. This does, notwithstanding, exclude that a revised version might provide a useful basis for future research regarding the evolution and development of tuberculation and spines in *Cypridea* and related taxa in context of their ecophenotypy and ontogenesis.

Andreev and Mandelstam (1968) described and figured another example of sexual dimorphism in *Cypridea* (see discussion of sexual dimorphism in Section 5.2.3 below for details).

Sohn (1969) erected a new subgenus of *Cypridea*: *Cypridea (Bisulcocypridea)* from Aptian[?] deposits of Nevada. This taxon is now regarded a separate genus closely related to *Cypridea* and integrated into the extinct family Cyprideidae Martin 1940 (see Horne and Colin 2005, and Table 1 herein).

From several boreholes penetrating the Purbeck Beds (Purbeck Group in modern terminology) of southern England, Anderson and Bazley (1971) described and reviewed many ostracod taxa with emphasis on their stratigraphic distribution and application for these beds, many of these being representatives of *Cypridea*, including some new species and subspecies. They (op. cit.) also defined and described the faunicycles for these deposits. As for the Warlingham Borehole in Surrey (England, UK), which documents a virtually complete ostracod sequence of the English Purbeck/Wealden, this was published in Anderson (1971).

Musacchio (1971) described, among others, several representatives of Early Cretaceous *Cypridea* from the Argentinian province of Neuquen. Among these were four new species and one new subspecies, all of which show an inverse valve size relation (see Sames 2011c, considered of low or none taxonomic significance here) but are otherwise very similar to well known contemporaneous taxa of Europe.

In a recapitulatory paper, Anderson (1973) gave a survey and review about the Late Jurassic to Early Cretaceous non-marine ostracod faunas (Purbeck/Wealden type) of the northern hemisphere, focusing on the dominating assemblages of representatives of *Cypridea* ("Cypridean assemblages"). Some subsequent authors mistook his assemblage scheme (op. cit., fig. 1) as zonation scheme (see Horne 1995, p. 648-651 for elucidation). Anderson (1973) also shortly outlined the until then known assemblages of England, Germany, The Netherlands, Denmark, Sweden, France, Spain, Switzerland, Poland, The Soviet Union, and North America, and listed relevant publications.

From Gabon (West Africa), De Klasz and Uliczny (1975) described some new nonmarine Early Cretaceous ostracod species, among them a species of *Cypridea (Sebastianites)* Krömmelbein (here considered questionably belonging to the Cyprideidae Martin, see Section 5.2.1 and Table 1), and another representative of the Cyprideidae Martin 1940.

With respect to the South American faunas of the Province Neuquen (Argentina), Musacchio and Chebli (1975) described several new species from the Chubut Group, among them three belonging to *Cypridea*.

In a more general but ground-breaking publication about speciation patterns in the Ostracoda, Sylvester-Bradley (1976) puts up polymorphism in *Cypridea* for discussion and some other ideas concerning intraspecific variation and reproduction mechanisms (parthenogenesis), as well as favoring the term "morphotypes" for several of Anderson's (1971) subspecies that occur in the same sample (a concept also followed herein). Sylvester-Bradley (1976) also was the first to consider polyploidy through interspecific hybridization as reason for polymorphism among representatives of *Cypridea*.

Brenner (1976) published his comprehensive work about ostracods and charophytes of the "Spanish Wealden" of NE Spain including, amongst others, 14 species of *Cypridea*, 5 of them he designated as new.

Guan (1978) erected the new subgenus *Cypridea (Guangdongia)* which is, however, considered being a representative of *Bisulcocypridea* Sohn 1969 here (see Section 5.2.1 and Table 1).

Within "The Stratigraphical Index of British Ostracoda", Kilenyi and Neale (1978) summarized the Purbeck/Wealden of England with the index ostracods figured, most of them belonging to *Cypridea*. With respect to the zonation scheme, however, Kilenyi and Neale (1978) mistook Anderson's (1973) assemblages as (bio-)zones (see Horne 1995, p. 648-651, and Horne 2009 for elucidation).

An important publication (and one of the few more recent ones) concerning North American representatives of *Cypridea* is that of Sohn (1979), who comprehensively described the ostracod fauna from the Lakota Formation, Black Hills area (South Dakota; also the main working area of the present author) wherein he erected the new genus *Longispinella* Sohn that is considered a subgenus of *Cypridea* here (see Table 1 and Section 5.4.3). Among other groups (e.g. his new family Trapezoidellidae), Sohn (1979) also discussed the family Cyprideidae Martin 1940 and presented a key to its genera, as well as that he emended the subgenera *Cypridea (Cypridea)* and *Cypridea (Pseudocypridina)*.

One of the major contributions to the taxonomy of *Cypridea* Bosquet is that of Szczechura (1981). Szczechura (1978) had had described many nonmarine ostracod taxa from the Upper Cretaceous of Mongolia and introduced the terms limen and guttur. Based on many new data from the "Polish-Mongolian Palaeontological Expeditions" (op. cit.), Szczechura (1981) expatiated upon *Cypridea* and morphologically similar forms which she merged into the Family Cyprididae Baird 1845, placing *Cypridea* under the subfamily Cyprideinae Martin 1940 (a view modified herein, see Section 5.2.1 above). This work (Szczechura 1981) is essential, because the author described

and, most important, figured many characters of the carapace margin (also internally and specifically the anteroventral area) in detail, and discussed their value for taxonomy, particularly for the position of *Cypridea* among morphologically similar contemporaneous ostracods and their suprageneric taxonomy. It is Szczechura's (1981) merit to have demonstrated that the internal features are essential to distinguish between *Cypridea* and superficially similar genera with beak/rostrum-like processes.

A major contribution concerning the Purbeck/Wealden ostracods of south-east England (UK) is the posthumously published synopsis (Anderson 1985) on their stratigraphic distribution based on Anderson's compilations, as he had nearly completed this work at the time of his death in 1982. For the first time (Anderson 1985), these ostracods were illustrated with SEM photographs, and the publication includes detailed schemes on their stratigraphic distribution.

In 1985, the "Atlas des Ostracodes de France" was published, containing the stratigraphically important taxa. Colin and Oertli (1985) therein gave an overview of the stratigraphy of the Berriasian to Valanginian taxa (Purbeck *sensu gallico*) of France, including several species of *Cypridea*.

Qi (1988) newly described the subgenus *Cypridea (Ordosia)* and four new species of it (as given in the Kempf Database Ostracoda, Kempf 1997a): *C. (O.) elongata*, *C. (O.) linguida*, *C. (O.) subdepressa* and *C. (O.) subelliptica*, the latter being the type species. Unfortunately, however, Kempf never received a copy of this publication. He took information in from a third source because Qi (1988) described the high number of about 120 new taxa but this was long ago and Kempf cannot retrace the source anymore (E. K. Kempf, written communication, November 2008). The present author also was unable to get a copy of Qi's (1988) article. Curiously, none of the mentioned species as well as the subgenus are mentioned in the voluminous Chinese "Atlas" of fossil Ostracoda, volume one (Hou et al. 2002) and, thus, the taxonomic position of these taxa has to be reappraised on the basis of the original publication.

A concise overview of the Mesozoic sequence of nonmarine ostracods of northern China as well as its faunas and assemblages has been given in Quiquing and Whatley (1990), who also extensively dealt with the *Cypridea* fauna of the uppermost Jurassic and the Cretaceous

Sztejn (1991) reviewed the taxonomy and biostratigraphy of the ostracods of the 'Purbeckian' of central Poland, confirmed the validity of the existing six ostracod zones, and described several new species, among which are eleven new species and subspecies of *Cypridea*.

Brouwers and De Deckker (1993) reported Late Maastrichtian taxa of, amongst others, *Cypridea* and *Bisulcocypridea* from Alaska. These, however, most probably immigrated from northeastern Asia.

Ye (1994, in English) gave a long anticipated synoptic account of the nonmarine Cretaceous stratigraphy in China (including the Jurassic-Cretaceous and Cretaceous-Paleogene transition) as subdivided into eight (northern China) and nine (southern China) ostracod assemblage zones by representatives of the Cypridoidea (mainly representatives of *Cypridea* and closely related taxa). However, since there are many taxonomic prob-

lems remaining to be reappraised which may have strong implications on the age determination of nonmarine Cretaceous deposits of China, the interpretations presented therein might become subject to more or less considerable modification.

Newer works about the NW German Late Jurassic to Early Cretaceous nonmarine ostracods are from Ulla Schudack, who dealt with the revision, documentation and biostratigraphy of these in her doctoral thesis (Schudack 1994; including several species of *Cypridea*), the results of which later flew into Elstner and Mutterlose (1996), Gramann et al. (1997), and Schudack (2004).

In a stratigraphically most significant contribution with respect to a modern ostracod zonation of the English Purbeck/Wealden, Horne (1995) critically reviewed and revised the ostracod biostratigraphy for the Purbeck/Wealden of England, as based on Anderson's (1939 *et seqq.*) work and proposed a new rigorously defined ostracod zonation scheme for these deposits. This zonation scheme also flew into the new book "Ostracods in British Stratigraphy" (Horne 2009). Anderson's (1967 et seqq.) schemes had proved to be largely unrepeatable due to inadequate definition.

With respect to the Lower Cretaceous of NW Germany (Berriasian-Valanginian, including the "German Wealden"), Elstner and Mutterlose (1996) revised its ostracod biozonation as developed by Wolburg (1949, 1959, 1962a) and proposed a new zonation scheme mainly based on representatives of *Cypridea*, that is, however, only applicable to the central part of the NW German Basin (op. cit., p. 122).

An important publication as to the stratigraphic range of *Cypridea* is that of Guan et al. (1997), who described *Cypridea (Cypridea) pingyiensis* sp. nov. from the Lower Eocene Middle Member of the Bianqiao Formation, Shandong (China), extending the stratigraphic range of *Cypridea* into the Early Eocene.

In a compendium of Devonian to Pleistocene fossil nonmarine ostracods of the U.S.A., Swain (1999) gave an overview of the known taxa, listed their stratigraphic distribution and occurrences chronologically, and refigured type specimens. The book is, in fact, a review of literature and does neither contain new or up-to-date information nor discussions, evaluations or refinement of data that exceed the original publications.

Nikolaeva and Neustrueva (1999) published a valuable taxonomic atlas of the Mesozoic ostracods of Russia and adjacent areas, refigured and reillustrated types of older workers so far only available as drawings, gave and reported revised taxonomic views, and added biostratigraphic schemes and recommendations.

From the Mongolian evidence and perspective, Khand (2000) outlined the Late Cretaceous to Early Paleogene development and evolution of nonmarine ostracod faunas and morphologically separated the taxa of the Cyprideidae Martin 1940 from representatives of the early Cyprididae Baird 1985, particularly the Talicyprideinae Hou 1982. In the same year, Khand et al. (2000) also published a revised overview on the (nonmarine) Cretaceous of Mongolia and the regional correlation, including its biozonation based on different fossil groups among which are ostracods including taxa of *Cypridea*.

Luger and Schudack (2001) described charophytes and ostracods from the "Wealden" of northern Somalia for the first time. The ostracod fauna is dominated by taxa of *Cypridea*, five species of which are described, two of them new. The maximum age of the fauna was given as earliest Aptian (op. cit.), potentially older in part.

As for the late Mesozoic to Paleogene nonmarine ostracods of China, Hou et al. (2002) published the huge atlas of Mesozoic to recent ostracods of China (part one with Cypridoidea and Darwinuloidea) with over 300 plates, describing, reviewing and (re-)figuring the local taxa that had been described at the time.

Mojon (2002), in his PhD thesis about sedimentology, micropaleontology, and biostratigraphy of Middle Jurassic to Lower Cretaceous deposits of the Jura platform (southeastern France and Western Switzerland) dealing with charophytes mostly, also figured and discussed Berriasian to Valanginian Purbeck/Wealden-facies ostracods as well as the biozonation and Tethyan-Boreal correlation in western Europe based on them.
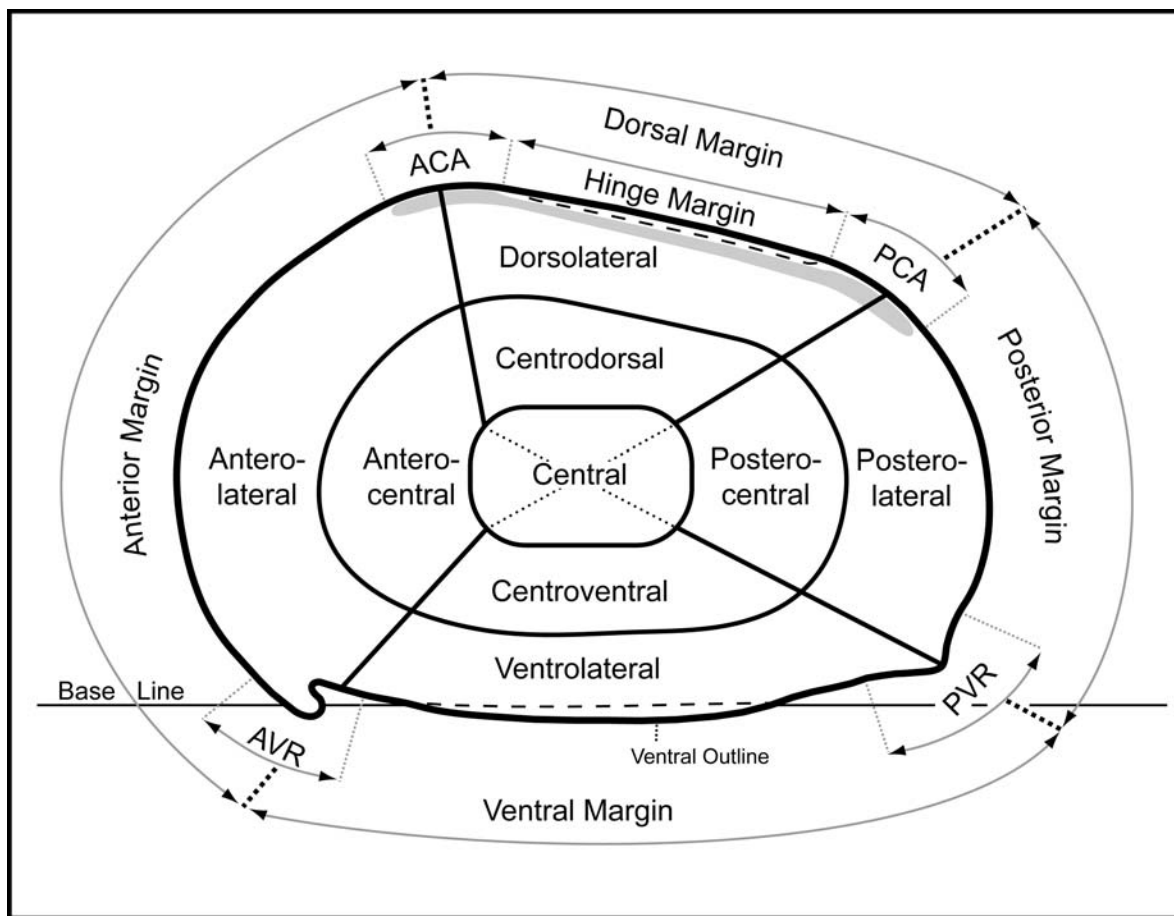
The so far earliest representatives of (true) *Cypridea* Bosquet (Late Jurassic, Kimmeridgian) were documented by Schudack and Schudack (2002) from the Middle Saurian Member of the Tendaguru Formation, SE Tanzania, East Africa.

Schudack (2004) revised the Late Jurassic to basal Early Cretaceous (Berriasian) ostracods of northeastern Germany–until then insufficiently analyzed (e.g. Wienholz 1968)–and newly documented their biostratigraphy in detailed range charts, including several lower Berriasian species of *Cypridea*.

In an important taxonomic paper, Horne and Colin (2005) analyzed the morphologic affinities of *Cypridea* s.l. (i.e., *Cypridea* including all its subgenera as given herein) to other cypridoideans, particularly focusing on the evaluation of some key features: the adductor muscle scar patterns and the complex structures of the anterior marginal zone (rostrum and alveolus and beak-like or lip-like anteroventral structures). The authors (op. cit.) concluded that the modern genus having the closest affinities to *Cypridea* Bosquet is the cypridid genus *Bennelongia* De Deckker and McKenzie 1981. According to Horne and Colin (2005), the adductor muscle scar pattern is not a sufficient character to indicate affinities of the family Cyprideidae Martin 1940 to other Cypridoidean families. The authors (Horne and Colin 2005, table 1) gave a table of the taxa included in the Cyprideidae Martin 1940, where they listed *Guangdongia* Guan 1978 as subgenus of *Cypridea* and *Longispinella* Sohn 1979 as separate genus within the Cyprideidae. This view is challenged herein (Table 1). *Guangdongia* Guan 1978 most probably belongs to *Bisulcocypridea* Sohn 1969 (Section 5.2.1), whereas *Longispinella* Sohn 1979 is here considered a representative (subgenus rank) of *Cypridea* Bosquet 1852 (Section 5.4.3).

As for the Mongolian Lower Cretaceous, Neustrueva et al. (2005) published a taxonomic atlas of late Mesozoic to Paleogene nonmarine ostracods of Mongolia including many species of *Cypridea*, therein refiguring and reillustrating types of older workers so far only available as drawings, reporting revised taxonomic views, and giving biostratigraphic charts.

In his PhD thesis, Stoica (2007, in Romanian) analyzed and described the Purbeck-type ostracods from the southern Dobrudja (Romania), their research history, geologic background and

TEXT-FIGURE 3
Schematic illustration of the terminology for outline, outline regions, margins and carapace regions of the genus *Cypridea*. Caparace regions modified based on Kesling (1951). ACA: Anterior Cardinal Angle. AVR: Anteroventral region. PCA: Posterior Cardinal Angle. PVR: Posteroventral region.

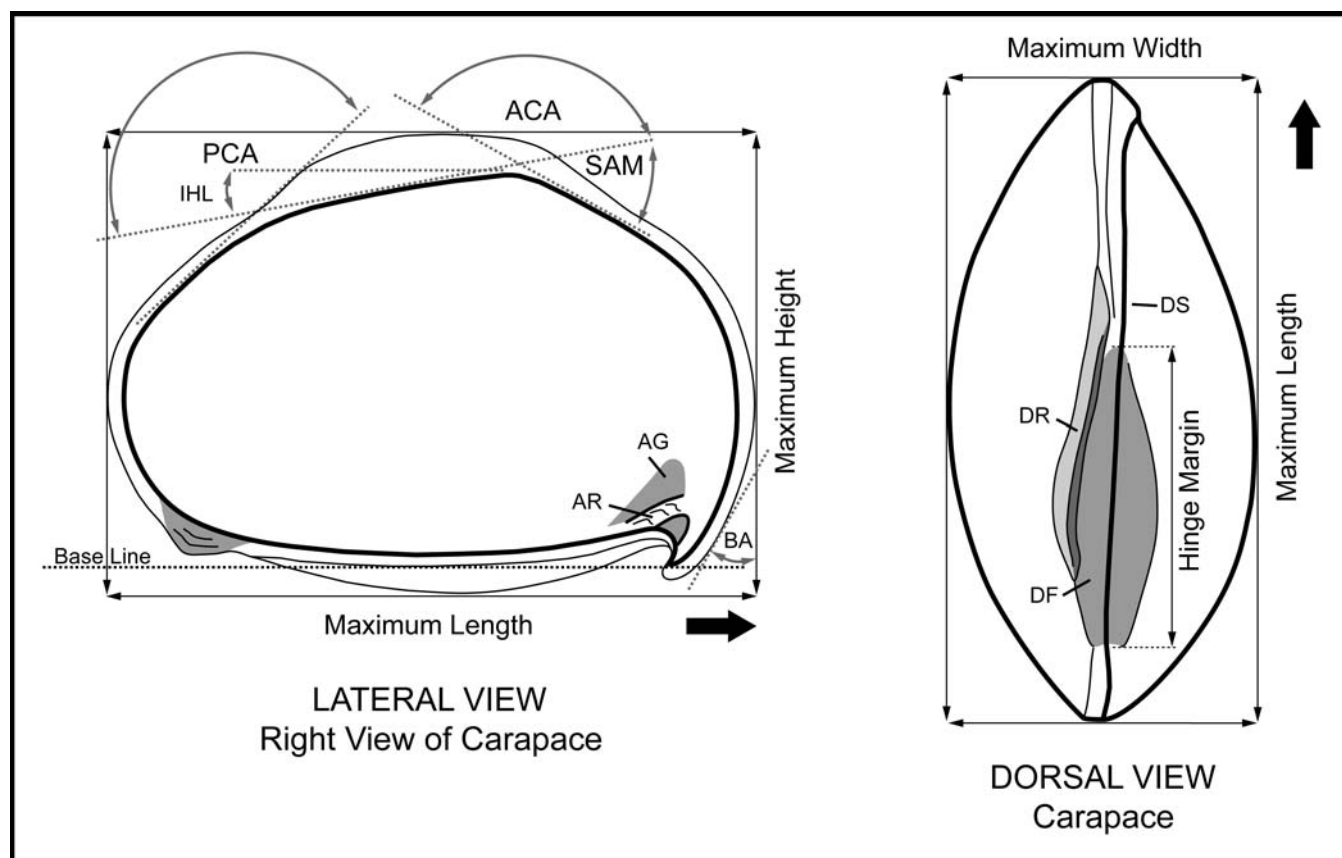stratigraphy as well as correlation and faunal association, including several species of *Cypridea*.

Do Carmo et al. (2008) emended *Cypridea* by adding the high degree of variability in outline and size of the rostrum and alveolar notch and the variable ornamentation (smooth, punctate or tuberculate) as well as integrating the species *Cypridea africana* (Krömmelbein 1965), formerly *Hourcqia africana* Krömmelbein (1965b). This view (Do Carmo et al. 2008) is partially challenged herein, and *Cypridea* is emended afresh (see discussion of the genus in Section 5.2.3 below).

In a recent applied publication, Arp and Mennerich (2008) described ostracod assemblages, including several species of *Cypridea*, from the Purbeck-type sediments of the upper part of the Münder Formation of NW-Germany, wherein they reconstructed paleoenvironments and cyclicity of these.

Sames (2008) confirmed the occurrence of Kimmeridgian representatives of true *Cypridea* from new samples from the type section of the Tendaguru Formation (Tanzania, East Africa) and discovered three species different from the one having been reported by Schudack and Schudack (2002) from the same (Middle Saurian) member of the Tendaguru Formation.

In the new "stratigraphic atlas" of British ostracods, Horne (2009) gave an updated account on the British Purbeck/Wealden (Berriasian–earliest Aptian) ostracods. This includes a definition of revised stratigraphic charts (adopted from Horne 1995) and the major ostracod zones (as defined by species of *Theriosynoecum*) and its subzones (Horne 1995, defined by species of *Cypridea*) as well as reproductions of Anderson's (1985) SEM photographs of relevant taxa and some new ones. Horne (2009) also gave a short synopsis of the current research status concerning stratigraphy, paleoecology and taxonomy, and perspectives for future research.

Sames et al. (2010b) erected the Middle to Late Jurassic (Bajocian to Kimmeridgian) and Early Cretaceous new genus *Praecypridea* Sames, Whatley and Schudack 2010 from Europe, North and South America, and Africa, which they consider to be the ancestor of *Cypridea* Bosquet 1852. *Praecypridea* does not have a true rostrum and alveolus yet, but a right-angled intersection of the anteroventral area instead, or a slightly developed beak-like anteroventral protrusion lacking an alveolus (no alveolar notch and furrow are developed). Neither does it show a true cyathus, but a cyathus-like protrusion instead (see Sames 2011c).

TEXT-FIGURE 4

Illustration of methods of measurement in *Cypridea* in relation to the carapace orientation. Note that parameters of length/height/width exclude ornamentation elements but do include carapace protrusions, i.e., where not congruent, the outline defines the outer delimitation prior to the margins (e.g. ventral ridge). This example demonstrates that in the strongly inequivalve case the protrusions of the LV overreach its own margin as well as the smaller RV, i.e., the LV has a much different shape based on the outline rather than based on the margins. Thus, the better measurements for the cardinal angles and inclination of the hinge margin have to be obtained from the RV. The ventral margin is oriented along the base line. ACA: Anterior cardinal angle, AG: Alveolar groove, AR: Alveolar ridge, BA: Bending angle (of rostrum), DF: Dorsal furrow, DR: Dorsal ridge, DS: Dorsal suture, PCA: Posterior cardinal angle, SAM: Inclination of the straight dorsal part of the anterior margin, IHM: Inclination of hinge margin in relation to base line.

Schudack and Schudack (2009a) revised the Lower Cretaceous ostracod biostratigraphy of the Iberian Chains (eastern Spain), and evaluated its local usability. The authors (op. cit.) differentiate 11 associations based on 87 species, 40 of these belonging to *Cypridea*. The Berriasian to Barremian ("Spanish Wealden") nonmarine associations are dominated by representatives of this genus.

Sames and Horne (in press) gave a comprehensive review on the princniples and stratigraphic application methods of latest Jurassic to Cretaceous nonmarine ostracod biostratigraphy. This is a synopsis of the history, problems and perspectives in this subject area that also deals some burning questions and gives recent examples as to proposals for solution.

Queiroz Neto et al. (2010; in prep.) propose(d) *Kegelina* gen. nov. of the family Cyprideidae Martin 1940, all the taxa of which having previously been assigned to *Cypridea*. The taxa of *Kegelina* exhibit a weakly developed rostrum in the larger LV, and just a weak alveolar notch in the smaller RV, even missing in some forms, and a weakly developed cyathus with transitions to a cyathus-like protrusion.
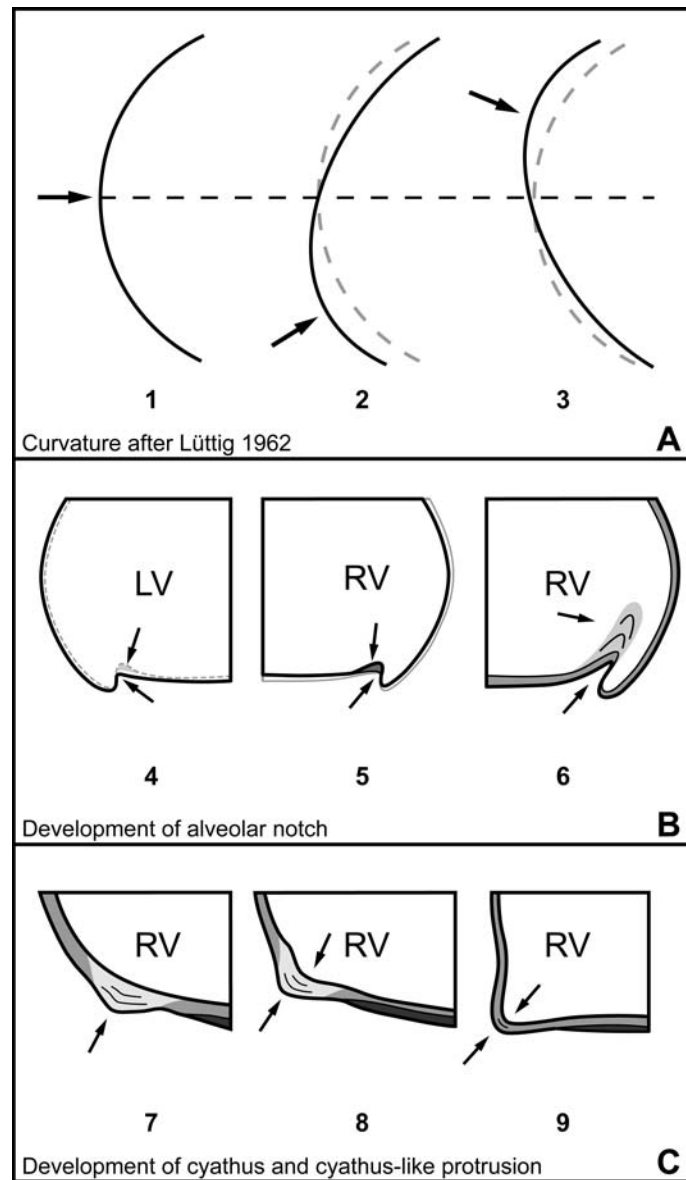
Sames (this work) emends and confirms the validity of the family Cyprideidae Martin 1940, emends the genus *Cypridea* Bosquet 1852 again based on a detailed revision of carapace terminology, integrates the genus *Longispinella* Sohn 1979 into *Cypridea*, challenges the validity of the subgenus *Ulwellia* Anderson 1939, and redescribes and emends some North American species of *Cypridea*.

With respect to the distribution mechanisms in context of reproductive modes, the reader is referred to Section 6.1 herein. As for the sexual dimorphism in *Cypridea*, the details are presented in the discussion under the genus' taxonomy in Section 5.2.3 right below. Table 1 summarizes the taxonomic notes and interpretation given above and below concerning the representatives of the family Cyprideidae Martin 1940 and the subgenera of *Cypridea*.

5.2.3 *Generic Taxonomy*

Genus *Cypridea* Bosquet 1852 **emend.**

Cypris granulosa sp. nov. – SOWERBY 1836, p. 345, pl. 21, fig. 4.

TEXT-FIGURE 5

A) Terminology of curvature of anterior and posterior ostracod carapace margins after Lüttig (1962). Arrows indicate the area of maximum curvature. These very useful terms are adopted here and translated into English: **1.** Equicurvate (in German "äquikurvat") means equally rounded, **2.** Infracurvate (in German "infrakurvat") stands for narrower rounded towards venter, **3.** Supracurvate (in German "suprakurvat") defines a dorsally narrower rounded margin.

B) Illustration of different degrees of the development of the alveolar notch. Arrows indicate the position of the (almost) absent alveolar notch (then it is the angular point of the angle between posterior part of rostrum and ventral outline) or the present alveolar notch (apex of the curve). **4./5.** Sketch of a left lateral view of a taxon with very weak (4, RV) to absent (5, LV) alveolar notch, like in many representatives of *Cypridea (Pseudocypridina)*, for example. Note that in the illustrated example (4 and 5), the alveolar notch is termed *absent* in the LV (4) because the ventral outline is not noticeable curved upwards and meets the posterior part of the rostrum in a purpendicular angle (see Sames 2011c for details) whereas in the smaller RV (5) the ventral outline right behind the rostrum is curved upwards causing a small alveolar furrow (upper arrow). **6.** Sketch of a right lateral view of a representative of *Cypridea* with a strongly developed alveolar notch in both valves (lower arrow; usually combined with a well-developed alveolar furrow as shown), e.g. *Cypridea alta* Wolburg 1959. Note that in forms with well-developed/deeply incised alveolar notch, the notch itself can be stronger developed in the *smaller* valve instead of the larger one. The alveolar furrow, however, is mostly stronger developed in the larger valve (see glossary for details).

C) Illustration of the development of the cyathus and the cyathus-like protrusion. Arrows indicate the apex of either the former or the latter in the larger valve only (7) or in both valves (8 and 9). **7.** 'True' cyathus: triangular extension of the posteroventral margin only developed in the larger valve, no indication of such extension in the smaller valve. This example shows the right lateral view of this particular region of *Cypridea (Pseudocypridina) piedmonti* (Roth 1933). **8.** Weakly developed cyathus-like protrusion: triangular extension of the posteroventral margin visible in both valves, distinct in the larger valve whereas only weakly indicated in the smaller valve. this example shows the right lateral view of this particular region of *Cypridea (Longispinella) longispina* (Peck 1941). **9.** Strongly developed cyathus-like protrusion: triangular extension of the posteroventral margin distinctly developed in both valves, even weakly acute in this example showing the right lateral view of this particular area of *Cypridea nitidula* Peck 1941.

pars*Cypridea* nom. nov. pro *Cypris* Müller 1776 – BOSQUET 1852, p. 47.

Pseudocypridina gen. nov. – ROTH 1933, p. 404 [syn. *Langtonia* Anderson 1939].

pars*Cypridea* – ANDERSON 1939, p. 294 [diagnosis therein not including all forms, e.g. "*Ulwellia*"].

Cyamocypris gen. nov. – ANDERSON 1939, p. 305.

Langtonia gen. nov. – ANDERSON 1939, p. 304 [syn. *Pseudocypridina* Roth 1933].

Morinina gen. nov. – ANDERSON 1939, p. 302.

Ulwellia gen. nov. – ANDERSON 1939, p. 300.

Cypridea – SYLVESTER-BRADLEY 1949, p. 130 [*Cypridea* s.l.].

Cypridea (Cypridea) – SYLVESTER-BRADLEY 1949, p. 135 [*Cypridea* s.s.].

non*Cypridea (Yumenia)* subgen. nov. – HOU 1958, p. 93.

Cypridea (Morininoides) subgen. nov. – KRÖMMELBEIN 1962, p. 471.

?*Cypridea (Sebastianites)* subgen. nov. – KRÖMMELBEIN 1962, p. 460

?pars*Hourcqia* gen. nov. – KRÖMMELBEIN 1965b, p. 68-69 [including *H. africana* Krömmelbein 1965b, *H. africana africana* Krömmelbein and Weber 1971, *H. africana confluens* Krömmelbein and Weber 1971].

non*Cypridea (Guangdongia)* – GUAN 1978 [this is most probably *Bisulcocypridea*]

Longispinella gen. nov. – SOHN 1979, p. 18.

?*Cypridea africana* (Krömmelbein) comb. nov. – DO CARMO et al. 2008, p. 793 [non *Hourcqia angulata angulata*, *H. angulata salitrensis*, *H. angulata sinuata*, *H. angulata symmetrica* Krömmelbein und Weber 1971].
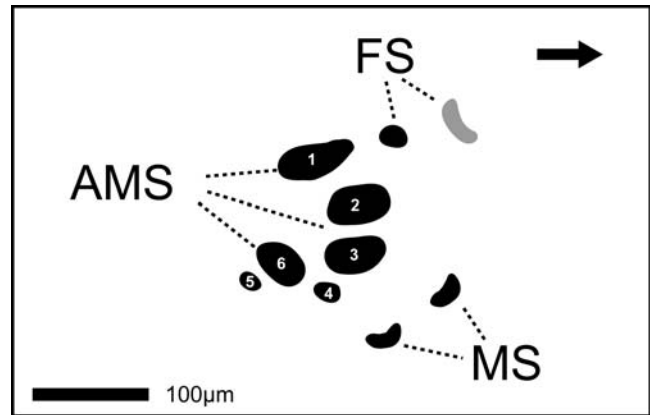
Type species (subsequent designation), lectotype: Cypris granulosa Sowerby 1836, p. 345, pl. 21, fig. 4, designated by Sylvester-Bradley (1947), p.VIII.

Remark: *Cypris granulosa* (Sowerby 1936) as given by Dunker (1846) is not identic to the type species of *Cypridea* Bosquet 1852 as designated by Sylvester-Bradley (1949), see Kempf (1980a, p. 17 for details).

Neotype: Cypridea granulosa (Sowerby 1836), designated by Sylvester-Bradley (1949), BMNH No. In 39024 (Jones' No. 229.13), The Natural History Museum, London.

Diagnosis (emend): Small- to medium-sized, rarely large, with ovate, rectangular, triangular or oblique-trapezoidal lateral outline. Anteroventral rostrum of highly variable shape, size, and reflexion always present, with adjoining alveolus posterior to it. Alveolar notch always present, though sometimes barely cognizable. Development of alveolar furrow highly variable, sometimes almost absent and often delimited by an alveolar ridge. Weakly to extremely inequivalve, LV>RV mostly, rarely with inverse (RV>LV) overlap but hinge always normal. Strong convex ventral overlap. Posteroventrally with a curved or triangular cyathus usually in larger valve only, sometimes hardly apparent; some forms with cyathus like protrusion (posteroventral extension in smaller valve also). Hinge margin distinctly incised (hinge incisure), causing the dorsal furrow. With or without local ornamentation elements (nodes and/or spines and tubercles). Surface finely to moderately punctate, rarely totally smooth, in the latter case also lacking any other ornamentation elements.

Remarks: The adductor muscle scar (AMS) pattern is not considered very diagnostic at genus level (also refer to Horne and Colin 2005, p. 27 for details). *Cypridea* is once more emended (last emendation by Do Carmo et al. 2008) for several reasons (see discussion below for explanation).

TEXT-FIGURE 6

Muscle scar pattern in *Cypridea* modified and recombined after Christensen (1968), Wolburg (1959), and Horne and Colin (2005). The sketch shows an *averaged* general pattern of the central muscle scar field of the LV as occurring in *Cypridea*. Main variations occur in size and shape of the scars of the adductor muscle scar field (AMS, Nos. 1-6), and their relative distances to a lesser degree, particularly the position of the posterior scars (5 and 6). Labeling of single scars adopted from Horne and Colin (2005). The general pattern of scars is constant. **FS:** Frontal scars (anterior one in grey because it has rarely been documented–for few species only–and, thus, its overall shape is somewhat unclear), **MS:** Mandibular scars.

Description: Carapace shape: Small to medium sized (usually 0.70-1.1mm), rarely large (e.g. *Cypridea gigantissima* Mojon 1990, 1.7-2.0mm, in Mojon and Médus 1990; and *Cypridea* cf. *clavata* of Jordan and Bless 1971, up to 2.1mm). Lateral outline variable, generally ovate modified in various ways: elongated ovate, rectangular, triangular or oblique-trapezoidal with many transitions. LV>RV, rarely inverse (never combined with inverse hinge), valve shape and valve size relation variable, either equivalve, subequivalve to strongly inequivalve, usually subequivalve to moderately inequivalve. Maximum height usually in front of, or otherwise close to, mid-length. Maximum width at around mid-length or between mid-length and 4/5 of length.

Anterior margin anteroventrally passing into a tapering rostrum of variable shape, width and length; bending backwards, bending angle between almost 0° to nearly 90°, usually around 30-60°. Point of rostrum mostly overreaching the ventral margin (more infrequent simultaneously protruding over the ventral outline), in some lineages barely or not at all reaching the ventral margin. Usually with, sometimes (almost) without an alveolar notch breaking the lateral outline in the anteroventral region immediately behind the rostrum which continues upwards as alveolar furrow/groove. Alveolar furrow extremely variable concerning degree of incision, shape, width and length (in some species taxa reaching up to 5/6 of height, causing a rostral bulge), sometimes almost or totally absent. Alveolar furrow ventrally delimited by an alveolar ridge in some species. Posteroventrally with a cyathus in the larger valve only, some forms with weaker cyathus in smaller valves also (transition to cyathus-like protrusion, see Text-fig. 7/C). Cyathus outline either rounded perpendicular to obtuse-angled, mostly not overreaching ventral and posterior valve margins, or (infrequently) tapering and then protruding over the posterior margin to a different degree.

Dorsal margin straight, rarely concave; dorsal outline slightly to strongly convex, sometimes feigned through a dorsal ridge. Dorsal suture generally straight, sometimes sinuous due to distortion by a dorsal ridge. Hinge margin incised (hinge incisure), forming a dorsal furrow with its flank being less inclined and wider in the larger valve (lateral offset, LO in Text-fig. 7/D). The hinge margin (not visible in lateral outer view) almost always (at least slightly) more or less inclined towards posterior end in relation to base line (Text-fig. 4, abbr.: IHL), rarely almost parallel to ventral margin. Ventral margin straight to convex, in many taxa with a ventral ridge (Text-fig. 7/C) in the larger valve.

Dorsal view compressed to elongated ovate or rather narrow elliptic, tapering towards both ends, stronger to the anterior end. In taxa with broadly developed and long alveolar furrow, the anterior end shows lateral constrictions. In case of the occurrence of a larger cyathus or a cyathus-like protrusion also slightly constricted laterally. Maximum width usually between around mid-length (in some taxa slightly anterior of it) and 3/5 of length.

Ventral overlap strong and convex (Text-fig. 7/C). If present, the alveolar ridge is well visible in ventral view and connects the rostrum and the ventral margin.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: Carapace surface finely to moderately punctate, smooth in some taxa. Diameter of puncta variable, generally larger (about 15-20μm) in centrolateral areas of the valves, and smaller (6-10μm) towards marginal areas, close to the margins being partially arranged in rows running parallel to these. Punctation intensity (depth of puncta) variable: all transitions from very faint and shallow to reticulation-like with deep puncta. Puncta mostly relatively uniform, punctation pattern relatively consistent. Several more or less evenly dispersed normal pores of 1-2μm diameter. Rostrum area often with a higher density of scattered normal pores.

2. Local ornamentation elements: With or without local ornamentation elements (nodes, spines, tubercles, node like tubercles, or combinations of these), but presence or absence as well as size and position of these being highly variable (see discussion for ornamentation in glossary also), as well as their distribution pattern. Most common are tubercles and node-like tuberculi, spines often larger but few in number, some forms with one pair of large spines only.

Internal characters: Inner lamella usually well developed, being broad anteriorly and moderate posteriorly with highest width antero- and posteroventrally (Text-figs. 7/E, 8 and 9). Narrow to moderately broad free inner lamella with maximum width at anteroventral and posteroventral areas of valves. With local widening of the inner lamella (where rostrum and alveolus occur). Marginal pore canals absent in the area above alveolar notch (attached area, Text-fig. 8). Interrupted selvage (Text-figs. 7/F, 8) along the posterior part of the rostrum. Larger valve often with posterior limen in cyathus area (Text-figs. 7/E and 9).

The hinge is tripartite, merodont (i.e., it has two terminal teeth in one valve with corresponding sockets in the other) and of lophodont type (i.e., tripartite with all elements being undivided, cf. Text-fig. 9), always "normal" (i.e., terminal hinge elements in the smaller valve, median hinge element in the larger valve), no inverse hinge known in *Cypridea*. Anterior terminal hinge element represented by a relatively long narrow tooth-like ridge being about 35-45° flexed towards venter in relation to the median element and fitting in a matching socket in the larger valve. Median hinge element represented by a simple and straight, narrow bar in the larger valve. No real median groove developed in the smaller valve, the hinge bar of the larger valve is only attached to the smaller with its ventral part, thus merely resting on the dorsal margin of the smaller valve. Posterior terminal hinge element about in line with the median hinge element, being represented by an elongated, slightly swollen tooth in the smaller valve fitting into a matching socket of the larger valve. All hinge elements smooth.
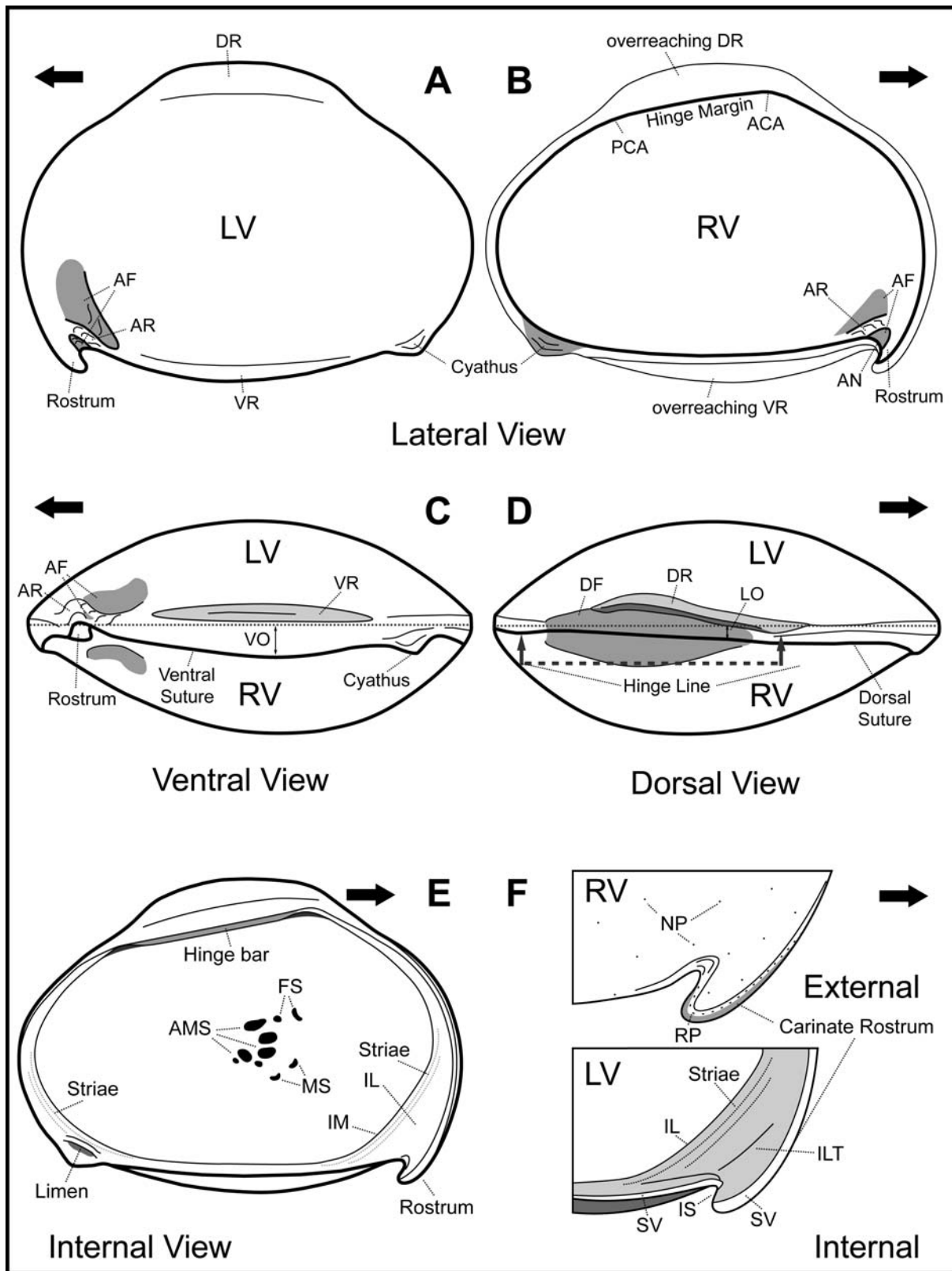
Remark: Sylvester-Bradley 1949, p. 132, claimed to have detected a faint crenulation of the posterior tooth in some well preserved specimens. However, a crenulation of these elements could not be confirmed thus far.

Muscle scar pattern: Adductor muscle scar (AMS) field consisting of 6 scars (see Text-fig. 6; labeling of individual scars adopted and modified from Horne and Colin, 2005). Number 1 to 4 are arranged in a row being convex towards anterior end, while 4 is often considerably smaller than 1-3. Scars 5 and 6 posterior of the row, while 6 is located somewhat higher than 5, but not above scar 2. Scar 6 mostly larger than scar 5, at about the same size of 1-3. Size of scar 5 is small, like 4. One round frontal scar, relatively small and close to adductor muscle scars 1 and 2, the second in front of the latter, being elongate and more or less crescentic. Two crescentic mandibular scars.

Remark: For detailed discussion and comparison of the AMS to taxa with similar patterns refer to Horne and Colin (2005, p. 27 and fig. 3 therein). Generally, the muscle scar field of *Cypridea* has rarely been given completely, particularly concerning the frontal scars, of which only one is often given. Christensen (1968, p. 23, fig. 6) gives one of the best photographs of the muscle scar pattern of *Cypridea* available from the literature, which is from an internal view of a fragment of *Cypridea* ex gr. *setina* (Anderson), nicely showing all central, frontal and mandibular scars as well as some dorsal ones.
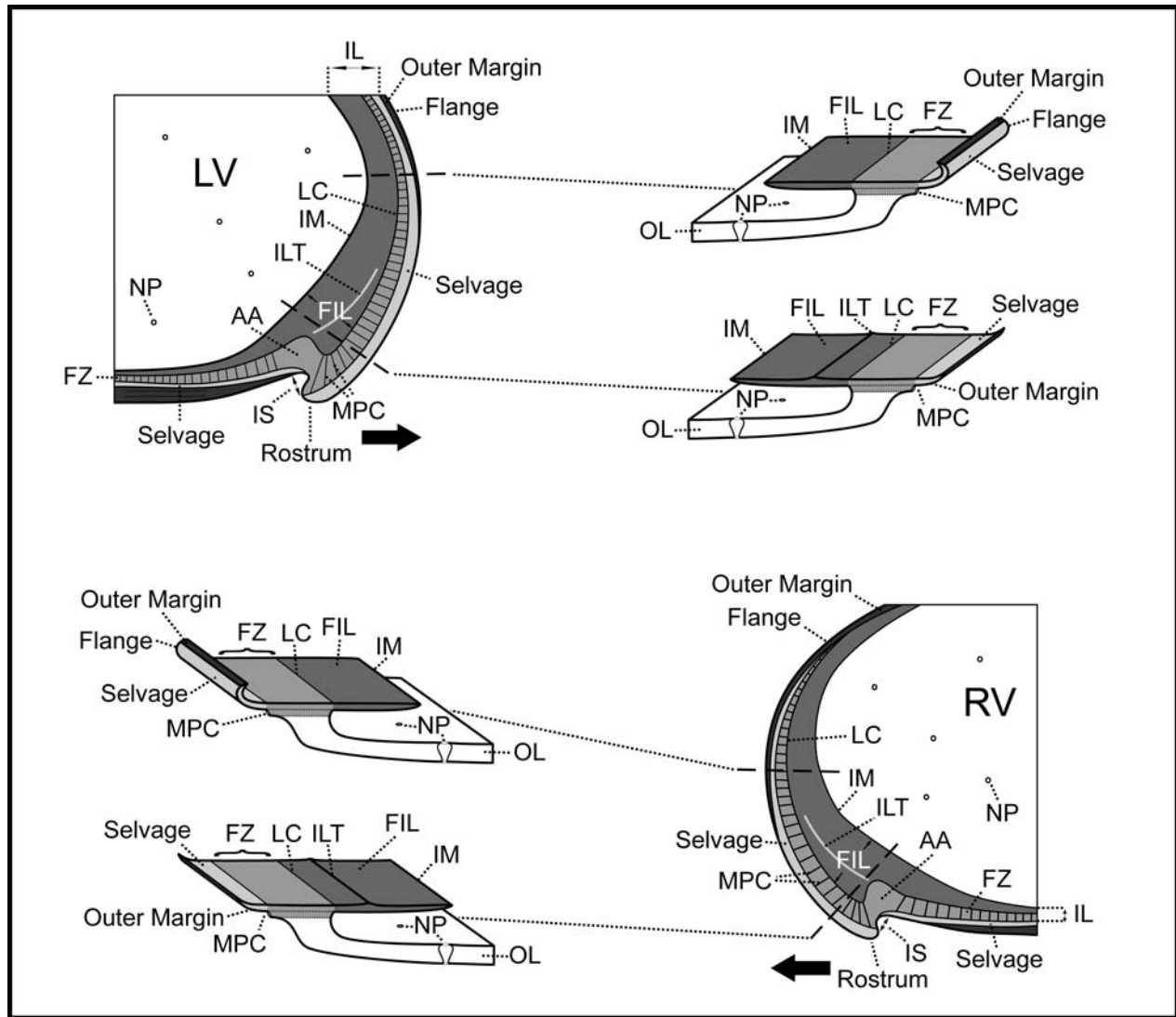
Sexual Dimorphism: Present in some representatives (listed right below, for illustration refer to Text-fig. 10). Presumed females generally more rectangular in lateral view, having a lower inclination of the hinge margin towards posterior end than the males and a higher maximum height (lower L/H-ratio) as well as being wider in dorsal view, thus appearing more inflated. Male dimorphs are by trend more elongate in lateral view than their female counterparts, having a higher inclination of the hinge margin towards posterior end (because of the narrower posterior margin), a lesser maximum height (higher L/H-ration) and narrower and stretched in dorsal view. The position of maximum width can be the same in both dimorphs, e.g. *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) herein, or not, e.g. *Cypridea gissarensis* Andreev 1968 (in Andreev and Mandelstam 1968), where the maximum width in the male is somewhat more posterior. Dorsal overreach of the left valve may be somewhat stronger in females.

Generally, the sexual dimorphism in Cypridoidea does not have to be pronounced and the morphologic variability among parthenogenetic females of one population can be higher than between males and females of sexual populations (e.g. Horne and Martens 1998).

TEXT-FIGURE 7

Terms for carapace description in *Cypridea* (without ornamentation elements). ACA: Anterior cardinal angle, AF: Alveolar furrow, AMS: Adductor muscle scars, AN: Alveolar notch, AR: Alveolar ridge, DF: Dorsal furrow, DR: Dorsal ridge, FS: Frontal scar, IL: Inner lamella; ILT: Inner list, IM: Inner margin, IS: Interrupted Selvage, MS: Mandibular scars, MZ: Marginal zone, LO: Flexure/Lateral offset, LV: Left valve, NP: Normal (lateral) pores, PCA: Posterior cardinal angle, RV: Right valve, SV: Selvage, VO: Ventral (convex, bow-shaped) overlap, VR: Ventral ridge.

TEXT-FIGURE 8
Detailed sketches of the internal views and sections of the anterior marginal zone of the LV and RV in *Cypridea*. Note that the extract of the RV captures a somewhat larger area (i.e. in height) than that of the LV. AA: Attached area, FIL: Free inner lamella, FZ: Fused zone (marginal zone), IL: Inner lamella, ILT: Inner list, IM: Inner margin, IS: Interrupted selvage, LC: Line of concrescence, MPC: Marginal pore channel, NP: Normal Pore. OL: Outer lamella.
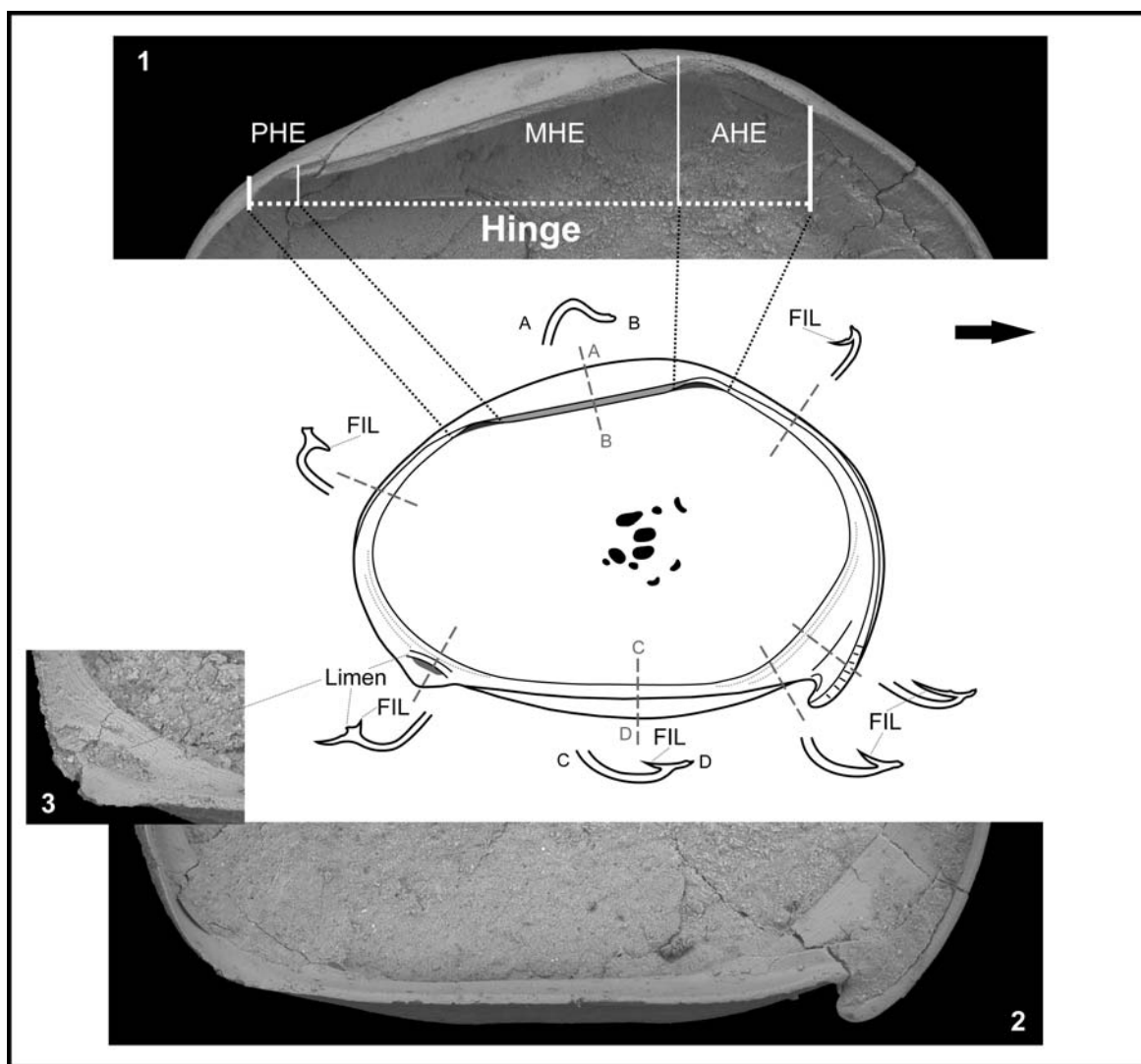
List of some selected representatives of Cypridea with sexual dimorphism (as presumed by herein and given in the literature; in alphabetic order)

- *Cypridea dunkeri carinata* Martin 1940 – Stoica (2007, p. 108, pl. 3-8)
- *Cypridea gissarensis* Andreev 1968 – Andreev and Mandelstam (1968, p. 80)
- *Cypridea (Longispinella) longispina* (Peck 1941) syn. *Cypridea (Longispinella) asymmetrica* (Sohn 1979) – herein
- *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *Cypridea (Pseudocypridina) henrybelli* Sohn 1979 – herein
- *Cypridea (Pseudocypridina) setina* (Anderson 1939) – herein
- *Cypridea subvaldensis* Hanai 1951 – Hanai (1951, p. 411, figs. 2-7)

Questionable sexual dimorphism

- *Cypridea clavata* (Anderson 1939) – in Nye et al. (figs. 10 D, G, presumed female; E, H and F, I, presumed male)
- *Cypridea obesa* Peck 1951 (herein)

Sexual dimorphism – discussion: The debate whether the reproductive mode of the Cyprideidae Martin 1940, particularly the *Cypridea*-lineage, is exclusively parthenogenetic or not reaches back to the early 1950's. Hanai (1951) already discussed females and males of *Cypridea subvaldensis* Hanai 1951. Although there have been some reports of presumed sexual dimorphism in *Cypridea* s.l. (*sensu* Sylvester-Bradley 1949) ever since, some authors persisted in the viewpoint that representatives of *Cypridea* reproduced entirely parthenogenetic, which, in conjunction with the desiccation and freezing-resistant resting egg, was presumed to have had facilitated the adaptive radiation and global dispersion of the group in latest

TEXT-FIGURE 9
Hinge area and sketches of cross-sections through the marginal zones of a LV of *Cypridea* (internal view), newly drawn as inspired by a figure by Sylvester-Bradley (1949, fig. 18) and complemented with photographs of the left valves upper (1) and lower part (2) of a *Cypridea (Pseudocypridina) laeli* Sohn 1979, and the cyathus (3) with limen of *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951. AHE: Anterior hinge element, FIL: Free inner lamella (absent in hinge area), MHE: Median hinge element, PHE: Posterior hinge element.

Jurassic to Early Cretaceous times (e.g. Whatley 1990, 1992). Whatley's ideas about the coherence of sex/parthenogenesis and dispersal in context with the differential success of the Cyprideidae have been challenged by Horne and Martens (1998, see Section 6.1 also). Sylvester-Bradley (1947, 1976) dealt with the subject of reproductive modes in *Cypridea* and suggested parthenogenetic reproduction in some (not all!) of its representatives. He (Sylvester-Bradley 1976) already pointed out that the high degree of polymorphism (the morphs either regarded as species, subspecies or variants by different authors) "… might be due to polyploidy after [interspecific] hybridization …" (Sylvester-Bradley 1976, p. 32, see Section 6.1 for more details regarding this topic).

Krömmelbein (1961) was the first to discuss and to provide evidence for sexual dimorphism of other representatives of the family Cyprideidae Martin 1940 (designated as subfamily Cyprideinae by Krömmelbein 1961), i.e., some species of *Paracypridea* Swain 1946: *Paracypridea langdoni* Krömmelbein 1961, *Paracypridea obovata obovata* (Swain 1946), *Paracypridea quadrirugosa weberi* Krömmelbein 1961 and *Paracypridea similis* Krömmelbein 1961. Krömmelbein (op. cit.) differentiated "a-forms" and "b-forms" of the mentioned taxa, interpreted the morphologic differences as sexual dimorphism while pointing out that he was not sure, which form would have to be designated as either of the sexual dimorphs. However, in the absence of direct indications, such as imprints of ovaries or tubes of the testes, as well as close recent relatives (the family Cyprideidae is extinct), Krömmelbein (op. cit.) already considered indirect carapace characters to distinguish the sexes: size relations, proportion of the quantity of the forms within a sample and specific morphologic characters (lateral widening of the posterior carapace half and ornamentation elements). Sohn (1969, p. B2), while mentioning the paper of

Krömmelbein (1961), stated that (sexual) dimorphism is unknown in *Cypridea*, but corrected this statement in a later publication (Sohn 1979, p. 13).

In 1968, Andreev and Mandelstam (1968) described and figured sexual dimorphs of *Cypridea gissarensis* Andreev (op. cit., p. 80-81, pl. 1, figs. 13a, b, male; and 14a, b, female) that differ in lateral and dorsal outlines, that is to say the male has a much less higher posterior margin and the hinge margin shows considerable inclination towards posterior end while the female is more oblong in lateral view whereas in dorsal view the male is less wide with its maximum width at 4/5 of length while the female is considerably wider and has its maximum width at or anterior of 3/5 of length.

Sohn (1979) took sexual dimorphism in *Cypridea (Pseudocypridina) piedmonti* and '*Longispinella*' *longispina*, recte *Cypridea (Longispinella) longispina*, into account, based on differences in the maximum carapace width in dorsal view. Regarding the latter, this case is interpreted differently and more complex here (see Section 5.4 under this species).

Stoica (2007) described and figured sexual dimorphism in *Cypridea dunkeri carinata* and his dimorphs satisfy the criteria of sexual dimorphism in *Cypridea* as given on top of this paragraph very well. Stoica's (op. cit.) evidence is well supported by numerous specimens that are very well preserved (Stoica, pers. comm., September 2007).

Altogether, the sum of facts given in the literature is evaluated, elaborated (refer to beginning of this paragraph above), and applied herein, see *Cypridea (Longispinella) longispina*, *Cypridea (Pseudocypridina) piedmonti* or *Cypridea (P.) setina* for example, and Text-fig. 10. Many a morphs of *Cypridea* as known to date that occur in the same samples and/or stratigraphic level–regardless whether having been determined species, subspecies or variants probably represent unrecognized sexual dimorphs.

A survey of the background and coherences (genetics, reproductive modes, evolutionary ecology etc.) is given in Section 6.1. In the past, sexual dimorphism in many fossil cypridoidean ostracods including *Cypridea* may have been overlooked due to a "cytheroid-centric" view on sexual dimorphism in the carapace shape, i.e., based on representatives of the Cytheroidea (deriving from the fact that these were studied more intensively). Carapaces of males of typical cytheroid species without broodcare are usually more elongate than females in lateral outline because of the large copulatory appendages to accommodate within the posterior part of the carapace. In those with broodcare, however (e.g. *Metacypris*, *Theriosynoecum*), males do not always appear more elongate since the females are larger with an posteriorly inflated carapace.
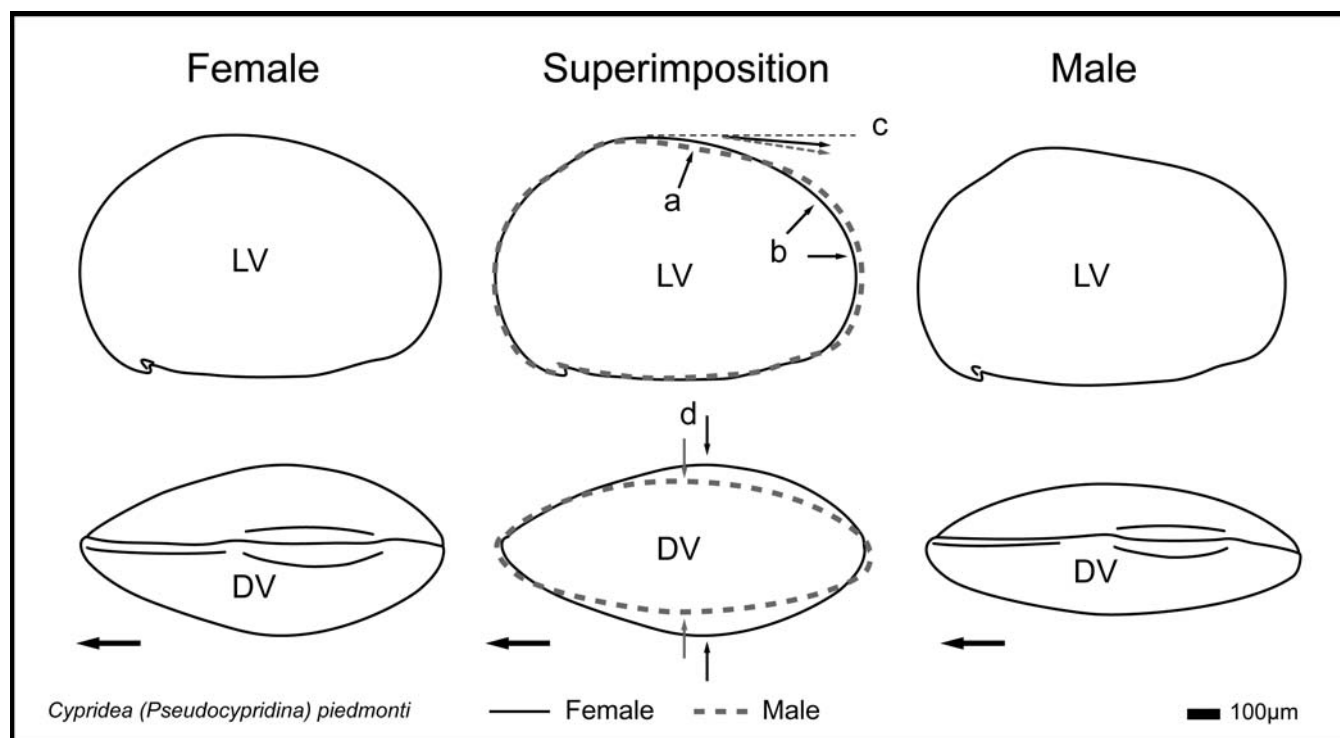
An identification of sexual dimorphism in many cypridoideans solely from the carapace shape may be difficult in many cases, particularly since the Cypridoidea neither have brood care (Martens et al. 1998a) that can lead to a much broader posterior carapace in the females (brood pouches) nor do they distinctly show the more elongate carapaces in the male dimorphs in comparison to the females.

General trends in ontogeny: Instars of *Cypridea* can, conditionally and not overall applicable (see discussion and remarks below), be identified through several characteristic features and trends. Younger instars tend to have a stronger inclined hinge margin (considerably more than 25°), thus being more triangular in lateral outline. In some forms the hinge margin is less incised and sometimes the dorsal outline between the cardinal angles is concave. Also, the surface characters appear coarser and more towards a reticulation rather than punctation (*sensu* Sames 2011c). However, this is considered an optic illusion caused by the fact that the diameter of the single elements of the surface characters (puncta) is the same as in adults, but they are less in number and closer to each other since the carapace surface is much smaller. The cyathus in the larger valve tends to be weaker developed and less prominent the younger the instar is. Concerning size, most adult specimens of representatives of *Cypridea* fall within a range of 0.7-1.1mm length (Nye et al. 2008), and thus, specimens with a maximum length considerably below 0.7mm are most probably juveniles.

Discussion and remarks concerning ontogeny: In the case of the plethora of taxa (many hundred) in *Cypridea*, many a species and/or subspecies are suspected to conceal either ecophenotypes, sexual dimorphs, and ontogenetic stages respectively (see Section 6.1 also). Wolburg (1959, p. 233) was the first one to take juveniles of *Cypridea* into account for taxonomy and to discuss ontogenetic lineages and their value for application, but he did not yet provide details on how to generally identify juveniles. Anderson himself (Anderson 1939, 1967, 1985, Anderson and Bazley 1971, Anderson et al. 1967) as well as Sylvester-Bradley (1949) seem not to have considered ontogenetic stages in their analyses and discussion of morphologic variations in *Cypridea*.

Jordan and Bless (1971) separated and described adult and juvenile(?) inverse specimens belonging to one species of *Cypridea (Ulwellia)* (Anderson 1939) in their perception and took one step further by morphologically characterizing the juveniles and highlighting ontogenetic trends, particularly regarding ornamentation, i.e., that the surface characters are coarser in the instars (reticulation like punctation) and finer (punctation) to absent in adults, and that the "sculpture", such as nodes, tubercles or spines (local ornamentation elements here, see Sames 2011c) tend to be more numerous and stronger developed in juveniles. Although ornamentation, particularly concerning the local ornamentation elements, is considered taxonomically insignificant to large extend as to designation and differentiation of species or genera of the Cyprideidae Martin 1940 leaving ecophenotypic effects out of consideration, it cannot totally be ruled out that in some forms there may be certain ontogenetic trends in *Cypridea* (see below). However, the problem regarding the line of argument of Jordan and Bless (1971) in conjunction with the discussion of ontogenetic trends is that, on the one hand, these authors convincingly discuss the enormous morphologic variability in the genus *Cypridea* and the possible occurrence of certain characters (normal and inverse valve size relation, maximum size, occurrence and degree of development of local ornamentation elements and surface characters) even within one species, but, on the other hand, the maximum length of their presumed juveniles (0.78-0.98mm) easily falls within the length range of most representatives of *Cypridea* (0.7-1.1mm, Nye et al. 2008), while the largest specimens are 1.25 to 2.10mm long. Although all the specimens come from one sample, the authors admit (Jordan and Bless 1971, p. 686) that they are not sure whether the material is autochthonous.

TEXT-FIGURE 10
Proposed identification of sexual dimorphism in representatives of *Cypridea* Bosquet 1852 as exemplified by means of *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) var. *henrybelli* (without nodes). Specimens to scale. Superimposition of both sexual dimorphs: female with black line, male with dashed grey line. LV: Lateral left view, DV: Dorsal view. a) difference in overreach of left valve over hinge line (stronger in female, not very pronounced here), b) difference in shape and maximum length (only slightly in this case), c) different inclination of the hinge margin (slightly in this case), d) considerable difference in degree (important character) and position (variable, not diagnostic) of maximum width.

More evidence for the possible ontogenetic character of ornamentation in Recent Cypridoidea has been given by Horne and Smith (2004) who described prominent tubercles (local ornamentation elements) in combination with pitted/reticulate ornament (area-wide ornamentation elements/surface characters, Sames 2011c) in juveniles and preadults (up to A-1) of the extant *Potamocypris humilis* (Sars 1924), while the adults are completely devoid of tubercles, being punctate to reticulation-like punctate, and just show faint indications of distortions of the punctation where the major tubercles were situated in the younger instars. Since this particular type of ornamentation has been described for the first time in the Cypridoidea therein (Horne and Smith 2004, p. 304) and *P. humilis* belongs to the family Cyprididae Baird 1845 and is thus not closely related to representatives of the extinct family Cyprideidae Martin 1940, no general conclusions can and should be drawn so far regarding the possible meaning of this character for other cypridoidean groups. However, the pattern of the tubercles is strikingly similar to that of many *Cypridea*, and the data provided by Horne and Smith (2004) implies that tuberculation/and or spines (local ornamentation elements) and its degree of development have at least to be considered to occur as ontogenetic characters in other taxa also, particularly *Cypridea* with its many highly spinose and/or tuberculate forms.

More recently, Nye et al. (2008) considered variably tuberculate subspecies of *Cypridea clavata* (Anderson 1939), including *Cypridea bogdenensis* Anderson 1967 and questionably

Cypridea insulae Anderson 1967 to be intrapopulational variants of a single species: *Cypridea clavata*. Their (Nye et al. 2008) adult forms show different degrees of variation ranging from nearly devoid of tubercles to strongly tuberculate as partially visible in the juveniles as well. The fact that all of these derive from the same very small interval at one locality makes a stronger argument for them all belonging to one species.

Altogether, the conclusion is that the identification of juveniles in *Cypridea* still remains problematic. Local ornamentation elements are not particularly significant for the designation of juveniles and due to considerable variation in lateral outline within the genus *Cypridea*, the narrow posterior margin (in comparison to the anterior one) in combination with the strong inclination of the hinge margin towards posterior end are not always reliable characters for the identification of juveniles as well. The same applies to the less well developed and protruding cyathus. What can be stated with some certainty is that a maximum carapace length being considerably less than the typical range of maximum length of most *Cypridea* species (0.7-1.1mm after Nye et al. 2008) points to juveniles.

Discussion: Synonymy: Most subgenera of *Cypridea* have been extensively discussed in the literature (see Section 5.2.2, Historic remarks, herein for synopsis and references as well as Horne and Colin 2005 and the list of valid subgenera of *Cypridea* below).

Yumenia Hou 1958 is excluded from being a representative of *Cypridea* Bosquet 1852 as well as the Cyprideidae Martin 1940 here for the reasons of lacking many diagnostic characters: rostrum, alveolus and cyathus as well as the incised hinge margin and the dorsal furrow. *Yumenia* has been placed into the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34).

As for *Cypridea (Ulwellia)* (Anderson 1939), the validity of this subgenus is strongly connected with the interpretation of the taxonomic significance of an inverse valve size relation, which is considered taxonomically insignificant here (see Sames 2011c, and 5.4.3 herein; *Ulwellia* has RV>LV). Although Anderson's (1939, p. 300) diagnostic features include several other morphologic characters (shape and hingement, as pointed out in the remarks), these turned out to occur among other *Cypridea* taxa also, and many subsequent authors, thus, focused on the inverse (RV>LV) valve size relation alone and simply assigned inverse representatives of *Cypridea* to this subgenus, regardless of the overall carapace shape and potential closer relationships. Therefore, the validity and the prevalent usage of the subgenus *Ulwellia* is challenged and rejected here (see discussion under the description of the subgenus in Section 5.4.3 for details).

Cypridea (Sebastianites) Krömmelbein 1962 is indicated with a question mark because of the strong trend towards a reduced rostrum and the dorsolateral sulcus at about mid-length. In his remarks to the diagnosis, Krömmelbein (1962, p. 460) noted that he included those forms into the subgenus which lack a rostrum, this group from which he also chose the type species ("subgenerotype"). Taxa with a rostrum, he (op. cit.) indicated with a question mark. From this point of view, *Sebastianites* would have to be excluded from being a representative of *Cypridea* and the taxa with (weak) rostrum i.e., those of *Cypridea (Sebastianites?)* Krömmelbein 1962 to be otherwise assigned to *Cypridea*. In his later publications including true or questionable representatives of *Cypridea (Sebastianites)*, Krömmelbein (1965b, Krömmelbein und Weber 1971) never again commented on the subject. Consequently, it also will have to be reviewed, whether *Sebastianites* can be furthermore considered as representative of the family Cyprideidae Martin 1940. This matter goes beyond the scope of this paper.

Guan (1978) erected the new subgenus *Cypridea (Guangdongia)* which is, however, considered being a representative of *Bisulcocypridea* Sohn 1969 here for the reason of, aside being similar to *Cypridea* and having a rostrum and alveolus, showing two dorsolateral sulci.

Longispinella Sohn 1979 is considered being a representative of *Cypridea* herein and designated as subgenus of the latter. According to more recent taxonomic concepts of *Cypridea*, Sohn's (1979, p. 18) diagnosis of *Longispinella* is based on few significant specific characters, and most characters included therein correspond to *Cypridea*. *Longispinella* has a well developed rostrum, alveolar notch and alveolar furrow, even the alveolar ridge (newly described in Sames 2011c) is present, as well as a cyathus and the incised hinge margin forming the dorsal furrow (for details refer to description and discussion of *Cypridea (Longispinella)* in Section 5.4 herein and the thereof described species).

Very recently, Do Carmo et al. (2008, p. 791) emended the diagnosis of *Cypridea*, and included some representatives of the genus *Hourcqia* Krömmelbein 1965(b) into *Cypridea* [*sensu lato*]. Based on advanced revision and information herein, however, it again became necessary to emend the genus for several reasons, as discussed right below.

Comments regarding the emendation: An emendation of *Cypridea* as well as its diagnosis became necessary afresh for the following reasons:

1) the revised terminology of some important characters (e.g. alveolus with its elements, ornamentation etc., Sames 2011c)

2) the different perception of the taxonomic significance of some characters (e.g. particularly local ornamentation elements as defined in Sames 2011c),

3) The changed status of *Longispinella* Sohn 1979, herein integrated into *Cypridea*,

4) the inclusion of a newly described character, the alveolar ridge, into the taxonomic analysis, as well as the inclusion of the hinge incisure, and the thereby caused dorsal furrow, plus the the cyathus and cyathus-like protrusion, respectively, into the diagnosis,

5) the recently emended diagnosis of Do Carmo et al. 2008, which is considered partially insufficient for the reasons given below.

The emendation of the diagnosis of *Cypridea* by Do Carmo et al. (2008) focuses on the rostrum (beak therein) mainly, while being very short and general regarding other characters and lacking many of the new facts as given here. Undoubtedly, the rostrum is one of the most diagnostic characters in *Cypridea*. However, the cases of the contemporaneous genus *Bisulcocypridea* Sohn 1969 or the much younger genus *Karshicypridea* Gramm and Burkharina 1967 show that a rostrum (or beak) alone, particularly in outer view only, must be considered insufficient to diagnose *Cypridea*. Based on the typical appearance of most representatives of *Cypridea* including its type species, only the rostrum in combination with a present alveolar notch (see Sames 2011c for discussion) and the, not always present, alveolar furrow as well as the cyathus are, altogether, diagnostic to *Cypridea*.

In the view of the present author, the diagnosis of the genus *Cypridea* should be kept as accurate and appropriate as possible to differentiate *Cypridea* from other taxa of the Cyprideidae (e.g. *Bisulcocypridea*, *Praecypridea* Sames, Whatley and Schudack 2010b), or to reduce problems in this context, at least. The weak development or absence of single characters in some subtaxa newly integrated is not considered a good reason to change or even adopt the diagnosis of a genus of which the type species as well as the majority of representatives do show all of these characters more or less well developed. If a diagnosis is changed or generalized, a detailed justification and discussion is necessary. Do Carmo et al. (2008, p. 791) only noted that " … the diagnosis proposed is emended in order to present a concept with the up-to-date synonym[y] list [therein]". Since synonymy and many morphologic characters of *Cypridea* are thoroughly described, revised and discussed herein, and led to new results, new emendation is proposed.

The inclusion of *Hourcqia africana* Krömmelbein 1965(b) into *Cypridea* as given and figured by Do Carmo et al. (2008) seems convincing thus far. However, the overall morphology of the

former is here considered relatively different from most representatives of *Cypridea* by belonging to a lineage with weak rostrum, very weak to absent alveolar notch (i.e., the ventral outline and ventral margin, if coincident, right behind the rostrum are not curved upwards but meeting the posterior part of the rostrum in a more or less perpendicular angle, as defined in Sames 2011c) and absent alveolar furrow. Do Carmo et al. (2008) provided no figure or photograph of the central muscle scar field of *Cypridea africana* (also not given by Krömmelbein 1965b), which is described as only consisting of 5 scars (anterior row only having 3 scars), and thus atypical. Therefore, the synonymy of *Hourcqia africana* Krömmelbein 1965(b) to *Cypridea* is considered to be in need of further investigation and for the present indicated with a question mark here.

Evolutionary trends: Aside from the fact that some early forms of *Cypridea* already may possess a weakly developed rostrum, alveolar notch plus alveolar furrow, and cyathus, there seems to be a general evolutionary trend from a more acute cyathus-like protrusion (Sames 2011c, Sames et al. 2010b)–sometimes combined with a strongly developed rostrum, alveolar notch and furrow in early forms–towards a weak and rounded, or even reduced, cyathus and weak or absent alveolar notch and furrow (see Section 6.3 for details).

List of valid subgenera of Cypridea (see discussion above for comments and also Table 1):
Cypridea (Cyamocypris) (Anderson 1939),
Cypridea (Cypridea) Bosquet 1852
Cypridea (Longispinella) (Sohn 1979) stat. nov.
Cypridea (Morinina) (Anderson 1939)
Cypridea (Morininoides) Krömmelbein 1962
Cypridea (Pseudocypridina) (Roth 1933) syn. *Langtonia* Anderson 1939

List of invalid or questionable subgenera of Cypridea (see discussion above, Table 1, and Sections 5.2.1 and 5.4.3 for details):
Cypridea (Guangdongia) Guan 1978 – moved to *Bisulcocypridea* Sohn 1969
Cypridea (Sebastianites) Krömmelbein 1962 – only questionably a taxon of *Cypridea* and even the Family Cyprideidae (to be investigated)
Cypridea (Ulwellia) (Anderson 1939) - rejected (herein, see Section 5.4.3 below)
Cypridea (Yumenia) Hou 1958 – lacking diagnostic features of the Cyprideidae, placed in the Trapezoidellidae Sohn 1979 by Nikolaeva and Neustrueva (1999, p. 34)

List of invalid species names for North America (unpublished theses of Looney 1948, Craig 1961, see Section 5.2.2 above):
Cypridea grandis sp. nov. Craig 1961
Cypridea hudsoni sp. nov. Craig 1961
Cypridea ovata sp. nov. Craig 1961
Cypridea trispinosa sp. nov. Craig 1961
Ulwellia crescenti sp. nov. Craig 1961
Cypridea laevicula sp. nov. Looney 1948
Cypridea sulcata sp. nov. Looney 1948 – preoccupied, used by Mandelstam 1955
Cypridea nodulata sp. nov. Looney 1948
Cypridea pyriformis sp. nov. Looney 1948

Stratigraphic range: Late Jurassic to Paleogene (Kimmeridgian to Lower Eocene).

Remarks: Recent publications revealed a longer stratigraphic distribution of 'true' *Cypridea*-species (taxa with true, fully developed rostrum and otherwise diagnostic characters). Schudack and Schudack (2002) and Sames (2008) demonstrated a Kimmeridgian occurrence of true *Cypridea* from the Tendaguru formation of Tanzania, East Africa while Guan et al. (1997) described *Cypridea (Cypridea) pingyiensis* Guan from the Lower Eocene Middle Member of the Bianqiao Formation, Pingyi, China.

Geographic distribution: Worldwide, except Australia and Antarctica (the following list was considerably complemented by Jean-Paul Colin, Cestas, France, which is gratefully acknowledged):

Europe: Denmark, Former USSR, France, Germany, United Kingdom (England), Ireland (offshore), Italy (Sardinia), The Netherlands, Poland, Portugal, Romania, Spain, Sweden, Switzerland.

Asia: China, Former USSR, Japan, Korea, Mongolia.

Middle East: Israel, Lebanon.

Africa: Angola, Cameroon, Chad, Democratic Republic of the Congo, Republic of the Congo, Ghana, Ethiopia (unpublished), Gabon, Liberia (unpublished), Morocco, Niger, South Africa, Sudan, Tanzania, Tunisia.

North America: Canada, U.S.A.

South America: Argentina, Bolivia, Brazil.

Paleoecology: Salinity: (Classification of brackish waters according to the Venice System as published by Oertli 1964): Presumed salinity tolerance: freshwater (0-0.5‰ TDS) after Neale (1988); freshwater to (β-)oligohaline (0-3.0‰ TDS) after Schudack, 1993. Indicative for lower alkalinity (<5-15mEq/L) by tentative analogue comparison with modern representatives of *Stenocypris* and *Mecynocypris* (Colin and Dépêche 1997). Dominantly freshwater, not to rule out that some taxa possible inhabited saline lakes (Horne 2002).

Habitat/life mode: Nonmarine temporal (ephemeral) waterbodies (pools, ponds), and in part nonmarine permanent water bodies (lakes) (Horne 2002). Benthic, crawling; possibly with swimming capability (Whatley 1990, 1992, Horne and Martens 1998).

5.3 Index of described taxa

Genus *Cypridea* Bosquet 1852
> *Cypridea nitidula* Peck 1941
> *Cypridea obesa* Peck 1951
> *Cypridea? minuta* (Peck 1951) emend.

> Subgenus *Longispinella* Sohn 1979 stat. nov. emend.
> *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979), emend.

> Subgenus *Pseudocypridina* Roth 1933 emend.
> *Cypridea (Pseudocypridina) laeli* Sohn 1979
> cf. *Cypridea (P.) moneta* Kneuper-Haack 1966
> *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979, emend.

Cypridea laevigata-group
Cypridea (Pseudocypridina) setina (Anderson 1939)
   Cypridea (Pseudocypridina) setina var.
   rectidorsata Sylvester-Bradley 1949
   Cypridea (Pseudocypridina) setina var. *setina*
   (Anderson 1939)

Cypridea alta-group
Cypridea ex gr. *alta* Wolburg 1959

Cypridea tuberculata-group
Cypridea ex gr. *tuberculata* (Sowerby 1836) cf.
C. tilleyi Loranger 1951

5.4 Description and taxonomy

5.4.1 *Preceding general remarks regarding the usage of subgenera and species-groups*

Establishing and using subgenera as classificatory category in paleontologic systematics is debatable but has proved to be quite useful. The past century revealed that experienced taxonomists can establish a good taxonomic system (i.e., a useful one) applying subgenera and subspecies. However, particularly the last few decades also revealed increasing discrepancies between taxonomy and nomenclature: By applying some articles of the International Code of Zoological Nomenclature (1999; e.g. article 43. – Principle of coordination, regarding the genus-group) workers have mixed up genera and subgenera, for example, and dealt with them at the same level or treated them as separate genera, thereby destroying a well justified taxonomy. Certainly, this is not generally wrong as long as the reasons to do so are given–which is often not the case–otherwise the differentiation of these taxa and included problems are nothing but elevated to a higher level (genus or tribus; I thank E. K. Kempf, Cologne, pers. comm. 2006, for pointing this out). The best way to avoid such problems is to avoid the erection of subspecies and especially new subgenera.

Be that as it may, we should not forget that taxonomy is a tool, and we do not need to–and should not–always stick to established taxonomic dogmata (e.g. Kaesler 1983). There are cases in which subgenera and/or species groups prove to be an excellent tool, and such a case is the biostratigraphic application of Mesozoic nonmarine ostracods, particularly as to representatives of *Cypridea* Bosquet 1852 (see right below and refer to Sections 6.1 to 6.3 for substantiation).

Subgenera are, by definition, taxa below genus and above species rank. In paleontology these are morphogroups comprising of taxa considered to belong to different species but sharing several characters that distinguish them from other groups within the same genus. They are believed to be related to each other and to have a common ancestor. Using subgenera is practical for the following reasons: Their usage allows a better handling of a high number of representatives of the particular genus they belong to, and their potential application as is the case for *Cypridea*, and can accelerate the process of identification by narrowing down the number of species coming into consideration. Furthermore, the application of subgenus names also allows a conservation and better traceability of the historical development of the taxonomy of a certain genus. Finally, subgenera (should) depict phylogenetic lineages.

Whether definition and application of subgenus names in paleontology makes sense or not, has been under controversial discussion for a long time. Nevertheless, the view held up here is

that it is possible and makes sense (for the reasons given above). Furthermore, the abandonment of the usage of subgenera in representatives of *Cypridea*, for example, would lead to the consequence having to give *Cypridea* a higher hierarchic rank. This would just but raise the problems to a higher level and destroy a well justifiable (and established) and applicable taxonomy and, therefore, such approach is dispensable and should be rejected.

In contrast, species groups are no nominal taxa but morphogroups believed to belong to one genus (and subgenus if applicable)–quasi "superspecies"–that represent a developing fossil "population" in more or less limited time and space or, alternatively, a phylogenetic lineage. Species groups should be possible to ascribe to a common principal form (ancestor) or include at least such species that appear to be closely related (Wolburg 1959, p. 238).

When a species group is defined and applied, this usually is an interpretation of representatives of a taxon that are:

1) assumed to belong to one genus (and subgenus, if applicable) by sharing its diagnostic characters,

2) differentiated based on characters considered not taxonomically significant at genus or subgenus level while at the same time interpreted as being too variable for a population of one species at a certain time and locality, and

3) considered closely related by depicting a species in development over time and space (ideally a phylogenetic lineage), thus representing a developing fossil population in more or less limited time and geographic area, and including a relatively high degree of morphologic variation that can be transitional over time and space.

Since the taxonomic significance of specific(!) morphologic characters may be highly debatable, the definition of species groups provides a practical tool for application (particularly biostratigraphy, e.g. Sames and Horne, in press) without having to clarify the taxonomic significance of all characters, allowing considerable variation of certain characters (e.g. outline, single ornamentation elements) and including even not clearly identified morphs, such as ontogenetic stages and sexual dimorphs. As pointed out by Wolburg (1959, p. 238) and as based on and supported by the interpretation of certain carapace characters (mainly local ornamentation, Sames 2011c, and lateral outline), an application of species-groups also has the advantage of giving a better image of the natural hierarchy of the to date existing, quite non-equivalent *Cypridea*-species (i.e., based on characters and/or combinations of characters of different taxonomic significance and value). This is practical for two reasons: a) an application is possible now, and b) the "real" biologic hierarchy of the taxa as well as that their phylogenetic relationships can be better examined and assessed without the distracting taxonomic details of a "wrong" taxonomy.

Therefore, working with species groups can be advantageous especially when applying representatives of the Cypridoidea (i.e., such forms with mixed reproduction, see also Section 6.1 for details) to biostratigraphy if taxonomy at species level is difficult due to high variability and particularly if no better option is available, that is, the application of species groups produces better results than any other method. This is the case in the application of taxa of *Cypridea* to many Upper Jurassic to Lower Cretaceous nonmarine deposits in the world. By exclusion of

carapace characters of high variability, doubtful taxonomic significance (at the particular taxonomic level but particularly at species level) or arguable stratigraphic range, the effects of uncertainties in taxonomy are reduced and supraregional correlations become more easily possible. That particularly applies to cases where areas with different paleoenvironment (e.g. different types of water bodies, salinities, supraregional and regional climates) are compared. It has to be admitted though that *Cypridea* Bosquet 1852, as it is defined at present, is a genus to which morphogroups can be easily applied, because some of its diagnostic characters or their development are unique amongst podocopid ostracods, and the significance of these characters at genus level is widely accepted. Thus, the genus is easy to identify and characters at (and below) genus level are more or less easy to distinguish.

Well-defined morphogroups also have the advantage that they are easy to identify and applicable (e.g. in biostratigraphy) by non-specialists after short training. Moreover, we deal with artificial categories that do not necessarily affect the taxonomic nomenclature. Particular attention, however, should be paid to their accurate definition (as accurate and conscientious as possible) as well as their clear indication and discussion! This has to be done by specialists.

Consequently, no new subgenera are established herein, except for the lowering of the rank of *Longispinella* Sohn 1979 to a subgenus of *Cypridea* Bosquet 1852. This is done herein and considered practical for the following reasons: Thereby, the consideration of all its taxa as species of *Cypridea* is indicated, while retaining the name has the effect to make it easier for other workers to follow descriptions and mentionings of such representatives through the literature. Indicating *Longispinella* as a subgenus of *Cypridea* also defines it as a morphogroup with specific characters that improves its (actual and potential) biostratigraphic usability. In contrast, the subgenus *Cypridea (Ulwellia)* (Anderson 1939) is rejected here (see below), since an inverse valve size (relation) is not considered taxonomically significant anymore it can occur in many different and not closely related representatives of *Cypridea*.

In summary, the taxonomic approach followed herein is geared to the targeted biostratigraphic application without loosing track of achieving an as realistic and comprehensible taxonomy and systematics as possible. The approach of pooling many (sub-)taxa of *Cypridea*, including geographically separated forms, is also consitent with new insights into the (partially enourmous) morphologic and genetic variability within recent cypridoidean species or populations in the context with specific dispersal and reproductive mechanisms (refer to Section 6.1 for details).

5.4.2 *Key to the described species in Cypridea*

1a Carapace surface with area-wide ornamentation (punctation)   2

1b Carapace surface smooth   *Cypridea (P.) setina*

2a Carapace devoid of dorsolateral sulcus (nonsulcate)   3

2b Carapace with dorsolateral sulcus   *Cypridea*? *minuta*

3a Moderately to strongly inequivalve   4

3b Slightly inequivalve to subequivalve   5

4a Dorsal ridge and small alveolar furrow   *Cypridea* ex gr. *alta*

4b Without dorsal ridge, large and wide alveolar furrow   *Cypridea (L.) longispina*

5a Rostrum indistinct, alveolar notch and furrow almost absent   *Cypridea obesa*

5b Rostrum small but distinct, alveolar notch distinct   6

6a Strongly developed rectangular cyathus-like protrusion   *Cypridea nitidula*

6b 'True' cyathus   7

7a Carapace surface moderately puctate   8

7b Carapace surface strongly tuberculate and punctate   *Cypridea* ex gr. *tuberculata*

8a Distinct alveolar notch, rostrum clearly overreaching ventral margins   *Cypridea (P.) laeli*

8b Alveolar notch weak to almost absent, rostrum very short   *Cypridea (P.) piedmonti*

5.4.3 *Descriptions of subgenera, species groups and species*

***Cypridea nitidula* Peck 1941 emend.**
Plate 1, Figures 1-8

Cypridea nitidula sp. nov. – PECK 1941, p. 301, pl. 43, figs. 1-5.
Cypridea nitidula Peck – PECK 1951, p. 312, pl. 49, fig. 5. – CRAIG 1961, p. 65, pl. 3, figs. 11-12 [unpubl.]. – PECK and CRAIG 1962, pl. 2, fig. 2. – SWAIN 1999, p. 121, pl. 13, figs. 9-11 [refigured from Peck 1941].
?*Cypridea nitidula* Peck – WICHER 1959, p. 45, pl. 9, fig. 4a, b.

Material: Six specimens from the collection of R. E. Peck, University of Missouri, Columbia, Missouri, U.S.A., in part badly preserved. Three specimens taken from the collection with permission of Raymond L. Ethington (University of Missouri, Columbia, U.S.A.) and deposited in the collections of the The National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A. under the numbers below.

USNM Numbers: USNM 544208-544210.

Dimensions (in mm): Overall length: 0.90-1.10

Specimens from the Peck collection:

    L: 0.99-1.10   H: 0.58-0.67   W: n/a

As given in the literature (various references):
    L: 0.90-1.00   H: 0.57-0.72   W: 0.38-0.51

Type locality and horizon: Not exactly given by Peck (1941). Draney Limestone(Sub-?)Formation at Tincup Creek Canyon, Freemont quadrangle, Idaho-Wyoming.

Holotype: U.M. 0-975-3, possibly lost. As stated before, the whereabouts of Peck's ostracod type material is unknown.

Diagnosis (emended): Medium sized (up to >1mm), punctate and slender species of *Cypridea* with equicurvate anterior margin, distinct but short and pointed rostrum, strong rectangular cyathus-like protrusion in both valves, dorsal and hinge margins considerably (15-20°) inclined to baseline towards posterior

end. Alveolar furrow narrow, reaching up to 1/3 of height. Prominent anterior cardinal angle, posterior cardinal angle strongly rounded and inconspicuous. Weak ventral ridge, ventral margin and outline nearly congruent.

Remarks: Peck (1941, p. 301) did not indicate and separate the diagnosis and the (short) description. However, Craig (1961, p. 65) gave a diagnosis in his Master's thesis which remained unpublished. Therefore, an emended diagnosis is proposed herein.

Description: Carapace Shape: Medium sized. Lateral outline suboblong with trend to a more triangular shape. Maximum length below mid-height, either at base line for the case that the cyathus is well developed and not broken, or at 1/3 of height by excluding the cyathus. Maximum height at anterior cardinal angle according to 1/3 of length, maximum width at about 3/5 of length. LV>RV, slightly overreaching and overlapping the latter along entire margin in lateral view, except for the hinge margin. Overreach somewhat stronger at ventral margin due to weak ventral ridge in LV. Overlap moderate at anterior and posterior margins, somewhat stronger at ventral margin due to convex tongue-like run of LV's selvage, weaker along hinge margin.

Anterior margin broad and equicurvate with moderately long straight dorsal part. Rostrum small and narrow, distinctly pointed towards apex and bent backwards with 60-70°, close-fitting, somewhat overreaching ventral margin and outline. Alveolus weakly developed, alveolar notch very weak to almost absent, alveolar furrow oblong, narrow and shallow, reaching up to about 1/3 of carapace height. Posterior margin of both valves narrow and about equicurvate to slightly infracurvate, meeting the ventral margin almost at right angle due to bearing a strongly developed cyathus-like protrusion with rectangular to pointed outline, its apex sometimes overreaching the posterior margins and its sides being slightly concave. Cyathus-like protrusion somewhat smaller in RV and being overlapped by its counterpart in the LV. Dorsal margin straight to slightly convex, considerably inclined (between 15° to 20°) to baseline of carapace towards posterior end, hinge margin straight. Anterior cardinal angle distinct, obtuse-angled with about 135-140°, somewhat protruding in LV. Posterior cardinal angle strongly rounded and indistinct, about 125°. Ventral margin straight to slightly concave, parallel to base line and meeting the posterior margin almost at right angle (cyathus). Ventral outline straight.

Weakly developed local lateral flattening/very weak depression of carapace at centrodorsal to anterocentral area, corresponding to the assumed position of the central muscle scar field.

Dorsal view elongated-ovoid. Hinge margin moderately indented, i.e., moderate dorsal furrow with left flank being broader and less inclined than right one. Along hinge margin, the smaller RV slightly overlaps the LV. At both cardinal angles, the overlap of the LV is somewhat stronger than elsewhere, and convex. Ventral view showing flattening and very weak ventral ridge in LV. Overlap along venter gently convex.

Ornamentation: 1. Area-wide ornamentation elements: Whole carapace regularly and distinctly punctated, including rostrum, alveolus and dorsal furrow. Diameter of puncta variable, larger (about 15µm) in centrolateral areas of the valves, and smaller (6-10µm) towards marginal areas, close to the margins being

partially arranged in rows running parallel to these. Several normal pores of 1-2µm diameter, more or less irregularly distributed, usually in between the puncta. Some normal pores swollen with up to 3µm diameter, having small tuberculi (15-20µm diameter) developed around them.

2. Local ornamentation elements: Usually weak or almost not present, characterized by few small tuberculi (15-20µm diameter) located close to anterior and posterior margins and arranged in rows parallel to them. Rarely with paired massive posterocentral spine of around 70-100µm diameter (Pl. 1, Fig. 5.).

Internal characters: Described as apparent from Peck 1941, pl. 43, fig. 3 (drawing, specimen not in collection, probably lost): Hinge merodont and of lophodont type. A straight ridge with slightly widened, elongated grooves anteriorly and posteriorly in the LV fits into corresponding groove and teeth in the RV. Inner lamella moderately broad with highest width anteroventral (widening of inner lamella) and posteroventrally (cyathus area), thereabouts the inner margin being much less curved. Inner lamella anteriorly and posteriorly reaching up to, and tapering off right below, the terminal hinge elements.

Muscle scar pattern: Neither observed nor documented in the literature.

Morphologic variation: Minor. Lateral outline relatively stable, sometimes the cyathus-like protrusion not very prominent (bent inwards diagenetically, or broken). Moderate variation in ornamentation (all probably ecophenotypic or ontogentic): presence, number and intensity in development of antero- and posterolateral small tuberculi, as well as absence or presence of the paired posterocentral major tuberculum/node like tuberculum.

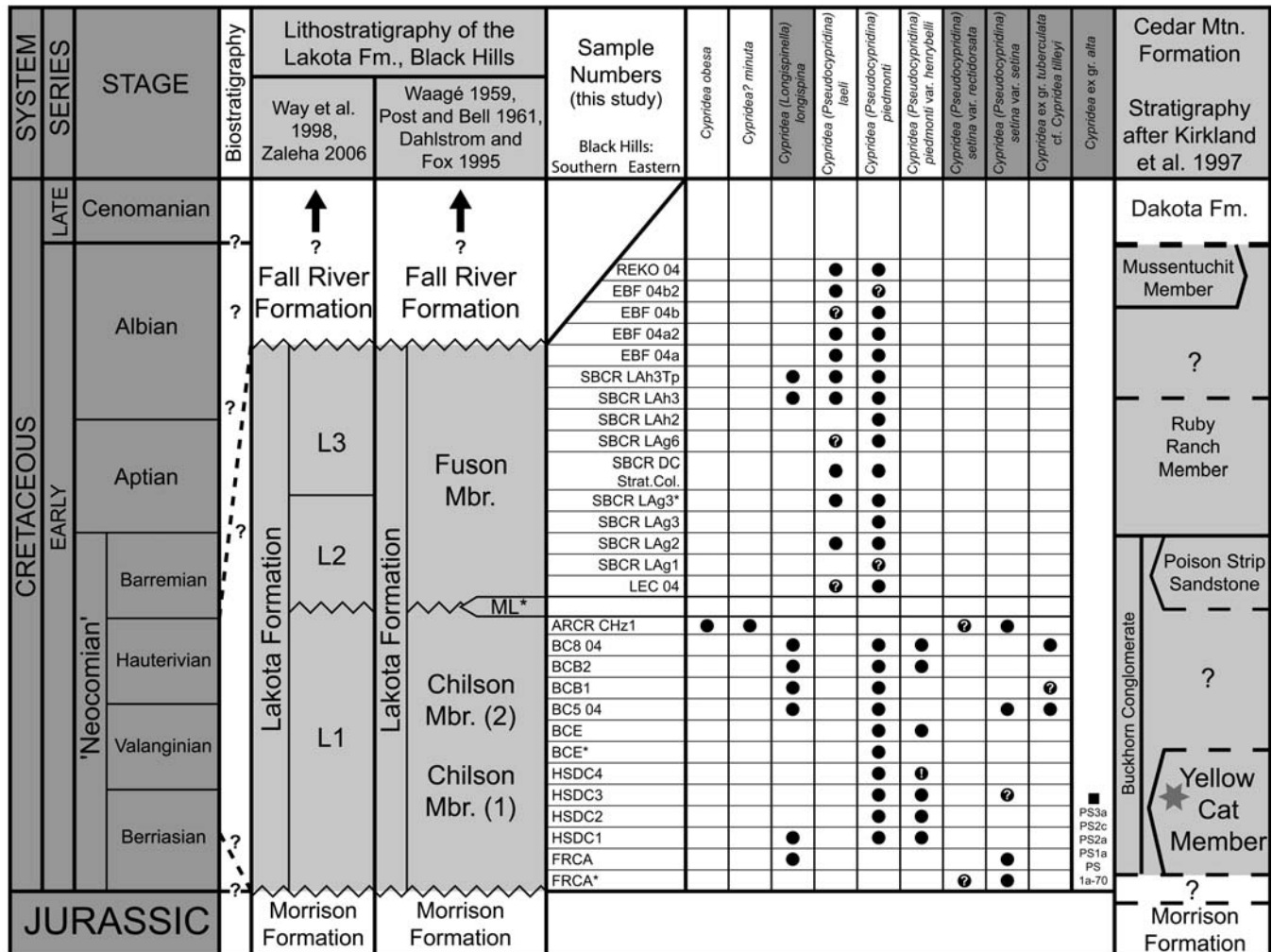*Ontogenetic variation:* Unknown thus far.

Dimorphism: Not observed.

Discussion: Remarks: Although none of the authors samples includes this species, it has been included here based on the material found in the collection of R. E. Peck at the University of Missouri because it is presumed to be a species of biostratigraphic utility (see below), particularly due to the fact that it is easy to identify by means of, amongst other features, its characteristic cyathus-like protrusion.

Discussion of synonymy and relations: Wicher (1959) listed *Cypridea nitidula* from the Recôncavo Bahiano of Brazil. He, however, gave no description and only two photographs (op. cit., pl. 9, figs. 4a, b) and from these, no accurate statement is possible. The original material is needed. The statement of Wicher (op. cit.) that the Brazilian specimens are rather small (0.97mm) in comparison with the North American ones (0.99-1.11mm) is not true.

Cypridea nitidula Peck 1941 shows striking similarities to the following species in lateral outline, presence and development of the cyathus-like protrusion, the development of the alveolar furrow, the surface characters, the common presence of a central to posterocentral pair of large spines, as well as shape and alignment of the rostrum:

a) *Cypridea aemulans* Anderson 1985 nom. nov. pro *C. acuta* Anderson 1971 (preoccupied by *C. acuta* Wicher 1959), inverse

Stratigraphic distribution chart — Lakota Formation, Black Hills. Column headers (taxa): *Cypridea obesa*; *Cypridea? minuta*; *Cypridea (Longispinella) longispina*; *Cypridea (Pseudocypridina) laeli*; *Cypridea (Pseudocypridina) piedmonti*; *Cypridea (Pseudocypridina) piedmonti var. henrybelli*; *Cypridea (Pseudocypridina) setina var. rectidorsata*; *Cypridea (Pseudocypridina) setina var. setina*; *Cypridea ex gr. tuberculata cf. Cypridea tilleyi*; *Cypridea ex gr. alta*.

Sample	obesa	minuta	longispina	laeli	piedmonti	henrybelli	setina rectidorsata	setina setina	tuberculata/tilleyi	alta	Cedar Mtn. Fm.
REKO 04				●	●						
EBF 04b2				●	❓						
EBF 04b				❓	●						
EBF 04a2				●	●						
EBF 04a				●	●						
SBCR LAh3Tp			●	●	●						
SBCR LAh3			●	●	●						
SBCR LAh2											
SBCR LAg6				❓	●						
SBCR DC Strat.Col.				●	●						
SBCR LAg3*				●	●						
SBCR LAg3					●						
SBCR LAg2				●	●						
SBCR LAg1					❓						
LEC 04				❓	●						
ARCR CHz1	●	●						❓	●		
BC8 04				●		●	●		●		
BCB2				●		●	●				
BCB1				●		●			❓		
BC5 04				●		●		●	●		
BCE						●	●				
BCE*						●					
HSDC4						●	❗				
HSDC3						●	●		❓		■ PS3a / PS2c
HSDC2						●	●				PS2a
HSDC1				●		●	●				PS1a / PS 1a-70
FRCA						●			●		
FRCA*							❓		●		

TEXT-FIGURE 11

Stratigraphic distribution of representatives of *Cypridea* in the Lakota Formation, Black Hills area, South Dakota. Taxa highlighted in grey also, or solely (black square), occurring in the Yellow Cat Member of the Cedar Mountain Formation (sample position indicated with grey star), San Rafael Swell, Utah.

This overview in this figure is not intended to establish a true lithostratigraphic or chronostratigraphic correlation. The stratigraphic succession of samples from different localities is only an approximation and may be subject to change when all faunal elements have been analyzed. A detailed correlation and stratigraphy is beyond the scope of this paper and will be dealt with elsewhere. For elucidation of the newer and older lithostratigraphic terminology (see references in table head) refer to Zaleha (2006). There are still conflicting discussions regarding parts of the lithostratigraphy, particularly the position of the Minnewaste Limestone Member (ML*), whether it be the top of L1 informal interval of the base of L2. The dated term "Neocomian", still widely-used but not well defined in the North American literature, is considered avoidable and confusing (see Sames et al. 2010a for discussion).

Symbols: Black circle ●: taxon present. Black circle with question mark ❓: taxon questionable in this sample (mostly resulting from bad preservation). Black circle with exclamation point ❗: ample occurrence (>1000 specimens) of the particular taxon. Black square ■: taxon solely occurring in the Cedar Mountain Formation. Grey star ✹: position of ostracod samples in the Cedar Mountain Formation (sample labels: PS)

Section labels: FRCA: Fall River Canyon Road (Text-fig. 2, loc. 3); HSDC: Horse Sanctuary/Devil's Canyon (Text-fig. 2, loc. 2); BC (BCE, BCB): Buck Canyon (Text-fig. 2, loc. 1); ARCR: Angell Ranch/Cheyenne River (Text-fig. 2, loc. 5); LEC: Little Elk Creek (Text-fig. 2, loc. 6); SBCR: Stage Barn Canyon Road (Text-fig. 2, loc. 8); EBF: East of road to Belle Fourche (Text-fig. 2, loc. 7), REKO: Boxelder Creek east of Blackhawk (Text-fig. 2, loc. 9, sample taken by Reko Hargrave 2004). PS: Cedar Mountain Formation east-northeast of the Ringtail Mine, Utah (Text-fig. 2, loc. 10).

species (RV>LV), Corfe (No. 26) to Nutfield (No. 44) faunicycles of Anderson 1985

b) *Cypridea asseri* Anderson 1967, inverse (RV>LV), Fairlight (No. 53) to Hawkhurst (No. 57) faunicycles of Anderson 1985

c) *Cypridea bispinosa* Jones 1878 (including *C. b. bispinosa* Anderson 1967, *C. b. birini* Jones 1878, *C. b. suthrigensis* Anderson 1967), inverse (RV>LV), Kingsclere (No. 51) to Cuckfield (No. 67) faunicycles of Anderson 1985

d) *Cypridea helenae* Anderson 1967, inverse (RV>LV), St. Leonards (No. 52) to Hawkhurst (No. 57) faunicycles of Anderson 1985

e) *Cypridea primaeva* Anderson 1941, Warren (No. 2) to Corfe (No. 26) faunicycles of Anderson 1985

f) *Cypridea paulsgrovensis* (Anderson 1939), inverse (RV>LV), Hastings (No. 41) to Fletching (No. 58) faunicycles of Anderson 1985

g) *Cypridea simplissima* Anderson 1985 nom. nov. pro *C. simplex* Anderson 1971 (preoccupied by *C. simplex* Galeeva 1955), Upper Soft Cockle (No. 10) to Hythe (No. 46) faunicycles of Anderson 1985

h) *Cypridea varians* Anderson 1971, Mountfield (No. 15) to Hastings (No. 41) faunicycles of Anderson 1985

i) *Cypridea wicheri* Wolburg 1959 (including all subspecies as listed by Anderson 1985, p. 33), Bacon (No. 31) to Bexhill (No. 42) faunicycles of Anderson 1985

It is noteworthy that all the European species of this morphotype are distributed in the Purbeck to Hastings groups of the English Purbeck/Wealden (up to the Cuckfield faunicycle No. 67 of Anderson 1985), an thus are of pre-Hauterivian age according to Hoedemaeker and Herngreen (2003). Even more intriguing is the fact that many of the English species have an inverse valve size, but those with normal valve size relation (LV>RV), i.e., *Cypridea primaeva*, *C. simplissima*, *C. varians*, *C. wicheri* as is also the case in *Cypridea nitidula* Peck 1941 are in trend even older, that is down to Hythe faunicycle No. 46 of Anderson (1985) being (lower) Valanginian following Hoedemaeker and Herngreen (2003). *Cypridea sagena* Anderson 1971, a species with normal valve size relation (LV>RV) as well that occurs in the English Purbeck from the Burwash (No. 14) to Nothe (No. 23) faunicycles of Anderson 1985 (Berriasian after Hoedemaeker and Herngreen 2003), is also considered to belong to this morphogroup but slightly differs in that its rostrum is not as strong bent backwards as in the other representatives.

To narrow the stratigraphic distribution of *Cypridea nitidula* down, it seems helpful to consider the normal and inverse valve size relation (see stratigraphic range below). The normal forms in England seem to be older by trend than the inverse ones, though with a big temporal overlap. However, aside from being considered taxonomically insignificant, the inversion of the valve size is as well considered to occur repeatedly in geologic times and to be possible to evolve in both directions.

There is little doubt that the forms of the *Cypridea nitidula*-like species group are all very similar. Many of Anderson's (1941, 1967, 1971, 1985) figures only show the partially disadvantageous view on the larger valve only, which makes it impossible to see the character of the cyathus ('true' cyathus of cyathus-like protrusion), and the degree of size differences between the valves, for example, especially when comprehensive descriptions are lacking.

Differential diagnosis: Cypridea nitidula differs from the other species described here in its strong and distinct cyathus-like protrusion in combination with a short but distinct rostrum that is strongly bent backwards. *C. nitidula* is easily distinguishable from the somewhat similar *C. obesa* by the distinct rostrum and

alveolar furrow, which is much lesser conspicuous in the latter species.

Paleoecology: As for the genus.

Faunal association: No information from the literature (Peck 1941, 1951, 1959; Peck and Craig 1962; Craig 1961), only tables of occurrences at the same localities are available.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Draney Limestone (Sub-?)Formation at Tincup Creek canyon about 1/2 mile east of the mouth of South Fork of Tincup Creek, Lower Cretaceous, Freemont quadrangle, Idaho-Wyoming (Peck 1941, loc. 5, equivalent to loc. 51P of Peck and Craig 1962).

+ Draney Limestone (Sub-?)Formation and shales, Lower Cretaceous, on the divide east of Draney Ranch in T. 8 S., R. 46 E., Crow Creek Quadrangle, Montana-Wyoming, U.S.A. (Peck 1941, 1951, loc. 9; equivalent to loc. 147P of Peck and Craig 1962).

+ Limestone and shale series, probably Draney Limestone (Sub-?)Formation. Early Cretaceous, along the road in Tincup Creek canyon at the extreme western edge of R. 45 E., T. 5 S., Freedom quadrangle, Idaho-Wyoming, U.S.A. (Peck 1941, 1951, loc. 7)

+ Draney Limestone (Sub-)Formation, Lower Cretaceous, along the Montpelier-Afton Highway in SE 1/4 NE 1/4 sec, 24, T. 29 N., R. 119 W., Lincoln County, Wyoming, U.S.A. (Peck 1941, 1951, loc. 14)

+ Draney Limestone (Sub-?)Formation and lower Bear River Formation, Early Cretaceous, on the north side of Thomas Fork Creek in the N 1/2 sec. 26, T. 28 N., R. 119 W., Cokeville quadrangle, Lincoln County, Wyoming, U.S.A. (Peck 1941, loc. 3a)

+ Draney Limestone (Sub-?)Formation, 0.7 of a mile east of the mouth of South Fork of Tincup Creek canyon, Freedom quadrangle, Idaho-Wyoming (Craig 1961, loc. 164-P therein)

+ Gannett Group, shales in and near the Peterson Formation, Lower Cretaceous, on the south side of the road in Tincup Creek canyon 1.7 miles west of Freedom School, T. 5 S., R. 46 E., Freedom quadrangle, Idaho-Wyoming, U.S.A. (Peck 1941, loc. 4 as referred to in Peck 1951).

Questionable occurrence

South America:

+ Recôncavo Bahiano, Ilhas Formation and Itaparica Formation, Early Cretaceous, Brazil (Wicher 1959)

Stratigraphic range in North America: As inferred from the English Purbeck/Wealden by comparison to a morphogroup of very similar species (see discussion of synonymy and relations above, and stratigraphic range outside North America right below) the most probable stratigraphic range is uppermost Tithonian to (uppermost) Valanginian.

Stratigraphic range outside North America: Not applicable for this species. As for the morphogroup including the inverse species (maximum range; see discussion of synonymy and relations above): uppermost Tithonian to uppermost Valanginian; excluding the inverse species (minimum range) uppermost Tithonian to (lower) Valanginian.

Cypridea obesa Peck 1951 **emend.**
Plate 1, Figures 9-15

*Cypridea obesa sp. nov. – PECK 1951, p. 318, pl. 50, figs. 19-21.
Cypridea obesa Peck – CRAIG 1961, p. 55, pl. 3, figs. 8-10 [unpubl.].
Cypridea obesa Peck – PECK and CRAIG 1962, pl. 2, fig. 5.
non*Cypridea obesa* sp. nov. – HAO et al. 1974, p. 42, pl. 14, figs. 3a-c.

Material: About 50 carapaces, moderately preserved, sample ARCR CHz1 (Angell Ranch Cheyenne River), Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, South Dakota, U.S.A. (Text-fig. 2, locality 5).

USNM Numbers: USNM 544211-544214.

Dimensions (in mm): Overall length: 0.76-1.10

Own specimens:
L: 0.94-1.08   H: 0.60-0.64   W: 0.48-0.56

As given in the literature (Craig 1961):
L: 0.76-1.10   H: 0.55-0.84   W: 0.60-0.83(?)

Type locality and horizon: Not clearly given by Peck. Samples came from the Cloverly Formation west and southwest of Lander, Wyoming (localities 32 and 33 of Peck 1951), from "shales associated with dense limestone beds above lowest variecolored beds and about fifteen feet below the prominent conglomerate" (Peck 1951, p. 310). Peck (op. cit) also referred to the bed 4 of the measured section given in Peck and Reker (1948, pp. 127, 132).

Holotype: U.M. 0-1205-3, possibly lost, the whereabouts of Peck's ostracod type material is unknown (present author's visit, summer 2005).

Diagnosis (emended): Highly angular in lateral outline with strongly inclined Dorsal/hinge margin. Weakly developed inconspicuous rostrum and alveolar notch, alveolar furrow almost absent. Whole carapace surface covered with reticulation-like punctation. Strongly obese, i.e., width about half or more than half the carapace's length.

Remarks: Peck (1951, p. 318) did not indicate and separate the diagnosis and the (short) description. However, Craig (1961, p. 56) gave a diagnosis in his Master's thesis but it unfortunately remained unpublished. Therefore, an emended diagnosis is proposed herein.

Description: Carapace Shape: Small to medium sized. Carapace subtriangular in lateral view with clear angularities. Maximum length below mid-height, maximum height at anterior cardinal angle at 1/3 of length, maximum width at or slightly anterior of 3/5 of length. LV>RV, slightly overreaching the latter along entire margin, LV with weak ventral ridge. Overlap weak at anterior and posterior margins, very weak at hinge margin, and moderate at ventral margin.

Anterior margin broad and slightly infracurvate with a moderately long, nearly straight dorsal part. Rostrum and alveolus weakly developed and inconspicuous, but cognizable in both valves. Alveolar notch narrow and weakly incising, alveolar furrow almost not developed (only faint depressions visible in ventral view). Rostrum blunt, bent backwards (circa 55°), and barely overreaching ventral margin, but not reaching ventral outline as defined by LV's ventral ridge. Posterior margin distinctly narrower than anterior one, infracurvate in general trend but with long nearly straight dorsal part steeply dipping (around 70°) towards posterior end. Ventral part of posterior margin strongly curved. Cyathus narrowly crescent with well rounded outer margin, cyathus angle about 105°, with slight trend to cyathus-like protrusion. Dorsal margin considerably sloping (around 20°) towards posterior end and very weakly convex in posterior part. Hinge margin straight with a total length of about half carapace length. Anterior cardinal angle rounded but well defined, obtuse angled with about 130° angular dimensions; posterior cardinal angle well rounded, poorly defined with around 130°. Ventral margin straight to slightly concave, ventral outline weakly convex defined by the weak ventral ridge of the LV.

Dorsal view very characteristic of the species: obese (=corpulent – name!), i.e., compressed-ovoid with high width in adults (L/W-coefficient less than 2, i.e., width about or more than half the carapace's length) and slightly pointed towards anterior and posterior end but the latter are well rounded. Hinge margin moderately incising forming a ralatively narrow dorsal furrow. LV with weak ventral ridge, ventral overlap moderate and slightly.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: Punctation with strong trend to reticulation; with pentangular to slightly elongated-elliptic, shallow fossae of about 20μm diameter and muri of about 5μm width as well as diffuse delimitation. Some variation and stronger gradation towards reticulation in less well preserved specimens. Towards all margins, the fossae become smaller, less well developed, and are somewhat more elongated parallel to the particular margin.

2. Local ornamentation elements: None (*sensu* Sames 2011c) do occur.

Internal characters: Unknown.

Muscle scar pattern: Unknown.

Morphologic variation: Minor variation regarding the definition/rounding of the posterior cardinal angle connected with a somewhat narrower posterior margin (?sexual dimorphism?, see below).

There seems to be some variation in the magnitude of the carapace's obesity (as already stated by Craig 1961), as well as some variation in the position of the maximum width. The former is most probably an ontogenetic feature, the latter doubtful for the following reasons: Drawings of dorsal and ventral views of the holotype (Peck 1951, pl. 50, figs. 19, 21) show a width of more than half the length but, as stated before, unfortunately the holotype is not in the collection. The photographs of other specimens in Craig (1961, pl. 88, figs. 8, 10, U.M. 0-1226-2) show the same whereas own specimens (Pl. 1, figs. 13, 14) have the maximum width always behind mid-length, at 3/5 or slightly anterior of total length. Since Peck's (1951) holotype as well as

much figured material is not in the collection, it cannot be verified how correct the drawings are and whether just the holotype shows this feature. As for Craig's (1961) specimens, one ventral view (pl. 3, fig. 8) seems to have the maximum width behind mid-length but this is not clearly apparent, and the other ventral view (pl. 3, fig. 10) is strongly dipped leftwards and appears to be as long as wide.

Therefore, based on numerous specimens in the author's own material the characteristic position of the maximum width is distinctly posterior of mid-length, at, or slightly anterior of, 3/5 of carapace length.

Ontogenetic variation: Own material (very few specimens, presumably not younger than A-2) specimens shows lesser obesity (Pl. 1, Fig. 14), with L/W-coefficient of or greater than 2, i.e., the width is half or less than half the carapace's length. Also, the surface characters are stronger trending towards reticulation.

Dimorphism: Not clearly identified (too few specimens). Some specimens (Pl. 1, Fig. 14) appear a bit more elongate and acute posteriorly due to a somewhat better defined posterior cardinal angle connected with a slightly narrower/less higher posterior margin. These might be male dimorphs or juveniles (A-1 or A-2?). The more obese specimen figured in Pl. 1, Fig. 13 might be a female.

Craig (1961, p. 56) already noted a variation in the obesity but was not able to determine "… if this was due to posthumous compression or if this is a valid variation of the species". However, for a better support of this hypothesis more and better preserved material is necessary and should become subject to a thorough morphometric analysis.

Discussion: Cypridea obesa Peck is a relatively atypical representative of its genus, a form with a very weakly developed rostrum and alveolus, and a high width that makes up more than half of the total carapace length. Also, it has a slight cyathus-like extension in the smaller right valve also, thus trending towards a cyathus-like protrusion.

The obesity, however, seems not to be as unique as Peck (1951) believed. For example, *Cypridea recta inflata* Wolburg 1959 or the much different species '*Pseudocypridina*' *sambaensis* Grekoff 1957 (fig. 20, pl. 3, figs. 47-49) also show the same feature. However, affilations of the latter species with *Cypridea (Pseudocypridina)* are doubtful and have to be verified by restudying the original material. To the best of the present author's knowledge, there are no other species known or published thus far, that show closer similarity to *Cypridea obesa* Peck 1959. Many species that seem similar to it at first glance are not as angular in lateral view, or either have a much stronger developed rostrum and alveolus, or these are totally absent.

As for the obesity, the diagnostic nature of this character debatable. Considered female dimorphs of other species of *Cypridea* have about similar length-width ratios, e.g. *Cypridea (Longispinella) longispina* Peck 1941 or *Cypridea (Pseudocypridina) piedmonti* (Roth 1933). Apart from sexual dimorphism the occurrence of which cannot yet be confirmed for *C. obesa* (see above) possible vertical compression has to be taken into account Craig (1961, p. 56-57). Diagenetic compression of the carapaces is quite common in nonmarine Early Cre-

taceous ostracods of the Western Interior and figured specimens given in the literature.

The species *Cypridea obesa* of Hao et al. (1974) does not belong to the genus *Cypridea*, but is a species of *Talicypridea* Khand 1977 instead.

Differential diagnosis: Cypridea obesa generally differs from other species described herein in its highly angular outline combined with a strongly inclined dorsal/hinge margin, its inconspicuous rostrum and almost absent alveolar notch and furrow as well as the strong obesity. *Cypridea nitidula* is clearly distinguishable from *C. obesa* by its strong rectangular cyathus-like protrusion and the distinct rostrum and alveolar furrow. Representatives of *Cypridea (Pseudocypridina) piedmonti* syn. *C. (P.) laeli* have a distinct rostrum and alveolar notch, the rostrum clearly overreaching the ventral margin. The same applies to *Cypridea (Pseudocypridina) laeli.*

Paleoecology: As for the genus.

Faunal association (see Text-fig. 11 also): In the present author's sample ARCR CHz1 associated with *Cypridea setina* (Anderson 1939), *Cypridea? minuta* (Peck 1951), some representatives of the Darwinulidae: *Alicenula?* sp. and some Ostracoda indet. (Candonidae?)

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Early Cretaceous, Fall River County, South Dakota, U.S.A. (this work, Text-fig. 2, locality 5)

+ Lakota Formation, Lower Cretaceous, cut on old road on north side of Fall River 3.2 miles east of 1940 city limits of Hot Springs, Fall River County, South Dakota, U.S.A. (Peck and Craig 1962, loc. D286)

+ Cloverly Formation, Lower Cretaceous, approximately 4 miles west of Lander, on the north side of Baldwin Creek, in S1/2 SE 1/2, Sec. 5, T. 33 N., R. 100 W., Fremont County, Wyoming, U.S.A. (loc. 32 of Peck 1951, same as Craig's 1961 loc. 21)

+ Cloverly Formation, Lower Cretaceous, approximately 3 miles southwest of Lander, about halfway between the roads in Squaw Creek and Middle Fork of the Popo Agie River, in sec. 15, T. 33. N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck 1951, lo. 33 equivalent to Craig 1961, loc. 95P)

+ Cloverly Formation, Lower Cretaceous, north side of Baldwin Creek 4 miles northwest of Lander, Fremont County, in sec. 9, T. 33 N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck and Craig 1962, loc. 658P; see specimen on pl. 1, fig. 10 herein).

Stratigraphic range in North America: As deduced from the association with *Cypridea (Pseudocypridina) setina* var. *setina* and its stratigraphic distribution in Europe: Early Cretaceous, upper Berriasian to lower Valanginian.

Stratigraphic range outside North America: Not applicable.

Subgenus *Ulwellia* Anderson 1939 **emend. and rejected**

*Ulwellia clavata sp. nov. – ANDERSON 1939, p. 300, pl. 13, figs. 1, 9a-b.
Cypridea (Ulwellia) stat. nov. – MARTIN 1940, p. 281.

Type species: Ulwellia clavata Anderson 1939

Original diagnosis: "Valves obovate or ovate-oblong. Antero-dorsal margin slightly concave. Postero-ventral angle of right valve reflexed. Carapace of medium thickness, evenly convex, widest in middle of in posterior half of shell. Surface smooth, punctate or reticulate, may be ornamented with spines or ridges. Right valve larger than left, overlapping it on all margins especially ventrally. Hinge-line knurled anteriorly and posteriorly. Beak and notch often very strongly marked" (Anderson 1939, p. 300).

Anderson also did remark: "This genus has been created for those species of the Rostrocypridae [literal error, recte Rostrocyprinae, i.e., with subfamily suffix, as newly erected by Anderson in this paper; declared invalid by Martin 1940, see Section 5.2.1 herein] in which the right valve is the larger. It is considered that this feature, like shape and hingement, is a character of generic importance, whereas sculpture and ornament are specific characters" (Anderson 1939, p. 300).

Discussion: Any of Anderson's (1939) given characters are here considered of no or rather negligible taxonomic significance, whether on generic or specific level. This applies to the slightly concave dorsal margin, the carapace thickness and mode convexity as well as the position of maximum width as well. The reflexed posteroventral angle of the RV (here the larger one), i.e., the cyathus, is not significant at species level (several representatives of *Cypridea* have this character) or genus level (possession of a 'true' cyathus is a diagnostic character of *Cypridea*). Surface characters, such as smoothness, reticulation (defined reticulation-like punctation for representatives of *Cypridea* in Sames 2011c, and used that way herein) and tuberculation, and the pattern of the latter two, are of no generic and minor specific significance. The inverse valve size (RV>LV) is not considered taxonomically significant here at all (see Sames 2011c). Larger, clearly marked rostra and alveolar notches do as well commonly occur in different representatives of *Cypridea* Bosquet and can be of subgeneric importance. The overall shape and development of the valve overlap is similar in most representatives of *Cypridea*, the variation of which mostly pertains the degree of intensity of overlap in different carapace regions. With respect to the shape of the hinge as given in Anderson's (1939) diagnosis above as more comprehensible explained by Sylvester-Bradley (1949, p. 132): "At the anterior end the *selvage* is swollen and overhangs the recess (the 'knurling' of Anderson 1939), partly hiding it in lateral view" is also not significant at species level, and occurs in many representatives of *Cypridea*.

What remains is that the validity of *Cypridea (Ulwellia)* (Anderson 1939) is strongly connected with the interpretation of the taxonomic significance of an inverse valve size relation, which is considered taxonomically insignificant here (see Sames 2011c). Although Anderson's (1939) diagnosis included several other morphologic characters as given above, many author's just focused on the inverse (RV>LV) valve size relation and simply assigned inverse representatives of *Cypridea* to the subgenus *Ulwellia*, regardless of the overall morphology and

potential relationships to "normal" forms of the same morphology (e.g. Anderson 1967, Christensen 1963, Hou 1958, Li 1984, 1988, Musacchio 1990, 1995, Peck 1951, Sohn 1967, Sylvester-Bradley 1949, Zhang 1985). In addition, the subgenus *Cypridea (Ulwellia)* has also been inconsistently used and applied by many authors (e.g. not used in Musacchio 1971 for several new inverse species, but applied in Musacchio 1990, 1995 for the same species).

Therefore, the validity and the prevalent usage of the subgenus *Ulwellia* are challenged here. Most of the included species should, therefore, have a morphologic equal counterpart except for the opposite ("normal") valve size relation (LV>RV) and the inverse forms should be considered a variety (mutant?) of the particular species. The remaining species are representatives of *Cypridea* with inverse valve size relation (RV>LV) and should be reassigned accordingly, i.e., without applying this subgenus name (but possibly another valid one) and for most of them the "normal" (LV>RV) counterparts can be looked for.

Consequently, the subgenus *Cypridea (Ulwellia)* (Anderson 1939) is rejected here. An application of the name *Ulwellia* should be avoided because it causes confusion in that it implies relationships between its "representatives" that do not exit. The genetic processes controlling the inverse valve size relation in ostracods (inversity of whole body symmetry?) remain to be investigated and discussed (see also 'inverse valve size' in Sames 2011c for discussion).

Cypridea? minuta (Peck 1951) **emend.**
Plate 2, Figures 1-15

*Ulwellia minuta sp. nov. – PECK 1951, p. 320, pl. 49, figs. 9-11.
Ulwellia minuta Peck – CRAIG 1961, p. 77, pl. 3, figs. 1-2 [unpubl.]. – PECK and CRAIG 1962, pl. 1, fig. 7.
Cypridea (Ulwellia) minuta – SWAIN 1999, p. 121, pl. 34, figs. 31-33.

Material: Few carapaces, badly preserved, sample ARCR CHz1 (Angell Ranch Cheyenne River), Chilson Member of the Lakota formation right below Minnewaste Limestone Member Fall River County, South Dakota, U.S.A. (Text-fig. 2, locality 5); few specimens figured from the Peck collection, badly preserved.

USNM Numbers: USNM 544215-544225.

Dimensions (in mm): Overall length: 0.71-0.88
Own specimens:

L: 0.71-0.84   H: 0.43-0.50   W: 0.35-0.40
As given in the literature (Craig 1961; Peck 1951 only gives a length around 0.8mm):
L: 0.71-0.8   H: 0.50-0.51   W: 0.40-0.50

Type locality and horizon: Not clearly given by Peck (1951). Samples came from the Cloverly Formation west and southwest of Lander, Wyoming (localities 32 and 33 of Peck 1951), from "shales associated with dense limestone beds above lowest varicolored beds and about fifteen feet below the prominent conglomerate" (Peck 1951, p. 310). Peck (op. cit) also refers to the bed number 4 of the measured sections given in Peck and Reker (1948, pp. 127, 132).

Holotype: U.M. 0-1202-2, possibly lost, the whereabouts of Peck's ostracod type material is unknown (author's visit, summer 2005).

Diagnosis (emend.): Inverse (RV>LV) form, suboblong in lateral outline, with concave indention of the dorsal outline at position of mid-length and dorsolateral sulcus at the same position. Anterior cardinal angle well defined, weak inclination (max. 10°) of the hinge and dorsal margins. Cyathus absent or very inconspicuous. Rostrum and alveolus well developed, alveolar furrow ventrally delimited by an alveolar ridge.

Remarks: Peck (1951, p. 320) did not indicate and separate the diagnosis and the (short) description, and assigned the species to *Ulwellia* Anderson 1939, which is rejected here. However, Craig (1961, p. 65) gave a diagnosis in his Master's thesis which remained unpublished. Therefore, an emended diagnosis is proposed herein.

Diagnosis as given by Craig (1961, p. 77): "Small, subquadrate form with distinct notch and beak, well defined anterocardinal angle, and with the dorsal margin indented at about mid-length."

Description: Carapace Shape: Small sized (below 1mm). Suboblong in lateral outline. Maximum length slightly below mid-height, maximum height at about 1/5 of length (at anterior cardinal angle), maximum width considerably behind mid-length, between 3/5 and 4/5 of length. RV>LV, weakly inequivalve, RV slightly overreaching LV along entire margin except for the ventral margin, where the overreach is moderate, intensified by a ventral ridge. Valve overlap moderate along anterior and posterior margins, somewhat stronger ventrally (ventral overlap), weak along hinge line.

Anterior margin broad and slightly infracurvate with short straight dorsal part, anteroventrally prolongating into a well-developed rostrum strongly bending backwards with 55-60°, that is not attached to the ventral margin and overreaches the ventral margin and can slightly overreach the ventral outline. Rostrum moderately broad with rounded point. Rostrum of smaller LV somewhat weaker developed. Alveolus well developed, alveolar notch distinct and moderately broad. Alveolar furrow elongate and slightly crescent and moderately incising, somewhat stronger developed in smaller left valve, and reaching almost up to mid-height. Alveolar furrow ventrally delimited by a weak alveolar ridge.

Posterior margin equicurvate and well-rounded, slightly narrower than anterior margin and having a short straight dorsal part. Occurrence and development of cyathus somewhat unclear due to bad preservation (posteroventral region mostly damaged) and insufficient figures and descriptions in the literature (see discussion below). However, three specimens from Peck's collection (Pl. 2, Figs. 10, 13, 14, 15; see discussion below also) clearly point to an absent cyathus.

Dorsal margin straight, dorsal outline slightly but distinctly concave (indention) at about mid-length. Hinge margin weakly inclined towards posterior end with circa 10°. Anterior cardinal angle well defined and only weakly rounded, circa 140°, posterior cardinal angle less distinct and strongly rounded, its angular dimension circa 140-150°.

Ventral margin straight to slightly concave, being coincident with the ventral outline in the smaller LV. Ventral outline in the larger RV considerably divergent from the ventral margin due to the RV's overreaching moderate ventral ridge.

Dorsal view elongate-ovate, laterally flattened towards both ends, the anterior end being somewhat more acute. With lateral constriction of variable degree at mid-length or slightly in front of it (caused by the dorsolateral sulci), more distinct in the assumed females (refer to item dimorphism below).

Ventral view showing slight anterolateral constriction caused by the alveolar furrow, as well as the ventral (tongue-like) overlap and the ventral ridge. Punctation less well developed ventrally.

Both valves with broad dorsolateral depression/sulcus at about or slightly anterior of mid-length, reaching down to almost 3/4 of height; the sulcus mostly being clearly delimited anteriorly and posteriorly by an edge.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: Whole carapace surface, including the dorsolateral sulci, covered by moderate to deep roundish to elongate-ovate puncta which are separated by broad muri, except ventral region where the punctation is weak or almost reduced. Puncta in the area where the central muscle scar field is located internally seem to be considerably deformed (elongated).

Several lateral pore canals (simple pores) of about 2-3µm diameter, more or less evenly distributed over the valve, some of these slightly widened up to 5µm.

2. Local ornamentation elements: No larger spines, tubercles or nodes reported in the literature or visible in the available material. Rows of few minor tubercles (around 10µm in diameter) in the anterolateral region along and close to the anterior margin and including the rostrum.

Internal characters: Unknown.

Muscle scar pattern: Unknown.

Morphologic variation: Minor. Some variation in the distinctness of the indention of the dorsal outline, some specimens almost lacking this character. Degree of development of punctation varying to some extend as well as the slight anterolateral tuberculation (absent or present). Some variation in maximum width and its position. Note: These statements are in part not considered fully reliable because the preservation of the material is bad.

Ontogenetic variation: No data.

Dimorphism: Sexual dimorphism tentatively assigned on the basis of few badly preserved specimens. Supposed female (Pl. 2, Figs. 2, 5, 6, 11, 12) ovate in dorsal view with distinct lateral constriction at about mid-length and position of maximum width at 3/5 of length. Supposed males (Pl. 2, Figs. 1, 4, 13, and 14) elongated-ovate with weak lateral constriction at mid-length and position of maximum width behind 3/5 of length.

Discussion: Cypridea? minuta (Peck 1951) is thus far only known from the Lower Cretaceous of North America. Its assignment to the Cyprideidae Martin 1940 is unquestionable based on the well-developed rostrum and alveolus. Its assignment to *Cypridea* Bosquet 1852, however, is debatable. *Cypridea? minuta* could either belong to *Cypridea* based on the rostrum, alveolus with well developed alveolar furrow and alveolar ridge–or be probably assigned to *Bisulcocypridea* Sohn 1969 based on the dorsal incision, the dorsolateral sulcus and

the potentially absent cyathus, in combination with rostrum and alveolus. As far as apparent from the few badly preserved specimens, the dorsolateral sulcus is not subdivided. Peck and Craig (1962, pl. 1, fig. 7 therein), however, pictured a drawing of a specimen with two distinct sulci being separated by a lobe, a specimen without number. Two specimens have been found in Peck's collection at the University of Missouri (SEM figures of these given here on Pl. 2, Figs. 13, 14), being labeled as *Ulwellia minuta* with the indication of having been figured in Peck and Craig (1962), one of them is figured here (Pl. 2, Fig. 13). Yet, both of these are badly preserved and none of them shows two sulci as well as all other specimens. Whoever did the drawings for the Peck and Craig (1962) publication, probably mistook the margins of the single sulcus for 2 separate sulci.

A single sulcus could be an ancestral state in the evolution towards *Bisulcocypridea*. *Cypridea? minuta* thereby potentially holds a key position (ancestor?) in the early evolution of *Bisulcocypridea* Sohn 1969 and a *Cypridea-Bisulcocypridea (-Ilyocypris?)*-lineage (refer to discussion of the family Cyprideidae Martin, Section 5.2.1 herein) and should be further investigated. Better material is essential to get more details of the carapace morphology.

An interesting thing to note and to investigate further is that *Cypridea? minuta* also possesses a well-developed alveolar ridge, which would also occur amongst representatives of *Bisulcocypridea* following the line of argument given above, and support a closer relation between certain *Cypridea*-lineages and *Bisulcocypridea*.

Cypridea? minuta shows some similarities to *Cypridea skeeteri* Peck 1951. Because of the two distinct sulci and absent cyathus, however, the latter is certainly a true representative of *Bisulcocypridea* Sohn 1969.

Differential diagnosis: Cypridea? *minuta* differs from the other *Cypridea*-species described here in its slight indention in the dorsal outline, and the dorsolateral sulcus. It is also the only form with inverse valve size relation (RV>LV) described among these.

Paleoecology: As for the genus.

Faunal association (see Text-fig. 11 also): In the present author's sample ARCR CHz1 associated with *Cypridea setina* (Anderson 1939), *Cypridea obesa* Peck 1951, some representatives of the Darwinulidae: *Alicenula?* sp.

No information about faunal association available from the literature (Peck 1951, Peck and Craig 1962, Craig 1961).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Lower Cretaceous, Fall River County, South Dakota, U.S.A. (this work Text-fig. 2, locality 5)

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, Calico Canyon south of Buffalo Gap [but NE of the town of Buffalo Gap!] in the SE1/4 sec. 24, T. 6 S., R. 6 E., Custer County, South Dakota, U.S.A. (Peck 1951

loc. 28, as equivalent to Peck and Craig 1962 and Craig 1961, loc. 184P [not Fall River County!])

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, partings in exposure of Skyline Drive, east of Hot Springs, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 29 as equivalent to Craig's (1961) loc. 439P as also listed in Peck's locality catalog)

Questionable occurrence:

West Africa:

+ Cocobeach Series, Lower Cretaceous, Gabon [then "Afrique Équatoriale Française – AEF", that is, "French Equatorial Africa"] after Grekoff (1953 and 1960); questionably because the species is only listed, neither figured nor described (correct taxonomy has to be verified on the original material)

Stratigraphic range in North America: As deduced from the co-occurrence with *Cypridea (Pseudocypridina) setina* [var. *setina*] and its stratigraphic distribution in Europe: Early Cretaceous, [upper] Berriasian to [lower] Valanginian.

Stratigraphic range outside North America: Not applicable (yet). A potential occurrence of *Cypridea? minuta* in West Africa as noted by Grekoff (1953, 1960b) remains to be verified.

Subgenus ***Longispinella*** Sohn 1979 **stat. nov., emend.**

v*Longispinella asymmetrica* gen. nov. sp. nov. – SOHN 1979, p. 18-19, pl. 4, figs. 7-20; pl. 5, figs. 1-7, 13-16.
Cypridea longispina sp. nov. – PECK 1941, p. 300, pl. 43, figs. 6-9.
non*Cypridea armata* sp. nov. – KRÖMMELBEIN 1962, p. 455, pl. 56, fig. 27a, b.
non*Cypridea tucanoensis* sp. nov. – KRÖMMELBEIN 1965a, p. 180, fig. 1a-c.
Cypridea daoudensis sp. nov. – ANDREU et al. 2003, p. 206, pl. 3, figs. 5-9.

Remarks: Sohn (1979) established *Longispinella* as separate genus and placed it within the Cyprideidae Martin 1940, a view still shared by authors in recent publications (e.g. Horne and Colin 2005). However, in the view of the present author this is not plausible anymore for the reasons given in the discussion below, and accordingly the status of *Longispinella* is changed to subgenus and placed within *Cypridea* s.l. (*sensu* Sylvester-Bradley 1949) herein.

Type species: Longispinella asymmetrica Sohn 1979

Diagnosis (emended): A small-sized (< 1mm) *Cypridea* with subtriangular outline. LV>RV, moderately inequivalve with distinct dorsal overreach of the larger LV. Rostrum pronounced, alveolus well-developed and broad, deep and broad alveolar furrow reaching up to mid-height (in some representatives?) being ventrally delimited by an alveolar ridge. Small but distinct cyathus-like protrusion. Dorsal outline, as defined by larger LV, slightly concave in hinge area. Carapace weakly to strongly punctate except for the anterolateral and posterolateral areas. Local ornamentation elements (tubercles, paired spines) may occur.

Sexual dimorphism presumed to occur, then being distinct: males much more elongate in lateral view and slender in dorsal

view; females more compact in lateral view and piriform in dorsal view.

Original diagnosis: "Relatively small, to 1 mm in greatest length, subtriangular in lateral outline; surface punctate, with one subcentral large spine, without nodes, small spines or ridges; rostrum and alveolus well-developed, cyathus usually subtriangular. Dimorphic in width of posterior." (Sohn, 1979, p. 18).

Other representatives: Cypridea daoudensis Andreu and Colin 2003 (in Andreu et al. 2003) => *Cypridea (Longispinella) daoudensis* Andreu and Colin 2003 (see discussion of synonymy below)

Discussion: This taxon was established by I.G. Sohn for "… those species previously referred to *Cypridea* Bosquet, 1852, that have a robust lateral spine on each valve and that do not have accessory smaller spines" (op. cit., p. 18). Since ornamentation, and particularly local ornamentation elements (*sensu* Sames 2011c) are considered taxonomically insignificant, and taking into account Sohn's diagnosis of the genus *Longispinella* (see above), which includes occurrence of rostrum, alveolus and cyathus, this diagnosis is considered insufficient to exclude taxa of *Longispinella* from *Cypridea*, and it remains strongly curious in the view of the present author that Sohn defined this new genus. Except for the single robust spine on each valve, *Longispinella* shows external features (internal features are unknown) all consistent with the genus *Cypridea* Bosquet: a rostrum, a well-developed alveolus with a distinct alveolar ridge (newly defined in Sames 2011c), a cyathus-like protrusion, a (weak) ventral ridge and the hinge incisure forming the dorsal furrow. Thus, there is no reason for establishing a new genus but rather many arguments to include this taxon into *Cypridea*, as, based on the available characters, had been done by Peck (1941) already.

The question, whether the definition and retention of a subgenus is justifiable in general is survey-like discussed in Section 5.4.1, but approved here. The subgenus *Longispinella* is here considered a well recognizable representative and "ancient" morphotype of *Cypridea*, therefore useful for application, and the retention of this name also facilitates and simplifies a tracing of representatives within the literature.

Presumed sexual dimorphism: Sohn (1979, p. 18) already included the statement " … dimorphic in width of posterior" in his diagnosis of *Longispinella* and presumed sexual dimorphism in his *Longispinella longispina* (Peck 1941). The view of the present author is that *Longispinella longispina* (Peck) of Sohn 1979 represents the female dimorph and *Longispinella asymmetrica* Sohn 1979 the male, as discussed in item "Dimorphism" of the species description of *Cypridea (Longispinella) longispina* below.

Phylogenetic considerations: Representatives of *Cypridea (Longispinella)* are considered to belong to a more primordial lineage of *Cypridea*. Its characteristics are: the strong (dorsal) overreach of the larger valve (i.e., considerably inequivalve) like present in several of such earlier groups of the older Early Cretaceous, e.g., the *Cypridea alta-, Cypridea angulata-, Cypridea lata-*groups of Wolburg (1959) ̄in the case of the *C. (Longispinella)*-lineage combined with a broad and deep alveolar furrow and a cyathus-like protrusion. The latter is assumed to be the plesiomorphic state within the evolution of a presumed *Praecypridea-Cypridea* lineage (see Sames et al. 2010b). *Cypridea*-lineages showing a considerable inequivalve carapace seem to be restricted to the Late Jurassic to older Early Cretaceous (Berriasian to Valanginian; up to Barremian?) interval (see Section 6.3 for discussion).

Discussion of synonymy: Sohn (1979) also assigned *Cypridea armata* Krömmelbein 1962 and *Cypridea tucanoensis* Krömmelbein 1965(a) from the Lower Cretaceous of Brazil to his *Longispinella*, along with *Cypridea longispina* Peck 1941. However, both taxa are strongly different from *Cypridea (Longispinella)* and considered not to belong in this group for the following reasons: As for *Cypridea armata* Krömmelbein 1962, its lateral outline is very different from species of *Cypridea (Longispinella)*, it only has a weakly developed rostrum and alveolus, and the paired "thorn" is no robust spine, but a tubercle instead. *Cypridea tucanoensis* Krömmelbein 1965(a) does not even have the "diagnostic" spine but only shows a "weak/flat, node-like protrusion, in an approximately postero/dorso-median position" (see diagnosis given in Krömmelbein 1965a, p. 180). This structure is hollow and neither well-defined nor distinctly pointed, and can thus not be designated as a (robust) spine but is an inflated tubercle instead. Altogether, *C. tucanoensis* rather fits into *Cypridea (Cyamocypris)* Anderson 1939 than into *Cypridea (Longispinella)* because its alveolar furrow is narrower that in the latter, the overreach of the LV is much stronger along the entire margin and the cyathus is much more rounded and wider.

Cypridea daoudensis Andreu and Colin 2003 (in Andreu et al. 2003) has all diagnostic characters of *Cypridea (Longispinella)* and is, therefore, included into the subgenus. It as well shows strong similarities to the type species of this subgenus particularly to the slender morphotype formerly designated *Longispinella longispina*, herein considered the male dimorph of *Cypridea (Longispinella) longispina* Peck 1941 (see discussion there for more details). Apart from that *Cypridea daoudensis* has a stronger degree of distinctness in its punctation and shows several smaller tubercles both characters not considered taxonomically significant its cyathus-like protrusion in the smaller RV is much stronger developed than that in *C. (L.) longispina*, no perpendicular ridge and sulcus do occur in the larger LV and no large spines are present. However, the latter characters are considered significant at species level (the spines might not even be significant at species level).

It is not totally clear, whether *Cypridea daoudensis* has an alveolar ridge, because Andreu et al. (2003) neither described such a character nor do the figured specimens explicitly show it. It seems, however, not to be present; if there is an alveolar ridge in *C. daoudensis*, it is very weak. This raises the (open) question about the taxonomic significance of the alveolar ridge–if it is taxonomic relevant, at what taxonomic level–as well as its function (see Sames 2011c for discussion).

Stratigraphic range: Early Cretaceous (Berriasian to Barremian?).

Geographic distribution: North America (U.S.A.); questionably Morocco, North Africa (*Cypridea daoudensis* Andreu and Colin 2003, in Andreu et al. 2003).

Paleoecology: Presumed salinity range as for the genus.

Cypridea (Longispinella) longispina Peck 1941 **syn. *C. (L.) asymmetrica*** (Sohn 1979), **emend.**
Plate 3, Figures 1-15

**Cypridea longispina* sp. nov. – PECK 1941, p. 300, pl. 43, figs. 6-9. – PECK and REKER 1948, pl. 3, fig. 22. – PECK 1951, p. 312, pl. 48, figs. 12-15. – SOHN 1958, pl. 1, figs. 1-4. – CRAIG 1961, p. 63, figs. 13-15. – PECK and CRAIG 1962, pl. 1, figs. 4, 21.
v*Longispinella asymmetrica* gen. nov. sp. nov. – SOHN 1979, p. 18-19, pl. 4, figs. 7-20; pl. 5, figs. 1-7, 13-16.
v*Longispinella longispina* (Peck 1941) – SOHN 1979, p. 19-29, pl. 4, figs. 1-6, pl. 5, figs. 8-12 and 17-23, pl. 7, figs. 5-7 [comb. nov.].
?*Cypridea (Cypridea)* cf. *longispina* Peck – CAO 1986, p. 241, p. 1, figs. 13, 14, 21, 22.
?*Cypridea (Cypridea) longispina* Peck – YE 1994, p. 292, fig. 9.

Material: About seventy carapaces, mostly moderately to well-preserved. Samples: PS1a-70 and PS2a (Yellow Cat Member of the Cedar Mountain Formation, Text-fig. 2, loc. 10). FRCA, HSDC1, BC5 04, BCB1, BCB2, BC8 04 (Chilson Member or L1 Interval of the Lakota Formation); SBCR LAh3 and LAh3Tp (Fuson? Member or L2/L3? Interval of the Lakota Formation, Text-fig. 2, locs. 1, 2, 3, 8).

USNM Numbers: USNM 544226-544234.

Dimensions (in mm): Overall length: 0.85-0.93

Own specimens:

Presumed females
     L: 0.85-0.93   H: 0.60-0.64   W: 0.45-0.47

Presumed males
     L: 0.85-0.91   H: 0.54-0.55   W: no data

As given in the literature (Peck 1941):

species *longispina*
     L: ~0.90   H: ~0.55   W: ~0.45

Type locality and horizon: Kootenai Formation, Montana. "Shales around a nodular limestone underlain by red clay along the road 1 mile southwest of Griffin, about 14 miles southeast of Great Falls, Montana, in T. 18 N., R. 4 E …" (Peck 1941, p. 288, locality 23).

Holotype: U.M. 0-974-1, whereabouts unknown (lost?).

Diagnosis (emended): LV>RV, strongly inequivalve, lateral outline more or less strongly rounded subtriangular. LV strongly overreaching the RV along dorsal margin. Rostrum well-developed, its point not overreaching the ventral outline, separated from the ventral margin by a broad alveolar notch. Broad and elongate alveolar furrow in LV, reaching up to slightly above mid-height, subtriangular in RV and not reaching mid-height. Alveolar furrow deeply incised and ventrally delimited by a strong alveolar ridge. LV anterocentrally with short perpendicular shallow sulcus, bounded anteriorly by a rounded ridge. Cyathus-like protrusion triangular and moderately strong developed. Coarsely punctate and mostly with paired and robust posterocentral spine being bent backwards. Strong sexual dimorphism.

Remarks: Peck (1941, p. 300) gave no particular indication of a diagnosis but only a short description of the species: "Carapace of medium size, subovate to subtriangular in lateral outline, highest just anterior to the middle; dorsal and ventral margins rounded, overlap strong. Anterior and posterior margins unequally rounded with a strong beak and notch, the posterior margin greatly contracted, almost pointed; cardinal angles prominent. Hinge deeply indented, with strong posterior slope, forming an angle of 35° or more with the long axis of the carapace. Ventral margin curved, almost parallel to longitudinal axis. Surface of the valves smooth [not true] except for a long blunt spine in the posterior ventral portion."

Description: Carapace Shape: Small sized. General shape of carapace in lateral view rounded subtriangular, tapering to posterior end. Maximum length at about 2/5 of height, maximum height at about 2/5 of length (at anterior cardinal angle), sometimes more backwards depending on the development of the LV's dorsolateral overreach (in the presumed females), but always anterior of mid-length. Maximum width (excluding spines) at about 3/5 of length or slightly anterior in females. LV>RV, distinctly inequivalve, LV moderately overreaching the smaller right valve along entire margin except for the dorsal margin, where the overreach is increased by a dorsal ridge in the LV, usually stronger developed in presumed females. Valve overlap strong, along entire margin, except hinge margin where the overlap is very slight or not existent.

Anterior margin broadly infracurvate, anteroventrally prolongating into a moderately pointed rostrum bending backwards with about 25-30°. Rostrum at the LV barely extending to the ventral margin line and never overreaching the ventral outline. Rostrum of smaller RV less developed, somewhat shorter and less pointed. Alveolus strongly developed with broad alveolar notch. Broad and elongate alveolar furrow in LV, reaching up to slightly above mid-height, subtriangular in RV and not reaching mid-height. Alveolar furrow deeply incised and ventrally delimited by a strong alveolar ridge, its outline in the LV being more rectangular-crescent, in RV triangular.

LV (only) with anterocentral short perpendicular shallow sulcus bounded anteriorly by a rounded ridge, the latter being located just behind upper end of alveolar furrow.

Posterior margin infracurvate, always narrower than anterior margin, well-rounded and relatively broad in females, narrow (half the width of the anterior one) and with long nearly straight dorsal part in male dimorphs. Cyathus-like protrusion moderately strong and triangular with an outer angle of about 130°, somewhat less conspicuous in males. Position of cyathus-like protrusion clearly in front of posterior margin's maximum extension, at about position of posterior cardinal angle.

Dorsal margin straight to slightly convex, not coincident with dorsal outline in both valves. Dorsal outline convex, particularly strong in the LV of the females due to strong dorsal overreach. Hinge margin straight to slightly concave, considerably inclined towards posterior end with about 30-35°. Cardinal angles more or less prominent, less distinct in LV. Anterior cardinal angle strongly rounded, circa 120°, posterior cardinal angle usually more distinct and less rounded, circa 140-145°.

Ventral margin straight to slightly convex, being coincident with the ventral outline in the smaller RV, but divergent from the latter in the larger LV due to ventral overreach.

Dorsal view of males elongated-ovate tapering towards anterior end, females ovate to piriform tapering towards anterior end. Both dimorphs with a slight lateral constriction anteriorly at po-

sition of alveolus. Hinge incision/dorsal furrow moderate, dorsal suture straight, lateral offset weak, slightly towards RV. Strong convex tongue-like overlap of LV in ventral view, also along the ventral ridge (Pl. 3, Fig. 6).

LV of both dimorphs with short perpendicular shallow sulcus bounded anteriorly by a rounded ridge, located anterocentrally just behind upper end of the alveolar furrow and considerably variable in its degree of expression.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: Surface covered with more or less regularly distributed roundish puncta of about 20μm diameter, often with very diffuse limitation, mainly occurring in and around the central region, attenuating towards anterior and posterior regions. No puncta in alveolus region and by trend in anterolateral region absent in general.

Valves with relatively regularly scattered normal pores of 1-2μm diameter and 40-50μm relative distance.

2. Local ornamentation elements: None, except one larger, posterocentral to posterior centroventral robust spine that is bending backwards. It seems as if there is a fine pore canal running through its center. Spines always pairwise occurring but not necessarily in exact opposite relative position. Quite the contrary, the relative position of the two spines can be quite divergent, vertically as well as horizontally. Size, shape and absolute position of these spines can vary considerably (see, for example, Sohn 1979, pl. 4, figs. 11, 13, 17; pl. 5, figs. 2, 4, 5). They can be straight or arcuate (always backwards), long (up to about 100μm) or very small and short, very acute or blunt, slender or sturdy, and even broad-conic, the diameter of their base varying between 20μm and 100μm, usually being about 40-60μm.

Although sometimes being small and hardly noticeable, there seem to be hardly any specimens totally devoid of spines (cf. pl. 5, fig. 19 in Sohn 1979). In most cases, specimens seeming to have no spines at first glance turned out to have either very small spines or these were broken off directly at the valve surface. However, due to their extreme morphologic variability these spines are not considered being of strong significant taxonomic value (see discussion below for mote details).

Internal characters: Not observed and unknown.

Muscle scar pattern: Unknown.

Morphologic variation: Aside from the strong sexual dimorphism (see below), mostly concerning the lateral outline, i.e., slightly variation in position of maximum height (between 2/5 of length and slightly before mid-length) and curvature of dorsal outline, being usually convex to straight, but sometimes slightly convex (mainly in those specimens having the position of maximum height/anterior cardinal angle somewhat more posterior). To a lesser extend, the size and degree of development of the anterocentral perpendicular ridge and sulcus in the LV varies. Concerning the pair of posterocentral spines, these may be present and then vary in their relative position to each other as well as their position on the valve, and in shape and size or absent.

There is some variation in the development of the surface characters, the reasons for which are not clear but may be ecophenotypic (salinity s.l.?, calcium concentration?). The

puncta are more or less distinct, depending on the width and intensity of the muri. This seems to be partially linked to the thickness of the valves (degree of calcification) rather than the preservation. Most of the present author's specimens, either well- or moderately preserved, show a diffuse limitation and elongation of the puncta in both morphotypes (considered sexual dimorphs here) whereas in the material of Sohn (1979, see pls. 4, 5 therein; and his collection at the USNM) well-delimited and diffuse puncta occur, but in both morphotypes as well.

Ontogenetic variation: No data available.

Dimorphism: Strong sexual dimorphism inferred and described herein: Females more compact in lateral view, somewhat higher maximum height (lower L/H-ratio), mostly with less well-defined (i.e., stronger rounded) posterior cardinal angle and well-rounded, relatively high posterior margin. In addition, the angular dimension of the females' anterior cardinal angle is somewhat lesser (117°-122°) than in males due to the stronger hinge margin inclination (~30°) of the former. Females piriform in dorsal view.

Males more elongate in lateral view, with lesser absolute maximum height (higher L/H-ratio), well-defined (i.e., weakly rounded) posterior cardinal angle, and low, weakly rounded posterior margin. Angular dimension of the anterior cardinal angle somewhat higher (125-130°) than in females due to lesser hinge margin inclination (~27°) of the males. Dorsal outline of males elongated elliptic with distinct anterior and somewhat weaker posterior lateral constriction.

Sohn (1979) presumed a sexual dimorphism within his *Longispinella longispina* only, indicated by the different width of the posterior end with his 'males' being narrower and females wider. However, these differences are minor and barely recognizable, and consequently considered to represent normal morphologic variation within females (or, hypothetically, may represent precocious sexual dimorphism). These specimens given in Sohn's (1979, p. 19) discussion as male dimorphs of his *Longispinella longispina* having also been inspected by the present author are diagenetically deformed (laterally compressed) to a different degree (Sohn 1979, pl. 4, figs. 3, 5; pl. 5, fig. 9, 19). It is, thus, no surprise that these specimens are more slender in dorsal view than the uncompressed ones considered females by Sohn (1979; pl. 5, figs. 12, 22).

Both, *Longispinella longispina* and *L. asymmetrica* of Sohn (1979) are herein inferred to belong to one species, *Cypridea (Longispinella) longispina* Peck 1941) and to represent sexual dimorphs, with *L. longispinella* (Peck 1941) of Sohn being the female dimorph and *L. asymmetrica* Sohn 1979 being the male dimorph, for the following reasons:

In contrast to Sohn's (1979, p. 19) diagnosis that his *Longispinella longispina*, amongst other things, differs from his *L. asymmetrica* in "… having a smaller perpendicular shallow sulcus bounded anteriorly by a rounded ridge behind the alveolus of the left valve, or not having that structure", the combined perpendicular sulcus and ridge in the LV are always present in the specimens of Sohn in the USNM collection (new SEM pictures taken, Pl. 3, Figs. 10, 11, 12 herein) as well as in the author's own samples. Even badly preserved and strongly diagenetically altered specimens show this character. It remains unknown why Sohn (1979) chose this character as one main reason to distinguish his two taxa. The other morphologic dif-

ferences as described above, well match typical characters of sexual dimorphism in cypridoid ostracods (if realized and visible in the carapace) and are strongly connected with the different shape and size of the sexual organs. In addition, both of Sohn's (1979) taxa (almost) always co-occur, in Sohn's samples as well as in the author's ones, which also is a strong argument against a separation of the two morphotypes into different species. Finally, both morphotypes are of the same overall size and show the same variation, distribution and pattern of puncta.

Altogether, under todays perspective of consideration, Sohn's (1979) arguments for establishing two species are very weak and a strong sexual dimorphism is much more probable.

Discussion: Both, *Cypridea (Longispinella) longispina* Peck 1941 and *C. (L.) assymetrica* (Sohn 1979) are combined under the former species because they are considered sexual dimorphs (see above) and representatives of *Cypridea* (*Longispinella*). This is supported by the fact that, if both forms are present (presumed males are missing sometimes), they always co-occur in Sohn's (1979) as well as in the present author's samples.

Although most likely, it is not possible to determine with certainty from the material available whether the occurrence of the large spines in *Cypridea (Longispinella) longispina* is always bound to a normal pore, because the spines are strongly mineralized (and diagenetically recrystallized?) and the fine central pore is often not observable. In addition, the causation as well as the processes controlling shape, size and position of this single pair of spines are unknown. Especially the spine in the smaller (right) valve seems to be highly variable in its position in the posterocentral to posterolateral area (Text-fig. 3).

The spines might or might not be characteristic at species level. Resulting from material and data from Sohn (1979), Peck (1941), and the present author's own observations, these spines are definitely no ontogenetic features since they are always present in adults, which would support the hypothesis that they are truly characteristic but not diagnostic at species level (see below). Degree of expression (and occurrence?) of the spines of the described species seems to be influenced, if not totally controlled, by extrinsic (abiotic environmental?) factors. Speculatively, these are also stronger developed when required as reaction to selection pressure caused by predators.

With regards to the area-wide ornamentation elements in *C. (L.) longispina*, its diffuse pattern and shape seems to be unique, but is, basically, a punctation (see Pl. 3, Figs. 1, 10, 14 herein, and Sohn 1979, pl. 4, figs. 9, 12, 13, pl. 5, figs. 18, 21, 23, for example). The reason for distortion or the superimposing (Pl. 3, Figs. 9, 13) of the puncta is not clear, though it might derive from strong calcification and thickening of the carapace that leads to swollen "muri" between the puncta.

The closer phylogenetic relationships of *Cypridea (Longispinella) longispina* are not yet well understood. Particularly the question of the taxonomic significance of the pair of robust lateral spines and the LV's anterolateral perpendicular ridge and sulcus are of interest. Although many representatives of *Cypridea* show a single pair of major lateral spines (in combination with total absence of other spines or tubercles) in their central, centrodorsal or posterocentral areas, these belong to morphologically strongly different groups (cf. Text-fig. 3; e.g. *Cypridea bispinosa bispinosa* Jones 1878, *Cypridea spinigera* Sowerby 1836, *Cypridea alta wicki* Wolburg 1959, as well as

many others). Therefore, the pair of spines is neither a good diagnostic character for *C. (L.) longispina* nor suitable to justify closer affinities between species with this character. The LV's (larger valves) anterocentral perpendicular ridge and sulcus in *C. (L.) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn) is unique among representatives of *Cypridea* and the representatives of the Cyprideidae Martin 1940. Its function is unknown and its taxonomic significance cannot yet be assessed.

However, even when disregarding the pair of spines and the LV's perpendicular ridge and sulcus in *C. (P.) longispina* syn. *C. (P.) asymmetrica*, the combination of the strong alveolar ridge, moderately incising alveolar notch, broad and long alveolar furrow, cyathus-like protrusion, punctation and the carapace being moderately inequivalve makes it difficult to find closer relations to other taxa of *Cypridea* thus far. There are, however, some similarities to *Cypridea dolabrata* (Anderson 1939) and its subspecies (variants) as well as *Cypridea inaequalis* Wolburg 1959 in general shape, lateral outline and the mode and degree of valve size relation, for example.

Discussion of synonymy: Cypridea (Cypridea) cf. *longispina* Peck of Cao (1986) is (very) questionably included here, because the specimens of Cao (op. cit.) are badly preserved and strongly deformed and the details not distinguishable from the photographs. The case remains to be reappraised on the original material.

Cypridea (Cypridea) cf. *longispina* Peck as figured (drawing) in Ye (1994, fig. 9B; from Cao's 1986 material and publication?) and given to be of Albian age is most probably no representative of *Cypridea (Longispinella) longispina* Peck 1941, because it is of different outline, it is not distinctly inequivalve, lacks the broad alveolar furrow as well as the cyathus-like protrusion, and the position of the spine is central (posterocentral to posterolateral in the latter). The specimen figured by Ye (1994) is much more similar to *Cypridea brevicornis* Peck 1941.

As for Ye's (1994) synopsis and as stated before (Section 5.2.2), there are problems remaining to be reappraised regarding the taxonomy of nonmarine Cretaceous ostracods of China, for example, before they can be applied to biostratigraphy. Such problems become apparent using the example of Ye (op. cit.), who, on the one hand cited *Cypridea (Cypridea)* cf. *longispina*, while at the same time (op. cit., Text-fig. 1, drawing) refigured "*Longispinella longispina* (Peck 1941)", having been correctly identified as far as evident from the drawing.

Differential diagnosis: Leaving aside the single robust pair of spines, *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979) differs from most taxa described here in its broad alveolar furrow and strongly developed alveolar ridge, in being strongly inequivalve with distinct dorsal overreach of the larger LV, and the larger valve's anterocentral to anterolateral perpendicular ridge and sulcus. *Cypridea* ex gr. *alta* is also strongly inequivale but clearly differs in being rather rectangular than subtriangular in lateral outline, in having a weaker rostrum and alveolus, a very distinct and strong dorsal ridge and a small and short alveolar furrow.

Paleoecology: As for the genus.

Faunal association (see Text-fig. 11 also): In the Lakota Formation: with *Theriosynoecum fittoni* (Mantell 1944) [see Sames 2011a, this theme issue], *Cypridea (Pseudocypridina) pied-*

monti (Roth 1933), *Cypridea (Pseudocypridina) laeli* Sohn 1979, *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, *Cypridea (Pseudocypridina) setina* (Anderson 1939), representatives of the family Darwinulidae Brady and Norman 1889, and representatives of the Trapezoidellidae Sohn 1979: *Trapezoidella trapezoidalis* (Roth), *Limnocypridea? morrisonensis* (Roth 1933).

In the Cedar Mountain Formation: with *Cypridea* ex. gr. *alta* Wolburg 1959, *Cypridea (Pseudocypridina) setina* (Anderson 1939), *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, representatives of the family Darwinulidae Brady and Norman 1889 (*Alicenula?* sp.).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available; as for this study, see Text-fig. 11):

North America:

+ Chilson Member of the Lakota Formation (corresponding to L1 informal interval after Way et al. 1998), Early Cretaceous, southern Black Hills, South Dakota, U.S.A. (Sohn 1979; and this study, Text-fig. 2, locs. 1, 3)

+ Fuson(?) Member of the Lakota Formation (corresponding to L2 and L3 informal interval after Way et al. 1998)

+ upper part of the Yellow Cat Member of the Cedar Mountain Formation north of Moab east-northeast of the Ringtail Mine, Utah, U.S.A. (this study, Text-fig. 2, loc. 10)

+ [lower] Lakota Formation on old road on north side of Fall River 3.2 miles east of 1940 city limit of Hot Springs, southern Black Hills, South Dakota, U.S.A. (Peck and Craig 1962, loc. D286 therein)

+ [lower] Lakota Formation, SW1/4 sec. 15, T 8 S., R. 4 E., Flint Hill quadrangle, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 30; Peck and Craig 1962, loc. D432 therein)

+ Cloverly Formation, north side of Baldwin Creek, approximately 4 miles NW of Lander, sec. 9, T. 33 N., R. 100 W. Mt. Arter SE quadrangle, Wyoming, U.S.A. (Craig 1961, loc. 21 therein)

+ Cloverly Formation, northwest end of Lander anticline, about 2 miles north of Lander, NW 1/4, sec. 12, T. 2 S., R. 2 E., Lander NW quadrangle, Wyoming, U.S.A. (Craig 1961, loc. 22 therein)

+ Cloverly Formation, Lower Cretaceous, approximately 3 miles southwest of Lander, about halfway between the roads in Squaw Creek and Middle Fork of the Popo Agie River, in sec. 15, T. 33. N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck 1951, loc. 33 as equivalent to Craig's 1961, loc. 95P)

+ Cloverly Formation, north side of Baldwin Creek 4 miles northwest of Lander, Fremont County, in sec. 9, T. 33 N., R. 100 W., Mt. Arter SE quadrangle, Wyoming, U.S.A. (Peck and Craig 1962, loc. 658P therein)

+ Cloverly Formation, southeast flank of Rawlins uplift northeast of Rawlins, MW1/4 sec. 6, T. 21 N., R. 86 W., Rawlins quadrangle, Carbon County, Wyoming, U.S.A. (Peck and Craig 1962, loc. 954P therein)

+ Kootenai Formation, along road 1 mile southwest of Griffin and about 14 miles southeast of Great Falls, in T. 18 N., R. 4 E., Montana, U.S.A. (type locality of the species, Peck 1941, loc. 23 therein and equivalent to Craig 1961, loc. 62aP therein)

Questionable occurrence:

Asia:

+ Lower Cretaceous deposits of China (Ye 1994).

Stratigraphic range in North America: As inferred from the faunal assemblage with *Cypridea (Pseudocypridina) setina*, *C. (P.) piedmonti* and *C. (P.) laeli* (Late?) Berriasian to Hauterivian(?).

Stratigraphic range outside North America: Lower Cretaceous (China)?

Subgenus ***Pseudocypridina*** Roth 1933 **emend.** Sylvester-Bradley 1949, **emend.**

v**Pseudocypridina piedmonti* gen. et sp. nov. – ROTH 1933, pp. 404-405, pl. 48, figs. 7a-h.
Cypridea piedmonti (Roth) comb. nov. – HARPER and SUTTON 1935, p. 625, pl. 76, figs. 12-15.
Langtonia setina sp. nov. – ANDERSON 1939, p. 305, pl. 12, figs. 7a, b; pl. 13, figs. 12a,b.
Cypridea (Pseudocypridina) setina rectidorsata subsp. nov. – SYLVESTER-BRADLEY 1949, p. 147, fig. 24.
Cypridea (Pseudocypridina) setina setina (Anderson) – SYLVESTER-BRADLEY 1949, p. 146.
Cypridea (Pseudocypridina) Roth – SWAIN 1961 in Moore, p. Q242.
Cypridea (Pseudocypridina) – KNEUPER-HAACK 1966, p. 187.
?*Cypridea granulosa* (Sowerby) syn. *Cypridea fasciculata* – ANDERSON 1971, p. 63.
?*Cypridea (Pseudocypridina) laeli* sp. nov. – SOHN 1979, p. 16, pl. 3, figs. 1-13, 24-25, 32; pl. 7, fig. 1; pl. 8, figs. 26-30.

Type-species (monotypy): Pseudocypridina piedmonti Roth 1933, Lakota Formation (Lower Cretaceous), South Dakota, U.S.A.

Diagnosis (emended): Relatively large *Cypridea* (up to 2 mm maximum length) with LV>RV overlap. Outline subovoid or suboblong to rounded pentagonal. Rostrum poorly to moderately developed, short and with its apex well-rounded. Alveolus consisting of a weak to almost absent alveolar notch and a short, weakly defined or even absent alveolar furrow. Cyathus crescent and indistinct. Surface finely and weakly punctate, rarely smooth. With or without nodes, with or without small scattered tubercles the latter being always smaller than the combined diameters of two puncta and usually occurring in antero- or posterodorsal areas, and/or ventral ridges. Never with large spines or tubercles, sometimes with nodes. Anterior cardinal angle at larger LV usually indistinct. Several scattered normal pores of 1-2μm diameter.

Note: The diagnosis is compiled after Swain 1946, Sylvester-Bradley 1949, and Sohn 1979 as well as emended and supplemented.

Remarks: A comprehensive list of many species that have been included within *Cypridea (Pseudocypridina)* can be found in Sohn (1979, p. 14-15). However, it is not the purpose of this paper to deal with a detailed revision of the subgenus and therefore, only taxa described and/or discussed herein are listed in the synonymy of this subspecies.

Harper and Sutton (1935, see synonymy on p. 625 therein), without any comment however, already considered this subgenus to be congeneric with *Cypridea*. Martin (1940) reduced all this far existing *Cypridea*-genera and subgenera (*Ulwellia* Anderson 1939, *Langtonia* Anderson 1939, *Morinina* Anderson 1939, *Cyamocypris* Anderson 1939) to the synonymy of *Cypridea*, comprising *Pseudocypridina* Roth 1933. In his revision of *Cypridea*, Sylvester-Bradley (1949) differs between the genus *Cypridea sensu lato*, comprising all the mentioned taxa as subgenera, and *Cypridea sensu stricto=Cypridea (Cypridea)*, thus being another subgenus of *Cypridea* Bosquet 1852. He (Sylvester-Bradley 1949, p. 127 and 146) quotes *Langtonia* to be a junior synonym of *Pseudocypridina*, considering the absence of punctation as insufficient to distinguish the two and states that Anderson's genotype of *Langtonia* (i.e., *Langtonia setina*) is also referable to *Pseudocypridina*. This view has been adopted by most authors (e.g. Wolburg 1959, Moore 1961, Sohn 1969, 1979, Horne and Colin 2005), including Anderson himself (e.g. Anderson 1962, 1971, 1985, Anderson and Bazley 1971), although not by all (e.g. Neustrueva 1989).

To review whether all the subgenera of *Cypridea* s.l. are considered valid and useful is not the purpose of this paper and will have to be analyzed and discussed elsewhere. In its current status, the subgenus *Pseudocypridina* Roth represents a morphotype that is relatively easy to identify and presumably represents a group of phylogenetically closer related taxa.

The assignment of *Cypridea (P.) laeli* Sohn 1959 to this subgenus is slightly questionable. While matching most diagnostic characters of *Pseudocypridina*, *Cypridea (P.) laeli* differs in having a relatively broad and deeply incising alveolar notch and a broad rostrum.

Leaving nodes or tubercles aside that are considered taxonomically insignificant, *Cypridea granulosa* (Sowerby 1836) syn. *Cypridea fasciculata* (Forbes 1855) according to Anderson (1971) well fits into this subgenus with respect to overall shape, development of rostrum, alveolus, and cyathus as well as the degree of valve inequality, a fact to be considered in future research.

Stratigraphic range: Lower Cretaceous (Berriasian) to Upper Cretaceous.

Geographic distribution: All continents, except Australia and Antarctica (no data).

Paleoecology: Presumend salinity tolerance as for the genus *Cypridea*.

Cypridea (Pseudocypridina) laeli Sohn 1979 **cf. C. (P.) moneta** Kneuper-Haack 1966, **emend.**
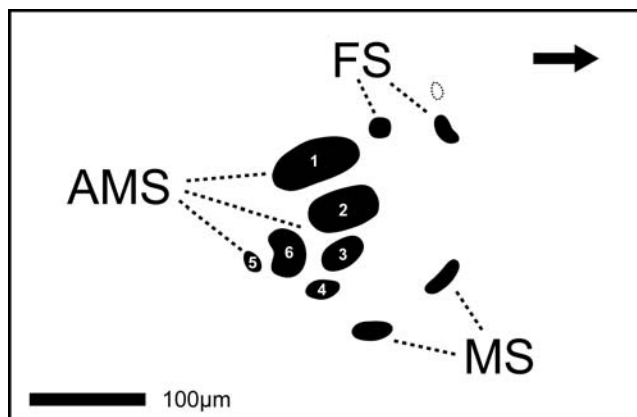Plate 6, Figures 1-15

v*Cypridea (Pseudocypridina) laeli* sp. nov. – SOHN 1979, p. 16, pl. 3, figs. 1-13, 24-25, 32; pl. 7, fig. 1; pl. 8, figs. 26-30.
v?*Cypridea (Pseudocypridina) moneta* sp. nov. – KNEUPER-HAACK 1966, p. 189, pl. 46, Fig. 21a-c.
?*Cypridea (Pseudocypridina) piedmonti* (Roth) – LI and ZHAO 1984, p. 191, pl. 2, figs. 4-6.
?*Cypridea (Pseudocypridina)* cf. *piedmonti* (Roth) – LI and ZHAO 1984, p. 191, pl. 2, figs. 1-3.
Cypridea (Pseudocypridina) laeli Sohn – SWAIN 1999, p. 120, pl. 12, figs. 41-44 [refigured from Sohn 1979].

TEXT-FIGURE 12
Muscle scar pattern in *Cypridea* (*Pseudocypridina*) *laeli* Sohn 1979. AMS: Adductor muscle scars, labeling of single scars adopted from Horne and Colin (2005), FS: Frontal scars (questionable bipartition of anterior scar indicated), MS: Mandibular scars.

?*Cypridea piedmonti* (Roth) – SCHUDACK and SCHUDACK 2009a, fig. 9, No. 18 [figured only].

Material: Few hundred carapaces and many valves, more ore less well preserve, mostly compressed. Samples: LEC 04?, SBCR LAg2, SBCR LAg3*, SBCR DC Strat. Col.?, SBCR LAg6?, SBCR LAh3, SBCR LAh3Tp, EBF 04a, EBF 04a2, EBF 04b?, REKO 04; all believed to be Fuson Member (L2/L3 informal interval after Way et al. 1998) of the Lakota Formation (see Text-fig. 11 also). Text-figure 2, locations 6, 7, 8, 9.

USNM Numbers: USNM 544261-544273.

Dimensions (in mm): Overall length: 1.12-1.23

Own Specimens:
L: 1.12-1.23   H: 0.71-0.75   W: ~0.5

No information in the literature (Sohn 1979).

Type locality and horizon: Lakota Formation at Inyan Kara Creek, Western Black Hills, Crook County, Wyoming NE1/4 sec. 20, and NW1/4 sec. 21, T. 51 N., R. 65 W. (Sohn 1979, p. 16); shale near top of Lakota Formation (Sohn 1979).

Holotype: USNM No. 129 644, figured in Sohn (1979, pl. 3, figs. 10-13) and Sohn (1958, *Pseudocypridina?* n. sp., pl. 1, figs. 9-12).

Diagnosis (emend): Medium sized (>1mm) representative of *Cypridea (Pseudocypridina)* emend. (herein). LV>RV, inequivalve, rounded-subovate outline with convex dorsal margin and strong ventral ridge in the LV. Hinge deeply incised, dorsal furrow very narrow, distinctly slender in dorsal view. Rostrum well-developed and distinctly overreaching the ventral margin in both valves and reaching the ventral outline of the LV as defined by the ventral ridge. Alveolar notch and groove short but distinct. Carapace surface finely punctate, may bear scattered minor tubercles.

Remarks: The emendation became necessary because Sohn (1979) partially integrated optional, taxonomically insignificant

characters (local ornamentation elements in the sense of Sames 2011c, considered ecophenotypic) in his diagnosis (given below), that is the anterodorsal node and the small tubercles, called spinelets by Sohn (1979).

The original diagnosis of Sohn (1979. p. 16) reads: "Subovate, with arched dorsal margin, ventral lateral ridge and dorso-anterior node on larger left valve; right valve with curved irregular ridge subparallel and slightly removed from dorsal margin. Surface finely punctate, with scattered minute spinelets more common on anterior and posterior quarters than on center."

Description: Carapace Shape: Medium sized (>1mm). Carapace strongly rounded-subovate in lateral view, outline defined by the larger LV. Maximum length slightly above mid-height, maximum height at mid-length or slightly in front of it (not defined by anterior cardinal angle), maximum width at 3/5 of length. LV>RV, inequivalve, LV slightly overreaching and overlapping the RV along entire margin. Overreach of LV stronger (moderate to strong) along ventral margin due to ventral ridge.

Anterior margin, almost equicurvate to slightly infracurvate in LV, infracurvate in smaller RV. LV with moderately long straight dorsal part of anterior margin, even longer in the RV, both inclined towards anterior end with about 25-30° in relation to base line. Well-developed carinate rostrum (in both valves Pl. 6, Fig. 4 and 5; see also Sames 2011c) with bending angle of 50-55°, its apex being well rounded in the LV, somewhat acute in the RV. Rostrum clearly separated from ventral margin by moderately broad and incising alveolar notch and distinctly overreaching the ventral margin of both valves and reaching (or sometimes slightly overreaching) the ventral outline of the larger LV. Alveolar furrow absent.

Posterior margin almost equicurvate in the LV, slightly infracurvate in the RV, in the LV ventrally passing into a weakly developed, well-rounded, narrow and crescent (true) cyathus, being very obtuse-angled (circa 150°).

Dorsal outline distinctly convex in LV, slightly convex in RV. Dorsal margin straight, dorsal margin and outline strongly divergent due to strong incision of hinge margin, the latter being moderately inclined towards posterior end with 10-15° (dorsal outline feigns stronger inclination). Anterior cardinal angle very inconspicuous in LV (often almost invisible owing to deeply incised hinge margin), better defined in RV, about 140-145°. Posterior cardinal angle well-rounded and inconspicuous in both valves, about 140°.

Ventral margin straight, almost coincident with ventral outline in smaller RV. Ventral outline of larger LV being strongly divergent from ventral margin and more or less distinctly convex depending on the development of the ventral ridge. Straight ventral ridge well-developed to strongly developed, often swollen (see discussion for details).

Carapace elongated-elliptic and slender in dorsal view (Pl. 6, Fig. 3), acute towards both ends, slightly more towards anterior end. Narrow but deep dorsal furrow with distinctly bulged flanks. Dorsal suture straight, at mid-width position with almost no lateral offset.

Ventral view showing strong ventral ridge (e.g. Sohn 1979, pl. 3, figs. 7) with distinct lateral offset towards LV and a moderate ventral tongue-like overlap of the LV.

Ornamentation: 1. Area-wide ornamentation elements: Whole carapace surface except rostrum and ventral ridge finely punctate with trend to reticulation-like pattern. Puncta often elongated about parallel to the margins outside the central area, ventrally sometimes forming weak striate rows.

2. Local ornamentation elements: Small, shallow and broad tubercles (minute spinelets of Sohn 1979) around the pores common, merely swollen normal pores and being of about 15-20μm diameter. Somewhat stronger and more acute tubercles in most of Sohn's (1979) specimens. All these tubercles seem to occur preferentially in posterolateral and anterolateral areas of the carapace, but also in the dorsolateral to central areas. No specific general pattern distinguishable.

Specimens of Sohn (1979, see discussion below for details) including the holotype having a large (up to about 80μm) anterodorsal node in the LV at position of the anterior cardinal angle (a character considered diagnostic by Sohn, op. cit., see original diagnosis given above). In addition, Sohn's specimens as figured by him (op. cit.; material also personally studied by the present author in Sohn's collection) have swollen, ridge-like protrusions of the margin of the dorsal furrow (running between the dorsal angles) in either both valves or the LV only, often slightly meandering. Ventral ridge also swollen and distorted ("inflated") and sometimes slightly meandering. All latter elements mostly lack any sign of surface characters.

Internal characters: Lophodont hinge with narrow (edged) hinge bar in the larger LV and narrow anterior and posterior teeth in the smaller RV, corresponding groove and sockets developed accordingly. Anterior tooth and socket considerably inclined (~40°) in relation to median hinge element, posterior tooth weakly to not inclined that way.

Inner lamella narrow posteriorly with maximum width in cyathus area, and moderately broad anteriorly with typical widening and straight inner margin above rostrum and alveolus. Interrupted selvage conspicuous.

Muscle scar pattern: Pattern as typical in *Cypridea* (see Text-fig. 6) with the following specifications (Text-fig. 12): dorsal adductor scar 1 largest and elongate; scar 2 parallel to the former but shorter and oblong; scar 3 smaller again, inclined in relation to the dorsal ones and rounded oblong; scar 4 the smallest of the anterior scars and ovate. Posterior scar 6 partially or fully covered in the material and, possibly not very exactly reproduced here, posterior scar 5 the smallest and ovate. Tiny roundish scar (dotted) above the anterior frontal scar.

Morphologic variation: Intraspecific, not ecophenotypically induced, variations mostly concerning slight variations in the lateral outline.

Variations assumed to be of ecophenotypic origin concern the local ornamentation elements: Occurrence or absence of 1) the anterodorsal node in the LV, 2) the tubercles, 3) the ridge-like protrusions of the carapace along the flanks of the dorsal furrow, and 4) the "inflation" or deformation of the ventral ridge (see first paragraph of discussion below for details).

Ontogenetic variation: Few data. The specimen figured on Plate 1, Fig. 10 (A-2? instar) shows the typical lower posterior margin associated with the somewhat stronger inclined posterior and hinge margins.

Dimorphism: Not identified with high confidence, but presumed to occur. Presumed females (Pl. 6, Figs. 1-3, 6, 13) stronger rounded and higher in lateral view and somewhat wider in dorsal view; presumed males (Pl. 6, Figs. 7, 9) more elongate-elliptic in lateral view and more slender in dorsal view. See also Sohn (1979, presumed females: pl. 3, figs. 1-9, 24-25 – same as in pl. 7, fig.1, pl. 8, figs. 26-30; presumed males: pl. 3, figs. 10-13).

Discussion: Taxonomic remarks: The taxonomy of *Cypridea (Pseudocypridina) laeli* Sohn 1979 has been problematic, because Sohn (op. cit.) had chosen an ecophenotype with strong morphologic peculiarities as the holotype, i.e., a specimen with an anterodorsal node, the ridge-like dorsal protrusions ("curved irregular ridge" of Sohn 1979), and the small tubercles, all considered of ecophenotypic origin (see Sames 2011c under the respective terms for explanation). Leaving the said characters out of consideration, the morphology of Sohn's specimens is that of the specimens described here. This statement is also supported by the fact that Sohn's specimens derive from one locality and horizon only (Sohn 1979). The strong ventrolateral ridge should not be considered diagnostic because there are also specimens of *C. (P.) piedmonti* with stronger developed ventral ridge (Sohn 1978, pl. 6, figs. 5, 10, 12, 21 for example) but otherwise clearly different from *C. (P.) laeli* (see differential diagnosis below). The present author's samples derive from three localities in the eastern Black Hills area (Lawrence and Meade counties of South Dakota) from many horizons (see Text-fig. 11 also), all of which, however, seem to derive from the same up to 10 m thick unit mainly comprising of claystones that may represent a large paleolake.

Possible closer phylogenetic relations of *C. (P.) laeli* to the associated and anteceding North American taxa–if there are some, this species might have been newly immigrated–have to be investigated further (continuous stratigraphic data necessary). This species resembles *C. (P.) piedmonti* at first glance only, but differs in detail, particularly in development of rostrum and alveolus (see differential diagnosis below). For that reason, its integration into the subgenus *Pseudocypridina* might also have to be discussed, because representatives of this subgenus typically have a more inconspicuous alveolar notch and a weaker developed rostrum.

As already noted by Sohn (1979), *C. (P.) laeli* resembles the *Cypridea fasciculata*-group, which is herein renamed *Cypridea granulosa*-group (see below), and the *Cypridea alta*-group of Wolburg (1959). *C. (P.) laeli* Sohn 1979, however, much more resembles the *Cypridea alta*-group with regard to its broad alveolar notch and the well-developed rostrum that is not almost attached to the ventral margin as is the case in the *Cypridea granulosa*-group. The occurrence and distribution pattern of small nodes, node-like tubercles or small tubercles (spinelets of Sohn 1979) as used by previous authors (e.g. Wolburg 1959, Sohn 1979, Schudack 1994) to distinguish between taxa are not considered taxonomically significant herein at all.

Cypridea (Pseudocypridina) laeli Sohn 1979 is definitely not a younger variation of *C. (P.) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979, but a separate lineage not

very closely related to the latter. Although *C. (P.) laeli* starts to set in later stratigraphically and only occurs in the upper, but not necessarily considerable younger part, of the Lakota Formation (Fuson Member?, see remarks to stratigraphic distribution right below), it does not replace *C. (P.) piedmonti* and distinctly differs in some characters (see above and differential diagnosis below).

Discussion of synonymy: Cypridea (Pseudocypridina) laeli Sohn shows strong similarities to *Cypridea (Pseudocypridina) moneta* Kneuper-Haack 1966 including *C. (P.) moneta logronana* Kneuper-Haack 1966. Although Kneuper-Haack (op. cit.) discussed similarities of her taxa to *C. (P.) piedmonti* (Roth)–*Cypridea (P.) laeli* Sohn 1979 had, of course, not yet been described at that time–all characters described by her, i.e., particularly the broadly-ovate lateral outline with the rounded cardinal angles and very inconspicuous posterior cardinal angle, the well-marked rostrum with the small but distinct alveolar notch do not match *C. (P.) piedmonti* (Roth) very well. The figures of Kneuper-Haack (1966, drawings, pl. 46, figs. 21a-c, 23) are misleading with respect to the surface ornamentation insofar that smooth specimens are shown. Kneuper-Haack (1966, p. 189) states that the surface of her specimens of *C. (P.) moneta* and *C. (P.) moneta longronana* is "smooth or with weak to stronger dimples [i.e., puncta]". As apparent from Kneuper-Haack's material (now in possession of Ulla Schudack, Freie Universität Berlin, Institut für Geologische Wissenschaften, Fachrichtung Paläontologie, Berlin, Gemany), the representatives of this *C. (P.) moneta* are punctated and the feigned smoothness of some specimens is due to preservation or diagenesis.

If *Cypridea (P.) moneta* Kneuper-Haack 1966 prooves to be a junior synonym of *C. (P.) laeli* Sohn 1979, priority would have to be given to the former, i.e., the oldest available name.

In a footnote to her foreword, Kneuper-Haack (1966, p. 167) has stated that after completion of her work (manuscript completed December 1960, that is long before the actual printing), among others, the comprehensive article of Wolburg (1959) was published, including many new taxonomic data. Kneuper-Haack (1966), therefore, concluded that many of her taxa could be assigned to one of Wolburg's (1959) taxa or groups and that many of her (Kneuper-Haack 1966) new species and subspecies would be mere "subspecies or mutants" (op. cit.; better: varieties) of Wolburg's (1959) taxa. After start of the printing, it was just possible to include some of the new data as footnotes (Kneuper-Haack 1966). *Cypridea (Pseudocypridina) laeli* Sohn 1979 and *C. (P.) moneta* Kneuper-Haack 1966 show strong affinities to the *Cypridea fasciculata*-group (synonym to *C. granulosa* according to Anderson 1971) of Wolburg (1959).

Cypridea (Pseudocypridina) cf. *piedmonti* of Li and Zhao (1984, pl. 2, figs. 1-3) has a distinct alveolar notch and furrow and more overall similarities to *Cypridea (Pseudocypridina) laeli* Sohn 1979 than to *C. (P.) piedmonti*. The attribution is, however, uncertain since the available figures alone are not significant enough to confirm it. The identification of *Cypridea (Pseudocypridina) piedmonti* of Li and Zhao (1984, pl. 2, figs. 4-6) cannot be confirmed as well for the same reasons, and, thus, the synonymy remains questionable. From the few characters apparent from the figures of the latter species, the specimens would have more similarities to *C. (P.) laeli* Sohn than

C. (P.) piedmonti (Roth), if they belong one of these species at all.

Cypridea piedmonti (Roth 1933) of Schudack and Schudack (2009a) is probably better to be assigned to *Cypridea (P.) laeli* Sohn 1979, but either assignment is somewhat uncertain due to the preservation of the specimens.

Remarks as for stratigraphic distribution: As for the stratigraphy, *Cypridea (P.) laeli* seems to be restricted to the upper part of the Lakota Formation (Fuson? Member), and therefore is a potential index fossil to correlate the beds of the Fuson Member (L2/L3 informal interval after Way et al. 1998). It can be used to correlate the eastern Black Hills sections (Text-fig. 2, locs. 6 to 9) as well as the Lakota Formation of the Western Black Hills (Sohn 1979, loc. 5).

The exact stratigraphic distribution of *C. (P.) laeli* in the eastern Black Hills (see Text-fig. 11, samples with question mark) is difficult to determine, because many of the samples (claystone) contain well-preserved but mostly compressed and broken specimens. Thus, it is sometimes difficult to distinguish *C. (P.) laeli* from *C.(P.) piedmonti* under the Light-Microscope, and numerous SEM-photographs from every sample are necessary.

Differential diagnosis: Cypridea (Pseudocypridina) laeli Sohn differs from *C. (P.) piedmonti* (Roth) syn. *C. (P.) henrybelli* Sohn in being more ovate in lateral outline and a bit larger in trend. More important is the better developed rostrum in the former, which is broader and longer than in the latter and distinctly overreaches the ventral margins. In addition, the alveolar notch is considerably deeper and broader in *C. (P.) laeli* and the rostrum is not (almost) attached to the ventral margin.

Apart from that, *C. (P.) laeli* is clearly distinguishable from other taxa dealt with here. Taxa of *Cypridea (Pseudocypridina) setina* as remaining representative of this subgenus entirely devoid of ornamentation elements with a smooth carapace surface. The other taxa are different in several characters: *Cypridea obesa* has a very weakly developed rostrum and an almost absent alveolar notch and furrow, and is strongly obese. *Cypridea nitidula* has a subtriangular lateral outline and a distinct cyathus-like protrusion.

The remaining taxa are strongly different (see there) and cannot be confused with *C. (P.) laeli*.

Paleoecology: As for the genus; freshwater if the synonymization with *Cypridea piedmonti* of Schudack and Schudack (2009a) from the Spanish Hauterivian-Barremian freshwater associations is correct.

Faunal association (see Text-fig. 11 also): In the Lakota Formation with *Theriosynoecum pahasapensis* (Roth 1933) [see Sames 2011a], *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* Sohn 1979, representatives of the family Darwinulidae Brady and Norman 1889, and representatives of the Trapezoidellidae Sohn 1979, that is, *Trapezoidella trapezoidalis* (Roth), *Limnocypridea? morrisonensis* (Roth 1933).

Stratigraphic and geographic distribution: (Stratigraphic terms follow the most recent terminology available):

North America:

+ Fuson Member(?) of the Lakota Formation, Lower Cretaceous, eastern Black hills, Lawrence and Meade Counties, South Dakota, U.S.A. (this study, Text-fig. 2, locs. 7, 8, 9)

+ Lakota Formation near top [Fuson Member?], Inyan Kara Creek – near Corral Creek, western Black Hills area, NE1/2 sec. 20 and NW1/4 sec. 21, T. 51 N., R. 65 W., Crook County, Wyoming, U.S.A. (Text-fig. 2, loc. 5 in Sohn 1979)

Questionable occurrence:

North America:

+ Fuson Member(?) of the Lakota Formation (L2? informal interval after Way et al. 1998), Lower Cretaceous, eastern Black Hills, Meade County, South Dakota, U.S.A. (this study, Text-fig. 2, loc. 6)

Europe:

+ Middle Enciso Group, Lower Cretaceous, northeastern Spain, Iberian Chains, Sierra de los Cameros, "Upper Purbeck" according to Kneuper-Haack (1966); Valanginian, Early Hauterivian to Barremian (after and Schudack and Schudack 2009a)

+ Iberian Chain, eastern Spain Early Cretaceous (Schudack and Schudack 2009a) designated *Cypridea piedmonti* therein):

- middle and upper Enciso Group of the eastern Cameros sub-basin, eastern Spain, Hauterivian to Barremian

- Torrelapaja Formation, Central Iberian Ranges, eastern Spain, Hauterivian to Barremian

- Polacos Formation, Maestrazgo sub-basin, eastern Spain, Early Hauterivian

- Artoles Formation, Maestrazgo sub-basin, eastern Spain, Barremian

Asia:

+ Tungulu Group, Lower Cretaceous, Xinjiang Autonomous Region, northeastern China

Stratigraphic range in North America: Lower Cretaceous, as deduced from similarity to *C. (P.) moneta* Kneuper-Haack 1966 (after and Schudack and Schudack 2009a): (Valanginian) Early Hauterivian to Barremian.

Stratigraphic range outside North America: If synonymous with *Cypridea moneta* Kneuper-Haack 1966 typically for Early Hauterivian to Barremian assemblages of the Iberian Chain, eastern Spain (Schudack and Schudack 2009a, designated *Cypridea piedmonti* Sohn therein).

Cypridea (Pseudocypridina) piedmonti (Roth 1933) **syn. *C. (P.) henrybelli*** Sohn 1979, **emend.**
Plate 4, Figures 1-15; Plate 5, Figures 1-15

v*Pseudocypridina piedmonti* gen. et sp. nov. – ROTH 1933, p. 404, pl. 48, figs. 7a-h.
Cypridea piedmonti (Roth) comb. nov. – HARPER and SUTTON 1935, p. 625, pl. 76, figs. 12-15. – CRAIG 1961, p. 45-47, pl. 1, figs. 4, 6, 10 [unpubl.]. – PECK and CRAIG 1962, pl. 2, fig. 3.
non*Cypridea (Pseudocypridina) piedmonti* (Roth) – SWAIN 1946, p. 550, pl. 83, figs. 10-12 [see Swain 1999, p. 123].

Pseudocypridina piedmonti Roth – PECK 1951, p. 319, pl. 48, fig.
  16-20. – PECK 1956, fig. 23.
v*Pseudocypridina piedmonti* Roth – SOHN 1958, p. 123, pl. 1, figs. 5-8.
v*Cypridea?* sp. – SOHN 1958, pl. 1, figs. 13-15, 16.
?*Cypridea (Pseudocypridina) piedmonti* (Roth) – WICHER 1959, p. 47,
  pl. 9, fig. 6.
Cypridea (Pseudocypridina) piedmonti (Roth) – SOHN 1979, p. 15,
  pl. 6, figs. 1-47.
Cypridea (Pseudocypridina) henrybelli sp. nov. – SOHN 1979, pl. 3,
  figs. 14-17; pl. 8, figs. 1-25.
non?*Cypridea (Pseudocypridina) piedmonti* (Roth) – LI and ZHAO
  1984, p. 191, pl. 2, figs. 4-6.
non*Cypridea (Pseudocypridina)* cf. *piedmonti* (Roth) – LI and ZHAO
  1984, p. 191, pl. 2, figs. 1-3.
Cypridea (Pseudocypridina) piedmonti (Roth) – SWAIN 1999, p. 122,
  pl. 7, figs. 29, 30; pl. 8, fig. 19; pl. 13, figs. 5, 19-22 [refigured after
  Roth 1933, Peck 1951, Sohn 1958, 1979].
Cypridea (Pseudocypridina) henrybelli Sohn – SWAIN 1999, p. 119,
  pl. 12, figs. 38-40 [refigured after Sohn 1979].
non*Cypridea piedmonti* (Roth) – SCHUDACK and SCHUDACK
  2009a, fig. 9 No. 18 [figured only].

Material: Several thousand carapaces and valves, moderately
to well-preserved. (#) indicates samples including *C. (P.)
piedmonti* var. *henrybelli*, which only seems to occur in the
lower Lakota Formation (Chilson Member). Chilson and Fuson
Members of the Lakota Formation (see Text-fig. 11 also). Sam-
ples: Lakota Formation: FRCA*?, HSDC1(#), HSDC2(#),
HSDC3(#), HSDC4(#), BCE*, BCE(#), BC5 04, BCB1,
BCB2(#), BC8 04(#), LEC 04, SBCR LAg1?, SBCR LAg2,
SBCR LAg3, SBCR LAg3*(#), SBCR DC Strat. Col., SBCR
LAg6, SBCR LAh2, SBCR LAh3, SBCR LAh3Tp, EBF 04a,
EBF 04a2, EBF 04b, EBF 04b2?. Localities: Text-fig. 2,
locs. 1, 2, 6, 7, 8 and 9.

USNM Numbers: USNM 544235-544260.

Dimensions (in mm): Overall length: 1.03-1.14

Own specimens:

C. (P.) piedmonti var. *henrybelli*
Presumed males
        L: 1.03-1.13   H: 0.61-0.69   W: 0.40-0.480
Presumed females
        L: 1.07-1.21   H: 0.71-0.76   W: 0.49-0.57

C. (P.) piedmonti
Presumed males
        L: 1.06-1.17   H: 0.67-0.71   W: ~0.45
Presumed females
        L: 1.14-1.22   H: 0.74-0.75   W: ~0.58

As given in the literature (various references):

C. (P.) henrybelli not given by Sohn (1979)

C. (P.) piedmonti
        L: ~1.08   H: ~0.72   W: ~0.52

Type locality and horizon: Chilson Member of the Lakota For-
mation, T. 4 N. R. 6 E., Meade County, 3 miles north of
Piedmont, South Dakota, U.S.A. (Roth's 1933 locality, corre-
sponding to Sohn's 1979 fig. 2, locality 8/USGS Mesozoic col-
lection locality: USGS 30998; about corresponding to
Text-fig. 2, locality 8 herein).

Holotype: USNM No. 70 473.

Diagnosis (emend): Rounded-suboblong species of *Cypridea
(Pseudocypridina)*, with moderate reticulation-like punctation
covering the whole surface. Alveolar notch very weak to almost
absent, alveolar furrow almost absent. Weak ventrolateral ridge.
LV barely or not overreaching RV along posterior margin in lat-
eral right view. Generally without local ornamentation ele-
ments, noding common, sometimes with small antero- and
posterolateral tubercles.

Remarks: Sohn's (1979, p. 15) original diagnosis: "A species of
Pseudocypridina with a ventrolateral ridge on left valve, with
few, small (less than twice the diameter of puncta), subdued,
scattered tubercles near end margins" is considered insufficient
for several reasons (see discussion below), and, thus, emended
here.

Description: Carapace shape: Medium sized (>1mm). Carapace
rounded-suboblong in lateral view. Maximum length at about
mid-height, maximum height at anterior cardinal angle (2/5 of
length), maximum width between half and 3/5 of length in both
sexes. Subequivalve, LV>RV, slightly overreaching and over-
lapping the latter along the entire margin except alveolar area.
Overreach of larger LV weaker at posterior margin, sometimes
even not apparent (Pl. 4, Fig. 2).

Anterior margin broad and almost equicurvate with a moder-
ately long straight dorsal part being inclined about 30-35° in re-
lation to base line of carapace (Text-fig. 4). Small tapering
anteroventral rostrum, strongly bending backwards with
50-60°, moderately overreaching the ventral margin, weaker
developed in smaller RV, there being narrower and less promi-
nent. The LV's rostrum also slightly overreaches the ventral
outline. Alveolus small and weakly developed, alveolar notch
narrow and weak. Alveolar furrow barely cognizable in both
valves, being very shallow and broadly triangular and some-
what stronger developed in RV, ventrally delimited by a very
faint alveolar ridge (e.g. Pl. 4, Fig. 1; Pl. 5, Fig. 1).

Posterior margin narrower than anterior one, equicurvate to
weakly infracurvate in larger LV, there passing into an obtuse
and well-rounded 'true' cyathus. Cyathus narrowly crescent, in-
distinct, with an ountline angle of circa 140-145°. Posterior
margin of smaller RV very slightly infracurvate to nearly
equicurvate.

Dorsal outline straight to weakly convex, in both valves slightly
overreaching the straight hinge margin and gently (8-14°) dip-
ping towards posterior end. Anterior cardinal angle rounded but
well cognizable, 135-140°, posterior cardinal angle strongly
rounded and relatively indistinct, even less distinct in smaller
RV, circa 130°.

Ventral margin straight to gently convex, ventral outline convex
in larger left valve through moderately overreaching ventro-
lateral ridge.

Dorsal view elongated-ellipsoid in males, more ovoid in fe-
males, tapering towards both ends, somewhat more tapering to
anterior end. Dorsal suture straight and indented in dorsal view
forming a moderate dorsal furrow with its left flank being
broader and less steep, resulting in a slight lateral offset towards
right valve. Overlap of LV somewhat stronger and arched at
both cardinal angles.

Ventral view shows arched, tongue-like overlap of the larger LV over the right one, with short, slightly concave part in front of the cyathus. Ventral ridge weak to moderately developed and displaced towards left side.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: Surface moderately punctate partially tending towards reticulation except for the marginal regions, the ventral ridge as well as the lateral nodes, if applicable (see local ornamentation elements below). Puncta rounded polygonal (pentangular) to roundish with a diameter of 20-30µm, becoming more elongated towards the margins forming rows parallel to the latter. Several irregularly scattered normal pores of 1-2µm diameter, almost always between the puncta, rarely having a marginal position inside the puncta.

Surface characters often distorted in the centrodorsal to dorsolateral regions of both valves, especially in these regions below anterior cardinal angle and anterior part of hinge margin (Pl. 5, Fig. 4). This involves lateral flattening or even a weak recess of the carapace in this area. The cause of this character remains unknown thus far. Speculatively, these distortions are caused by tractive force of the organs that connected to the carapace by the dorsal muscle scar group during the soft stage of the molting process. At the nodes, surface characters strongly distorted or missing (i.e., extremely stretched until not visible anymore).

2. Local ornamentation: With or without scattered, usually improminent and very shallow, conic tuberculi developed around the somewhat bigger normal pores in between the puncta, located generally outside the central and centrolateral areas of carapace. Diameter of tubercles observed and documented in the literature (Sohn 1979) always smaller than two times the diameter of a punctum.

Occurrence of circular to perpendicular elliptic true nodes common (these specimens have formerly been designated as a discrete species, *C. (P.) henrybelli* Sohn 1979). The position of the nodes is consistent, being antero- and posterocentrally. Nodation greatly varies in number and intensity (height) of the development of the nodes (Pl. 5, Figs. 1-5, 7-14), but much less in length and width. One, two, three or four nodes can occur, their occurrence not usually being pairwise. Nodes generally stronger developed in the LV and anterocentrally stronger than posterocentrally. The latter does sometimes not apply, if all four nodes are present (Pl. 5, Figs. 11, 12). Consistent succession of intensity of node development realized (Pl. 5, Figs. 7-12), always starting with the a weak anterocentral node in the LV (Pl. 5, Fig. 7) only, followed by a somewhat stronger anterocentral node and a weaker posterocentral one in the LV only (Pl. 5, Fig. 8) or with a weak anterocentral node in the RV also (Pl. 5, Fig. 9), the latter then being weaker than the posterocentral one of the LV. The following stage shows strong anterocentral nodes in both valves, a strong posterocentral node in the LV (about as strong as the anterior one in the RV, both less strong than anterocentral of the LV), and a weak posterocentral node in the RV (Pl. 5, Fig. 10). Last stage is with all four nodes more or less strongly developed, the anterocentral one in the LV being the largest and the other three of about the same size (Pl. 5, Figs. 11, 12), not ruling out some minor variations.

Remarks: The noding pattern in *Cypridea (Pseudocypridina) piedmonti* var. *henrybelli* is nearly the same as that of the recent cytheroid ostracod species *Cyprideis torosa* (Jones). Interestingly, although the former belongs to the superfamily Cypridoidea whereas *Cyprideis torosa* belongs to the Cytheroidea (genus name of the latter might be misleading), the pattern of the primary nodes is nearly the same (four nodes, antero- and posterocentrally), thus raising the question, if the causes of the noding process in both cases might be more or less or exactly the same, which seems to be the case. More research is wanting. There are many more Mesozoic and Cenozoic ostracods showing this pattern of noding. Additionally, like in *Cyprideis torosa*, "erratic" additional nodes can occur in representatives of *Cypridea* (not to confuse with obvious node-like tuberculi *sensu* Sames 2011c, like in *Cypridea verrucosa* Jones or *Cypridea morula* Anderson, for example), that might point to higher environmental stress, like assumed for *Cyprideis torosa* (see Keyser 2005, and references therein).

Internal characters: Hinge lophodont (*sensu* Sylvester-Bradley, 1956). Hinge line about half the length of carapace. Narrow (edged) hinge bar in the larger LV resting on the margin on the margin of the smaller RV (no real corresponding groove developed) combined with narrow anterior and posterior teeth of the RV with corresponding grooves in the LV. Anterior tooth and socket considerably inclined (~40°) in relation to the hinge bar, posterior tooth and socket weakly inclined (~15-20°).

Inner lamella anteriorly moderately broad with typical local widening of inner lamella and straight inner margin in alveolus area, narrow posteriorly with maximum width and straight inner margin in cyathus area. With anterodorsal and posterodorsal flange, stronger developed anteriorly, and, in overall trend, stronger in the LV.

Harper and Sutton (1935, pl. 76, fig. 15, specimen upside down, anterodorsal part broken away, valve filled with sediment) already figured some internal features.

Muscle scar pattern: Unknown.

Dimorphism: Sexual dimorphism assumed herein, as already tentatively mentioned by Sohn (1979, p. 15) for *Cypridea (Pseudocypridina) piedmonti*. Presumed females (e.g. Plate 5, Figs. 1, 2, 10) somewhat higher and ovate in lateral view with a convex dorsal margin and wider (piriform) in dorsal view, presumed males (e.g. Plate 5, Figs. 3, 12, 13) less high and more slender in lateral view with a more straight dorsal margin and elongate-elliptic in dorsal view.

Morphologic variation: Minor, except presumed sexual dimorphism (see above) and noding (see local ornamentation above).

Ontogenetic variation: Few data available. Presumed late ontogenetic stages (A-1 to A-2, Plate 4, Figs. 3, 6?, 7) show somewhat lower posterior margin, a somewhat stronger inclination of the hinge margin and generally follow the morphology of the male(?) dimorph.

Discussion: Sohn's (1979) diagnosis of *Cypridea (Pseudocypridina) piedmonti* (see above) is considered insufficient, because the ventrolateral ridge or the small "scattered tubercles" (op. cit., p. 15) are not diagnostic in general (refer to the description of the genus *Cypridea*, Section 5.2.3, and to Sames 2011c under 'ornamentation'). Additionally, this diagnosis is unsuitable to differ *C. (P.) piedmonti* from *C. (P.) henrybelli* Sohn (see right below), and from *C. (P.) laeli*, respectively (the

latter also having a ventrolateral ridge and can show minor tubercles). The ventrolateral ridge is mostly well visible in Sohn's material (USNM collection).

Cypridea (P.) henrybelli Sohn 1979 is considered a junior synonym of *C. (P.) piedmonti* (Roth 1933) here for several reasons. Sohn's (1979, p. 17) original diagnosis for *C. (P.) henrybelli* is as follows: "Straight backed, with anterodorsal angulation, finely punctate; commonly with distinct nodes at mid-height on anterior and posterior quarters of each valve; sometimes one or both nodes may be smaller, more subdued, or entirely missing on the right valve." However, neither the "straight back" (i.e., the straight dorsal margin) nor the anterodorsal angulation (i.e., a weakly rounded anterior cardinal angle) and least of all, the punctation, are diagnostic. Sohn (1979) did not include a differential diagnosis of his species, but from his plates the inconsistency between his diagnosis and the assigned specimens becomes apparent: Specimens assigned to *C. (P.) piedmonti* by him have the straight dorsal margin and weakly rounded anterior cardinal angle (Sohn 1979, pl. 6, figs. 25, 29/31, 35/36, 42/45), while specimens of Sohn's *C. (P.) henrybelli* have a convex dorsal margin and a strongly rounded anterior cardinal angle (op. cit., pl. 8, figs. 1/3, 10, 21), for example. The nodes are not taxonomically but rather ecophenotypically significant. Altogether, both of Sohn's species do share the same characters except for the nodes, and show similar morphological variations, which are interpreted as intraspecific variations (particularly the presumed sexual dimorphism) herein. In addition, in the authors own samples, *Cypridea (P.) piedmonti* var. *henrybelli* also does always co-occur with *C. (P.) piedmonti*. For unknown reasons, a faunal association of these was not mentioned by Sohn (1979) under his item "geographic distribution" of both taxa.

With reference to noding in *C. (P.) piedmonti* var. *henrybelli*, Sohn (1979, p. 17) already discussed the problem but did not draw the correct consequences (that is, its taxonomic insignificance) and did not yet take ecophenotypy into consideration.

However, Craig (1961, p. 46) already discussed the nodes as variation of the same species (although he did and could not yet explain its origins) for the reasons that all other characters are the same as in the unnoded forms. He also figured a noded specimen and assigned it to *Cypridea piedmonti* (op. cit., pl. 1, fig. 4).

Roth (1933) as well as Harper and Sutton (1935) had considered *C (P.) piedmonti* to occur in the Morrison Formation of the Black Hills area by mistake, later taken over by Peck (1951, 1956). Sohn (1958) demonstrated these to having derived from the Lakota Formation.

Cypridea (Pseudocypridina) piedmonti, as had been described and figured by Swain (1946, p. 550, pl. 83, figs. 10-12), is rather *Cypridea? salvadoriensis* Krömmelbein 1962 as indicated by Swain (1999, p. 123). A personal examination of the specimen (USNM 103 845, author's visit 2006) showed that this specimen is not well preserved and probably a juvenile of a thus far unidentified species of *Cypridea (Pseudocypridina)*.

The specimens designated as *Cypridea?* sp. and figured by Sohn (1958) have been examined by the present author and, although not specifically indicated by Sohn (1979), are representatives of *C. (P.) piedmonti* var. *henrybelli*. The one specimen

of *Cypridea?* sp. as figured by Sohn (1958, pl. 1, figs. 13-15) became the holotype of the latter (Sohn 1979).

Pseudocypridina piedmonti Roth as figured in Peck (1951, 1956) had been considered to be of Late Jurassic age by mistake (taken over from Roth 1933 and Harper and Sutton 1935) and to derive from the Morrison Formation, an interpretation having been challenged and disproven by Sohn (1958). Having not been considered in a later stratigraphic overview of Peck (1959) anymore, this species, then designated *Cypridea piedmonti* (Roth), was mentioned to occur in the Lakota Formation in Peck and Craig (1962), but not listed in the overview of the distribution of species (op. cit., fig. 1).

The specimens assigned to *C. (P.) piedmonti* (Roth) by Wicher (1959) do not belong to this species. Wicher (1959, p. 47) himself stated that his identification were tentative, because the single adult specimen is crumpled and the others are juveniles. The latter, however, Wicher (op. cit.) indicated not to correspond to the specimens of Swain (see above), but to resemble the figures of the North American specimens (i.e., Roth 1933, Harper and Sutton 1935). However, lacking any description, this is considered highly doubtful here because the specimen figured by Wicher (1959, pl, 9, fig. 6) does not show any similarities to *C. (P.) piedmonti* at all, not even a rostrum is visible.

The identification of *Cypridea (Pseudocypridina) piedmonti* of Li and Zhao (1984, pl. 2, figs. 4-6) cannot be confirmed due to the taxonomically insufficient characters visible from the figures.

Cypridea (Pseudocypridina) cf. *piedmonti* of Li and Zhao (1984, pl. 2, figs. 1-3) has a distinct alveolar notch and furrow and more overall similarities to *Cypridea (Pseudocypridina) laeli* Sohn 1979 than to *C. (P.) piedmonti*.

Schudack and Schudack's (2009a, fig. 9, number 19 therein) *Cypridea piedmonti* (Roth 1933) as figured is similar to the North American species, but the identification cannot be fully confirmed from this moderately preserved specimen. It is more likely to be related to *Cypridea (Pseudocypridina) laeli* Sohn 1979 (see there).

Discussion of phylognetic relations: Sohn (1979) related his *Cypridea (Pseudocypridina) henrybelli* to the *parallela*-line of the *Cypridea valdensis-parallela*-group of Wolburg (1959) on the basis of lateral outline and rostrum. All representatives of the latter group, however, have a much stronger (broader) developed rostrum, the alveolar furrow is much more distinct (deeper and longer, reaching up from 1/5 to 3/4 of height), and the hinge margin relatively long and slightly inclined and, therefore, this view is not followed here.

Cypridea (Pseudocypridina) piedmonti syn. *C. (P.) henrybelli* has much more similarities to the *Cyridea granulosa*-group. This group has been first defined as "*fasciculata*-group" by Wolburg (1959), who already pointed out the close relation of *Cypridea fasciculata* (Forbes 1855) to *C. granulosa* (Sowerby 1836) and *C. buxtorfi* Martin 1958. Consequently, Anderson (in Anderson and Bazley 1971, p. 63-68) synonymized *Cypridea fasciculata* with *C. granulosa*, the former being the junior synonym, but retains the two morphologic variants as subspecies of *Cypridea granulosa* for the reason that they do not completely overlap stratigraphically. Kilenyi and Neale (1978. p. 304) also pointed out that all transitions between these two morphotypes

exist but followed Anderson (in Anderson and Bazley 1971) in retaining his subspecies *Cypridea granulosa granulosa* (Sowerby) and *C. granulosa fasciculata* (Forbes 1855) for their biostratigraphic value in the English Purbeck. Schudack (1994, p. 20-21) as well followed this view for the reason that a partial stratigraphic separation is also observable in contemporaneous deposits of NW-Germany, and could detect the transition of one form (subspecies) to the other in her material.

Representatives of the *Cypridea granulosa*-group should be considered to be included into *Cypridea (Pseudocypridina)* because of the fact that they show many diagnostic characters of the latter (see above). Except for the taxonomically insignificant nodes and tubercles, *Cypridea (Pseudocypridina) piedmonti* syn. *C. (P.) henrybelli* shows strong similarities to *Cypridea granulosa* (Sowerby 1836), in general shape, development of rostrum and alveolus, the narrow cyathus, the ventrolateral ridge and the slight valve inequality. More research is necessary for clarification. For the moment it can be stated that *Cypridea granulosa* and representatives of this group could be probable ancestors, or members of an ancestral lineage, of a somewhat younger lineage to which *Cypridea (Pseudocypridina) piedmonti* syn. *C. (P.) henrybelli* belongs to.

Differential Diagnosis: Cypridea (Pseudocypridina) piedmonti (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979 differs from *C. (P.) laeli* Sohn 1979 in being less ovate in lateral outline and a bit smaller in trend. More important is the weaker developed rostrum in the former, which is narrower and shorter than in *C. (P.) laeli* and barely overreaching the ventral margins. In addition, the alveolar notch is inconspicuous to absent (*sensu* Sames 2011c) in *C. (P.) piedmonti* and the rostrum is almost attached to the ventral margin, while in *C. (P.) laeli* the alveolar notch is clearly defined and the rostrum separated from the ventral margin.

Cypridea (Pseudocypridina) piedmonti (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979 is clearly distinguishable from other taxa dealt with here. *Cypridea (Pseudocypridina) setina* as remaining representative of this subgenus shows no ornamentation at all. The other taxa are different in several characters: *Cypridea obesa* has a very weakly developed rostrum and an almost absent alveolar notch and furrow, and is strongly obese while *Cypridea nitidula* has a subtriangular lateral outline and a distinct cyathus-like protrusion.

The remainig taxa described here are totally different in their overall characters and cannot be confused with *C. (P.) piedmonti* (Roth 1933) syn. *C. (P.) henrybelli* Sohn 1979.

Paleoecology: Generally, as for the genus. *Cypridea (P.) piedmonti* var. *henrybelli* is considered to point to low salinity (rapid desalination during moult, e.g. through strong rainfall into ponds) and/or low calcium content as derived from the recent *Cyprideis torosa* (see Keyser 2005, and discussion of ornamentation elements in Sames 2011c). On a long term trend, this may point to more variable (seasonal?) climate with periods of regular heavy rainfall.

Faunal association (see Text-fig. 11, and Sohn 1979): In the Lakota Formation associated with *Cypridea (Longispinella) longispina* (Sohn 1979), *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951. Taxa other than *Cypridea* (with respect to *Theriosynoecum* see Sames 2011a): associated with

Theriosynoecum fittoni (Mantell 1844) and with *Theriosynoecum pahasapensis* (Roth 1933). Also, with representatives of the Darwinulidae Brady and Robertson 1889 (*Alicenula?* sp.) and of the Trapezoidellidae Sohn 1979 (see therein also).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member (both varieties) of the Lakota Formation, Lower Cretaceous, southern Black Hills, South Dakota, U.S.A. (Sohn 1979; and this work, Text-fig. 2, locs. 1-4, 6-9), and Fuson(?) Member of the Lakota Formation (*C. (P.) piedmonti* only, see Text-fig. 11), eastern Black Hill area, South Dakota, U.S.A.

+ Lakota Formation North of Sturgis, eastern Black Hills area (Craig 1961)

Stratigraphic range in North America: Valanginian to Barremian (Sohn 1979, this work).

Stratigraphic range outside North America: Unknown.

Cypridea laevigata-group

Description: Taxa of *Cypridea* with small, reflexed rostrum (bending angle > 45°) and being devoid of any ornamentation elements (area-wide as well as local ones), i.e., having a completely smooth carapace surface. Rostrum small, alveolus inconspicuous, cyathus narrow and lunate. Highly variable in lateral outline.

Remark: This group so far includes all taxa of *Cypridea (Pseudocypridina) setina* (Anderson 1939) and *Cypridea laevigata* (Dunker 1836). Whether all known variants can be included (see synonymy list in Schudack and Schudack 2009b, p. 316-317) or not, remains to be reappraised (see discussion below).

Discussion: Wolburg (1959) had established the *Cypridea setina*-group for those species of the "German Wealden" that are completely smooth and, according to Wolburg (op. cit.), correspond to the diagnosis of the genus *Langtonia* Anderson 1939. In his first attempt to correlate the Upper Purbeck of England to the "German Wealden", Anderson (1962) revised the group and included several of his new subspecies (regarded variants herein) into the group, most of them subspecies names for morphologic variants having previously been described by Wolburg (1959).

In a recent work Schudack and Schudack (2009b) synonymized the species *Cypridea setina* (Anderson 1939) herein *Cypridea (Pseudocypridina) setina* and *Cypridea laevigata* (Dunker 1846) under the oldest valid name: *Cypridea laevigata* (Dunker 1836), because of their identical diagnostic characters. Schudack and Schudack's (2009b) line of argument is comprehensible, their view is, however, not completely followed herein for the reasons given below (see discussion of *Cypridea (Pseudocypridina) setina*). Schudack and Schudack (2009b) also accounted all subspecies of *Cypridea setina* and *C. laevigata* (see Sylvester-Bradley 1949, Anderson 1962, 1971, 1985, Anderson et al. 1967, Kneuper-Haack 1966) as varieties, a view shared by the present author for the reasons that

a), these subspecies are often not well defined or figured and, therefore, irreproducible, and b), rarely have limited stratigraphic or paleogeographic distribution and their stratigraphic ranges partially overlap considerably or several of these even co-occur in one assemblage. A circumstantial revision of *Cypridea setina* s.l. and *Cypridea laevigata* s.l. (according to Anderson's concept, Anderson 1962, Anderson in Anderson, Bazley and Shephard-Thorn 1967, Anderson in Anderson and Bazley 1971), i.e., emphasizing a close analysis of the varieties including sexual dimorphism, genetics of mixed reproduction in the context of morphologic variation within a population, and ontogeny, remains to be conducted.

However, until the details of this problem can be sorted out (see discussion of *Cypridea (P.) setina* below), all variants are pooled here under the *Cypridea laevigata*-group and the morphotype names (species and variants) are retained and dealt with separately, wherever justifiable for practical reasons as to biostratigraphic application.

This paper deals with and discusses two variants of *Cypridea (Pseudocypridina) setina* (Anderson 1939) occuring in the Lower Cretaceous of North America and Europe: *Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949 and *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939).

With respect to the presumed uniqueness (and, thus, diagnostic character) of a totally smooth carapace surface in *Cypridea (Pseudocypridina) setina* and *Cypridea laevigata* among Early Cretaceous taxa of *Cypridea* it has to be mentioned that 1) there is one other smooth species, *Cypridea tenuis* Anderson 1967 from the Upper Weald Clay Formation (Weald sub-basin) and Vectis formation (Wessex sub-basin) of southern England, the closer relations of which are as yet not clear, and 2) there are some data of older representatives of *Cypridea* also showing this character.

In his Master's thesis, Sames (unpublished, Freie Universität Berlin, Germany, 2002, p. 22, pl. 2, figs. 6-8) described two taxa of *Cypridea*, *Cypridea* sp. B and *Cypridea* sp. C, from the Middle Saurian Member (Kimmeridgian, see Sames 2008) of the Tendaguru Formation (Upper Jurassic to Lower Cretaceous of southeastern Tanzania, East Africa), most probably belonging to one species. These forms, considered to represent members of an early lineage of *Cypridea*, are smooth and devoid of any ornamentation elements, and show a distinct cyathus-like protrusion in combination with a weak dorsal furrow, a well-developed and broad rostrum, as well as inconspicuous to almost absent alveolar notch and furrow. No statements concerning possible phylogenetic relationships of the Tanzanian species and *Cypridea (P.) setina* can be made so far, the absence of ornamentation elements in representatives of *Cypridea* may, or may not, be a plesiomorph character a presumed *Praecypridea-Cypridea* lineage (Sames et al. 2010b).

Cypridea (Pseudocypridina) setina (Anderson 1939) **emend.**

?*Cypris laevigata* sp. nov. – DUNKER 1846, p. 59, pl. 13, fig. 25.
*Langtonia setina sp. nov. – ANDERSON 1939, p. 305, pl. 12, figs. 7a, b; pl. 13, figs. 12a,b.
Cypridea setina (Anderson) – MARTIN 1940, p. 287 [comb. nov.].
Cypridea inornata sp. nov. – PECK 1941, p. 301, pl. 44, figs. 33-36.
Cypridea (Pseudocypridina) setina rectidorsata subsp. nov. – SYLVESTER-BRADLEY 1949, p. 147, fig. 24.

Cypridea (Pseudocypridina) setina setina (Anderson) – SYLVESTER-BRADLEY 1949, p. 146.
Cypridea (Pseudocypridina) setina acerata subsp. nov. – ANDERSON 1962, p. 25, pl. 1, figs. 7, 8.
Cypridea (Pseudocypridina) setina camelodes subsp. nov. – ANDERSON 1962, p. 25, pl. 1, fig.6.
Cypridea (Pseudocypridina) setina dotica subsp. nov. – ANDERSON 1962, p. 25, pl. 1, figs. 3, 4.
Cypridea (Pseudocypridina) setina erumna subsp. nov. – ANDERSON 1962, p. 24, pl. 1, fig. 5.
Cypridea (Pseudocypridina) setina fiteriensis subsp. nov. – KNEUPER-HAACK 1966, p. 187, pl. 45, fig. 19.
Cypridea setina bellatula subsp. nov. – ANDERSON 1971, p. 82, pl. 17, figs. 2-3.
Cypridea setina deburghi subsp. nov. – ANDERSON 1971, p. 83, pl. 18, fig. 1.
Cypridea setina florida subsp. nov. – ANDERSON 1971, p. 84, pl. 17, fig. 8.
Cypridea setina pelota subsp. nov. – ANDERSON 1985, p. 31, pl. 11, fig. 10.
?*Cypridea setina acerata* Anderson – LI 1988, p. 1249, textfig. 3, fig. 23.
?*Cypridea setina bellatula* Anderson – LI 1988, p. 1249, textfig. 3, fig. 24.
?*Cypridea setina florida* Anderson – LI 1988, p. 1249, textfig. 3, fig. 22.

Preceding remarks: In a recent publication, Schudack and Schudack (2009b) consider *Cypridea setina* (Anderson 1939) to be a junior synonym of *Cypridea laevigata* (Dunker 1846). Though accepted in priciple, this view is not (yet) followed herein for all cases for the reasons given in the discussion below). Taxa of *C. laevigata* are therefore not included in the synonymy list here (see extended synonymy list in Schudack and Schudack 2009b, p. 316-317).

Lectotype: GSM Mik(M) 535001, formerly GSM 60682, as selected by Sylvester-Bradley (1949), syntypy with *Cypridea setina* var. *setina* (Anderson 1939).

Diagnosis (emend.): Small to medium sized (circa 0.90-1.40mm), considerably variable in lateral outline: rounded oblong or trapezoidal to elongate ovate. Carapace surface smooth, completely devoid of any ornamentation elements. LV>RV, rarely inverse (RV>LV), slightly overreaching the latter along entire margin. Rostrum weakly defined, never overreaching the ventral outline of the larger valve. Alveolar notch distinct but weakly developed, alveolar furrow barely developed, triangular and very shallow. Slight indication of alveolar ridge. Cyathus weakly developed, narrow and strongly rounded ("lunate").

Remarks: The diagnosis has been emended here to point out the highly variable lateral outline, the complete absence of ornamentation elements (which is almost unique among uppermost Jurassic and younger taxa of *Cypridea*–when *Cypridea lavigata* is synonymized with it) and to include inverse and larger forms.

Description - Remarks: The representatives of this species have relatively few and consistent characters, except for their high variation in lateral outline. Since this is interpreted to be related to sexual dimorphism and different reproductive modes (see below and discussion Section 6.2, the *Cypridea (P.) setina* case) as well as that the variants have different stratigraphic and, in particular, different (paleo-)geographic distributions, the variants of particular interest in this study are described separately (refer to the particular variants of this species described below). As for the application aspect, that is biostratigraphic utilization in North America, dealing with the variants and their stratigraphic and (paleo-)geographic separately is hoped to potentially allow a higher biostratigraphic resolution in future studies

once more data regarding their stratigraphic distribution is available from areas outside Central to Western Europe.

Muscle scars: As figured by Wolburg (1959, pl. 5, fig. 16 – refigured in Text-fig. 13 herein) for *Cypridea setina* (Anderson 1939).

Christensen (1968, p. 23, fig. 6) gave a very good photograph of an internal view of a fragment of "*Cypridea* ex gr. *setina* (Anderson)", nicely showing all central, frontal and mandibular scars as well as some dorsal ones. The correct taxonomic designation, however, cannot be verified from this fragment, and in the description Christensen (1968, p. 22) only stated that the "… fragments [are] of more ore less smooth thin valves of a large *Cypridea* with diminutive rostra …".

Dimorphism: Sexual dimorphism conjectured herein (see below fordiscussion). *Cypridea (Pseudocypridina) setina* var. *rectidorsata* is conditionally believed to be the female dimorph capable of parthenogenetic reproduction, whereas *C. (P.) setina* var. *setina* is tentatively assumed to represent a male dimorph (see remarks right below and of the particular variants for details, and also Section 6.2). This conclusion is made by analogy to morphologic trends in the carapace shape of modern cypridoid ostracods–although sexual dimorphism does not have to be apparent in the valve shape of Cypridoideans according to Horne and Martens (1998).

Remarks: Lacking distinct differences in the width of the posterior end of the carapace, one "classic" general trend presented in many older textbooks for Mesozoic to recent ostracods is that female carapaces often are more compact in lateral view, i.e., shorter in relation to the height due to the smaller female reproduction organ. Male carapaces often tend to be more elongate, i.e., having a longer posterior end because of the space needed for the large hemipenises. This, however, might not be the case since in the Cypridoidea males additionally have Zenker's organs (sperm pumps) anterodorsally of the hemipenises, which may lead to higher posterior ends in the males as well.

Taking a mixed reproduction into consideration for (at least some) representatives of *Cypridea* and for *Cypridea (P.) setina* in particular, a parthenogenetic population can only emanate from a sexual population (see Martens et al. 1998b, for example). As given by Anderson (1985), however, *Cypridea (P.) setina* var. *rectidorsata*, tentatively presumed to be the female dimorph herein, starts to occur considerably earlier stratigraphically than all other variants of this species or the probably synonymous *Cypridea laevigata*, particularly those variants believed to be potential male dimorphs of either of these (see below). This should not be possible but may be a problem of inaccuracy in the definition of this variant and could probably be solved by revision of Anderson's material from the Studland to Greenwood faunicycles (cycles Nos. 30-33, Anderson 1985). *C. (P.) setina* var. *setina*, tentatively presumed be the male dimorph herein, is the most dominant variant in deposits from North America, as far as known. If the American populations should mainly represent populations of parthenogenetic females deriving from passively transported eggs, *C. (P.) setina* var. *rectidorsata* and similar morphotypes (see discussion under this variant below) should be the dominant form, and not *C.(P.) setina* var. *rectidorsata*. This problem is not yet satisfactory solved and has to be further investigated.

Morphologic variation: Within *Cypridea (Pseudocypridina) setina*, variation is almost exclusively expressed in the lateral outline as far as known, because only sparse data of the internal features are available. (However, if taxa of *Cypridea laevigata* are considered, this also concerns the position of the rostrum in relation to the ventral margin and its bending angle).

Discussion:

Discussion of synonymy: Then North American species *Cypridea inornata* Peck 1941, also given as *Pseudocypridina inornata* (Peck) or *Cypridea (Pseudocypridina) inornata* Peck in different publications (see stratigraphic and geographic distribution below), is considered synonymous with *Cypridea (Pseudocypridina) setina* (Anderson 1939) here, particularly with *C. (P.) setina* var. *setina* (Anderson). Peck's (1941) description and figures as well as the specimens in his collection (excluding the type material the whereabouts of which are unknown) match the latter species. The specimen figured by Peck (1941, pl. 44, fig. 35) looks different and had been excluded from being synonymous with *C. inornata* by Craig (1961) and assigned to a new species, *Ulwellia crescenti* Craig 1961, which is a *nomen nudum* since Craig's work remained unpublished. Its assignment to *Cypridea (P.) setina* is probable but could not be verified because the material is not in the collection (University of Missouri, Columbia, author's visit, summer 2005). However, in his description of the latter, Craig (op. cit.) designated its surface as "unornamented" (i.e., smooth and lacking local ornamentation elements), and, thus, Peck's (1941, pl. 44, fig. 35) specimen as well as those of "*Ulwellia*" *crescenti* Craig 1961 are likely to belong to *C. (P.) setina*.

Cypridea setina acerata Anderson, *C. setina bellatula* Anderson and *C. setina florida* Anderson as given by Li (1988, as figures in the stratigraphic chart) cannot be taxonomically verified from these drawings and are therefore given with questions mark. Actually, all three forms given in Li (op. cit.) look quite different from *Cypridea (Pseudocypridina) setina* in general and its variants in each case: in outline and development of rostrum and alveolus.

The question, whether *Cypridea setina* (Anderson 1939) and *Cypridea laevigata* (Dunker 1846) belong to the subgenus *Pseudocypridina* or may represent a separate lineage, remains to be investigated further.

The specimen (topotype) of *Cypridea (Pseudocypridina) setina* var. *florida* Anderson 1971 figured in Anderson (1985, pl. 18, fig. 17, right view of carapace) was photographed in unfavorable orientation and does not show the rostrum this way. Illustrations (drawings) in Anderson 1962 (pl. 1, fig. 8, holotype as designated by Anderson 1971) and Anderson (1971, pl. 17, fig. 8) are preferable in this case. The same applies to *Cypridea (Pseudocypridina) setina* var. *deburghi* Anderson 1971, also unfavorably figured in Anderson (1985, pl. 6, fig. 7) and not showing the rostrum. The holotype as pictured in Anderson (1971, pl. 18, fig. 1 in right lateral view) does show the rostrum.

Discussion of retention and preference of Cypridea (P.) setina to C. laevigata: Schudack and Schudack (2009b), in their special note on the taxonomic inconsistencies of *Cypridea setina* Anderson 1939 (op. cit., therein) and *Cypridea laevigata* (Dunker 1846), pooled these two species and their subspecies under the name with priority, *Cypridea laevigata*, and designated all known subspecies of both species varieties of the lat-
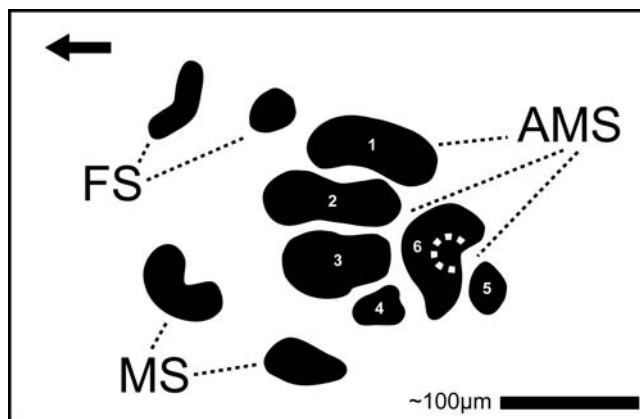
ter. While the latter is accepted here (see above), the two variants described here are listed under the *Cypridea laevigata*-group to draw attention to the problem but are still given under the species name *C. (P.) setina* for the following reasons (I thank David J. Horne, QMUL, London, UK, for pointing out important details on this issue):

1) The central issue concerning this problem is, how much variation one considers to be "admissible" in one species, which in this case concerns large shape differences in lateral outline and the development (position and degree of reflexion) of the rostrum, not having yet taken sexual dimorphism and ontogenetic stages into consideration. Even if *Cypridea (P.) setina setina* (Anderson 1939) and *Cypridea laevigata* (Dunker 1846) are synonymized, a large number of subspecies (variants herein; see synonymy list in Schudack and Schudack 2009b) remains, some of which still might justify separate species. Depending on the taxonomic concept, the whole group could be regarded as a valid genus–*Pseudocypridina*. Altogether, this problem cannot be completely sorted out before the range of morphological variation in the taxa from English Purbeck and Wealden assemblages has been (re-)studied.

2) *Cypridea (P.) setina* is the by far more widely used name, regarding the frequency of usage in general, in biostratigraphy and by most authors from different countries, and, thus, it is applied here, particularly to avoid confusion when dealing with the stratigraphic literature. *Cypridea (P.) setina* is a very useful index taxon for biostratigraphic correlation since its stratigraphic range is relatively restricted (upper Berriasian to [lower, if not synonymized with *C. laevigata*] Valanginian), and since it is easily identifiable by the absence of all ornamentation elements, which is unique among almost all representatives of *Cypridea*. Until the taxonomic problems have been solved (see above), it appears best for the their stratigraphic application in general to regard all taxa as representatives of the *Cypridea laevigata*-group and not giving the unjustified impression of taxonomic or stratigraphic precision by using the subspecies or variety names, respectively.

If, as Schudack and Schudack (2009b) have suggested, *Cypridea (Pseudocypridina) setina* (Anderson 1939) is a junior synonym of *Cypridea lavigata* (Dunker 1846) and all varieties of both species are included (see synonymy list in Schudack and Schudack 2009b) the stratigraphic range of what could be the called the *Cypridea laevigata*-group would be extended to the top of the Valanginian, with a total range of upper Berriasian to uppermost Valanginian: *C. (P.) setina* (Anderson 1939) occurs from the Studland to Rye faunicycles (cycles Nos. 30 to 47) of Anderson (1985), which is upper Berriasian to lower Valanginian according to Hoedemaeker and Herngreen (2003). *Cypridea laevigata* (Dunker 1846) occurs from the Mupes to Cuckfield faunicycles (cycles Nos. 35 to 67) of Anderson (1985), being upper Berriasian to uppermost Valanginian according to Hoedemaeker and Herngreen (2003). However, as indicated in fig. 5 of Anderson (1985, p. 12), the maximum abundance of the latter species is Mupes to Lydd faunicycles (cycles Nos. 35 to 49), that is upper Berriasian to lower/middle Valanginian (Hoedemaeker and Herngreen 2003), which is approximately the same as the distribution of *Cypridea (P.) setina*.

Nonetheless, as the North American example presented here shows, some distinguishable varieties (as described below)

TEXT-FIGURE 13
Muscle scar pattern in *Cypridea (Pseudocypridina) setina* (Anderson 1939) redrawn after Wolburg (1959, pl. 5, fig. 16). The sketch shows the pattern of the central muscle scar field of the RV. AMS: Adductor muscle scars, labeling of single scars adopted from Horne and Colin (2005), the spot in scar No. 6 as indicated here by the white dotted line was outlined by Wolburg (1959) and not specifically explained. FS: Frontal scars, MS: Mandibular scars.

seem to be stratigraphically applicable (with caution), besides the fact that an application of either the varieties or the *Cypridea laevigata*-group as a whole is a step forward as to the nonmarine Lower Cretaceous stratigraphy in North America (see Sames et al. 2010a). The estimated Upper Berriasian maximum ages of the Lakota Formation based on the occurrence of species of *C. (P.) setina* var. *setina* seem to be supported and confined by associated charophytes (Martín-Closas, Sames and Schudack research in progress).

Differential diagnosis: Cypridea (Pseudocypridina) setina is different from all other species discussed here in having a totally smooth carapace that is devoid of any ornamentation elements.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation, Lower Cretaceous, southern Black Hills Area (Text-fig. 2, locs. 1, 3 and 5), South Dakota, U.S.A. (this work)

+ Yellow Cat Member of the Cedar Mountain Formation, Lower Cretaceous, Text-fig. 2, loc. 10, Utah, U.S.A. (this work)

As for older reports of occurrences in North America, the forms were formerly designated and published under *Cypridea inornata* Peck 1941, *Pseudocypridina inornata* (Peck 1941) or *Cypridea (Pseudocypridina) inornata* Peck 1941:

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, southeastern Black Hills area, South Dakota, U.S.A. (Peck 1951, Peck and Craig 1962)

+ Chilson Member of the Lakota Formation, Lower Cretaceous, Black Hills area, (Peck 1951, Peck and Craig 1962)

+ Lakota Formation [Chilson Member], Lower Cretaceous, southern Black Hills area, South Dakota, U.S.A. (Sohn 1979)

+ Cloverly Formation, Early Cretaceous, southeastern flank of Rawlins uplift, Wyoming, U.S.A. (Peck and Craig 1962)

+ Kootenai Formation, Lower Cretaceous, Montana, U.S.A (Peck 1941)

Europe:

+ Studland to Rye faunicycles (cycles Nos. 30 to 47) of Anderson (1985) as equivalent to upper Purbeck Group (Durlston Formation) to Lower Wealden Supergroup (Ashdown and lowermost Wadhurst formations of the Hastings Group), that is *Cypridea propunctata* to *Cypridea menevensis*-subzones of Horne (1995); upper Berriasian to lower Valanginian according to Hoedemaeker and Herngreen (2003)

+ *Cypridea setina*-zone of Clements (1993) "Upper" Purbeck; Broken – Shell Limestone Member, *Unio*-Member and Upper 'Cypris' Clays and Shales Member of the Durlston Formation, type-section of the Purbeck-Limestone Group, Durlston Bay, Swanage, England, UK; upper Berriasian according to Hoedemaeker and Herngreen (2003)

+ Middle to upper "German Wealden 3 to 5 (W3 to W5)" after Wolburg (1962), NW Germany; upper Berriasian to lower Valanginian according to Hoedemaeker and Herngreen (2003)

+ North Celtic Sea and Fastnet Basin, offshore southern Ireland, occurrence of *C. (P.) setina dotica*, Early Valanginian, Ainsworth et al. (1987)

+ lower 'Purbeck' of the southern Dobrudja, Romania, Zavoiana Member of the Amara Formation *Cypridea dunkeri* to *Cypridea granulosa* zone, Berriasian (Stoica 2007)

+ Cabretón Beds of the Urbión Group Northern Spain, Iberian Chains, Sierra de los Cameros, "Middle Purbeck" according to Kneuper-Haack (1966)

Stratigraphic range in North America: Upper Berriasian to lower Valanginian as inferred from the distribution in Europe; maximum distribution up to upper Valanginian (if considered junior synonym of *Cypridea laevigata*).

Stratigraphic range outside North America: Europe (best data): Upper Berriasian to lower Valanginian; up to uppermost Valanginian if considered junior synonym of *Cypridea laevigata*).

Cypridea (Pseudocypridina) setina var. rectidorsata Sylvester-Bradley 1949
Plate 7, Figures 9-10, 13-15

pars*Langtonia setina* sp. nov. – ANDERSON 1939, p. 305, pl. 12, figs. 7a [non 7b].
Cypridea inornata sp. nov. – PECK 1941, p. 301, pl. 44, figs. 33-34, 36, [35 questionable].
Cypridea (Pseudocypridina) setina rectidorsata subsp. nov. – SYLVESTER-BRADLEY 1949, p. 147, fig. 24.
pars*Pseudocypridina inornata* (Peck) – PECK 1951, p. 319, pl. 48, figs. 10, 11 [non pl. 48, figs. 8, 9].
Cypridea inornata? Peck – SOHN 1958, pl. 1, figs. 17, 18.
Cypridea rectidorsata Sylvester-Bradley – WOLBURG 1959, p. 293, pl. 5, fig. 1.

Cypridea (Pseudocypridina) setina rectidorsata Sylvester-Bradley – ANDERSON 1962, p. 23, pl. 1, fig. 1.
Cypridea rectidorsata Sylvester-Bradley – WOLBURG 1962a, p. 211, pl. 31b, fig. 8.
Cypridea setina (Anderson) – WOLBURG 1962a, p. 211, pl. 31b, fig. 12.
non*Cypridea setina* (Anderson) – WOLBURG 1962a, p. 211, pl. 31b, figs. 9-11 [*C. setina setina*].
Cypridea setina rectidorsata – ANDERSON and BAZLEY 1971, p. 84, pl. 16, fig. 9.
Cypridea (Pseudocypridina) inornata (Peck) – SOHN 1979, p. 15-16, pl. 3, figs. 18-23 [non pl. 7, figs. 2-4].
Cypridea setina ssp. 1 – STOICA 2007, p. 11, pl. 11, figs. 1-3; pl. 12, figs. 1-3; textfig. 72a, b.

Material: Few carapaces, questionably in samples of the Lakota Formation BCE, FRCA, and ARCR CHz1 (Text-fig. 2, loc. 1, 3 and 5, Chilson Member of the Lakota Formation). Some carapaces from the Cedar Mountain Formation (upper part of the Yellow Cat Member), sample PS 1a-70, Text-fig. 2, loc. 10. See Text-fig. 11 also.

USNM Numbers: USNM 544282, 544283, 544286-544288.

Dimensions (in mm): Overall length: 1.05-1.24

Own Specimens
(Presumed females)
     L: 1.05-1.24   H: 0.63-0.73   W: ~0.48

As given in the literature (various references):
(Presumed females)
     L: ~1.05   H: ~0.68   W: ~0.50

Type locality and horizon: Chilcomb Down No. 1 Borehole, Hampshire, at 1710 ft., Hastings Group of the Wealden Supergroup.

Holotype: Actual number is In. 39180 (BMNH, London) as selected by Sylvester-Bradley (1949).

Diagnosis: A variety of *C. (P.) setina* with rounded-oblong carapace, dorsal outline and margins straight in both valves. Anterior and posterior margins of about equal height, inclination of dorsal margin and outline weak to barely cognizable.

Description: Carapace Shape: Small to medium sized. Carapace shape in lateral view oblong, well-rounded and slightly to barely tapering towards posterior end. Maximum length slightly below middle height, maximum height at 2/5 of length (at anterior cardinal angle), maximum width at or hardly behind middle length. LV>RV, weakly inequivalve, LV slightly overreaching RV along entire margin except for the point and posterior part of rostrum and alveolus. Overreach (excluding cyathus) most distinctive at anterodorsal margin, posterodorsal margin including posterior hinge margin; at ventral margin stronger overreach due to ventral ridge of LV. Overlap moderate at anterior and posterior margins, strong at ventral margin. No overlap at hinge margin area.

Anterior margin broad and slightly infracurvate, ventrally prolongating into a well-developed rostrum, with a moderately long, slightly convex dorsal part. Rostrum moderately bending backwards with about 45°, its point slightly overreaching the ventral margin of the smaller RV, but hardly ever reaching the ventral outline of the LV. Alveolus weakly developed, with slightly incising and narrow alveolar notch in LV, somewhat

stronger developed in RV. Alveolar furrow hardly present in both valves, triangular, very shallow and rather developed as a weak anteroventral lateral flattening, being ventrally delimited by a very weak alveolar ridge.

Posterior margin equicurvate to slightly infracurvate, only slightly narrower than anterior margin. LV's posterior margin ventrally passing into a narrow crescent cyathus being obtuse and rounded.

Dorsal margin partly incised (hinge), dorsal outline about straight in both valves, weakly inclined towards posterior end with an angle of about 45°. Anterior cardinal angle rounded, obtuse but relatively well-marked, about 140-145°. Posterior cardinal angle well-rounded, gently passing into posterior margin and, thus, its apex is difficult to position, about 145-150°. Hinge margin straight to slightly concave, about 1/3 of total carapace length, overreached by both cardinal angles.

Ventral margin straight to slightly concave; convex venter in larger LV feigned through weakly developed overreaching ventral ridge.

Carapace elongated-ovate (drop-shaped) in dorsal view, tapering towards anterior end. Hinge margin weakly incised, forming a shallow furrow of moderate width and with nearly no lateral offset of the dorsal furrow.

Ventral overlap strong and moderately convex. Ventral view showing diffusely delimited ventral ridge of overlapping LV. A vague outline of alveolar furrows and alveolar ridges visible in ventral view.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: None. Surface smooth with very few simple pores of 1-2μm diameter, barely to detect; evenly scattered with a mean distance of about 70μm to each other.

2. Local ornamentation elements: None, totally absent.

Internal characters: Not well known. Free inner lamella of moderate width anteroventrally, posteroventrally being narrow (cf. sketches of Sylvester-Bradley 1949, fig. 25).

Muscle scar pattern: As figured by Wolburg (1959, pl. 5, fig. 16 – refigured in Text-fig. 13 herein) for *Cypridea setina* (Anderson 1939).

Morphologic variation: Some variation in dorsal outline, which can be straight to slightly convex.

Ontogenetic variation: No data.

Dimorphism: Sexual dimorphism present as tentatively assumed herein in analogy to morphologic trends in modern ostracods. *C. (P.) setina* var. *rectidorsata* is considered to be the female dimorph of *C. (P.) setina* var. *setina* herein (see also under dimorphism of the latter taxon below), because it is somewhat shorter and higher, thus appearing more compact (see Section 6.2 also).

Discussion: This variety has not been frequently reported from North America, based on the few published (formerly under the name *Cypridea inornata*) and own data available. From the two samples of the Lakota Formation the occurrence of this variant is questionable, because of the bad preservation. Unquestion-

able is its presence in the Yellow Cat Member of the Cedar Mountain Formation, Utah (see Pl. 7, Figs. 13, 14).

If *Cypridea (Pseudocypridina) setina* (Anderson 1939) and *Cypridea (Pseudocypridina) laevigata* (Dunker 1846) are synonymized (refer to discussion of *Cypridea (P.) setina* above), this has consequences on the stratigraphic distribution of the species. In addition, the following variants of *C. (P.) laevigata* (being regarded subspecies by F. W. Anderson in Anderson et al. 1967) are believed to be synonymous to *C. (P.) setina* var. *rectidorsata* by the present author:

a) *Cypridea (Pseudocypridina) laevigata* var. *hawkhurstensis* Anderson 1967

b) *Cypridea (Pseudocypridina) laevigata* var. *philpottsi* Anderson 1967

c) *Cypridea (Pseudocypridina) laevigata* var. *subquadrata* Anderson 1967

Differential diagnosis: In contrast to *Cypridea (Pseudocypridina) setina* var. *rectidorsata*, *C. (P.) s.* var. *setina* is more elongate (higher L/H-coefficient), has a distinct inclination of the dorsal margin and outline with its posterior margin is distinctly narrower than the anterior one, and thus tapering towards posterior end in lateral view. In dorsal view, it appears very elongate, only slightly tapering towards anterior end.

As for the species *Cypridea (P.) setina* in general (see above), this variety is, likewise, different from other species described here in lacking any ornamentation elements.

Paleoecology: As for the genus.

Faunal association (See Text-fig. 11 also): In the present author's sample ARCR CHz1 (Lakota Formation) associated with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea? minuta* (Peck 1951), *Cypridea obesa* Peck 1951 some representatives of the Darwinulidae: *Alicenula?* sp., and some Ostracoda indet. (Candonidae?). In sample PS2a (Cedar Mountain Formation) associated with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea (Longispinella) longispina* Peck 1941 and *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Yellow Cat Member of the Cedar Mountain Formation, Lower Cretaceous, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10, this study)

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, Calico Canyon south of Buffalo Gap [but NE of the town of Buffalo Gap!] in the SE1/4 sec. 24, T. 6 S., R. 6 E., Custer County, South Dakota, U.S.A. (Peck 1951 loc. 28, as equivalent to Peck and Craig 1962 and Craig 1961, loc. 184P [not Fall River County!])

Europe:

+ Studland to Battle faunicycles (cycles Nos. 30 to 40) of Anderson (1985) as equivalent to upper Purbeck Group (Durlston Formation) to Lower Wealden Supergroup (Ashdown and low-

ermost Wadhurst formations of the Hastings Group), that is *Cypridea propunctata* subzone of Horne (1995); upper Berriasian to lowermost Valanginian according to Hoede-maeker and Herngreen (2003)

+ lower 'Purbeck' of the southern Dobrudja, Romania, Zavoiana Member of the Amara Formation *Cypridea dunkeri* to *Cypridea granulosa* zone, Berriasian (Stoica 2007)

Questionable occurrence:

North America:

+ Chilson Member of the Lakota Formation, Lower Cretaceous, Buck and Devil's canyons, southern Black Hills Area (Text-fig. 2, locs. 1 and 2), South Dakota, U.S.A. (this work)

Stratigraphic range in North America: As inferred from the English Purbeck/Wealden: upper Berriasian to lower Valanginian; maximum distribution up to upper Valanginian (if synonymized with *Cypridea laevigata*).

Stratigraphic range outside North America: Upper Berriasian to lower Valanginian. Up to upper Valanginian if *Cypridea (Pseudocypridina) setina* is synonymized with *Cypridea (Pseudocypridina) laevigata* (Dunker 1846), some variants of which are also very oblong and similar to *C. (P.) setina* var. *rectidorsata* (refer to discussion right above).

Cypridea (Pseudocypridina) setina var. setina (Anderson 1939)
Plate 7, Figures 1-8, 11-12

pars*Langtonia setina* sp. nov. – ANDERSON 1939, p. 305, pl. 12, fig. 7b [not 7a].
Cypridea inornata sp. nov. – PECK 1941, p. 301, pl. 44, figs. 33, 34, 36 [35 questionable].
Cypridea (Pseudocypridina) setina s*etina* (Anderson 1939) comb. nov. – SYLVESTER-BRADLEY 1949, p. 146.
pars*Pseudocypridina inornata* (Peck) – PECK 1951, p. 319, pl. 48, figs. 8, 9 [non pl. 48, figs. 10, 11].
Cypridea inornata? Peck – SOHN 1958, pl. 1, figs. 17, 18.
Cypridea setina (Anderson) – WOLBURG 1959, p. 294, pl. 5, figs. 2, 15-17. – WOLBURG 1962a, p. 211, pl. 31b, figs. 9-11.
Cypridea (Pseudocypridina) setina setina (Anderson) – ANDERSON 1962, p. 24, pl. 1, fig. 2.
non*Cypridea setina* (Anderson) – WOLBURG 1962a, p. 211, pl. 31b, fig. 12 [*C. setina rectidorsata*].
Cypridea setina setina (Anderson) – ANDERSON and BAZLEY 1971, p. 85, pl. 17, fig. 10.
pars*Cypridea (Pseudocypridina) inornata* (Peck) – SOHN 1979, p. 15-16, pl. 7, figs. 2-4 [non pl. 3, figs. 18-23].
v*Cypridea setina setina* (Anderson) – ANDERSON 1985, p. 31, pl. 5, fig. 9 [lectotype].
Cypridea setina ssp. 2 – STOICA 2007, p. 113, pl. 11, figs. 4-7; pl. 12, figs. 4-6.

Material: About 200 carapaces and few valves, moderately to well-preserved. Samples: PS 1a-70, PS 2a, SKM 060705 (=PS 2c), Yellow Cat Member of the Cedar Mountain Formation, Text-fig. 2, loc. 10. FRCA*, FRCA, BC5 04, ARCR CHz1, Chilson Member of the Lakota Formation. Few specimens from the Peck Collection, University of Missouri, Columbia (MO), U.S.A.

USNM Numbers: USNM 544274-544281, 544284-544285.

Dimensions (in mm): Overall length: 0.95-1.41

Own specimens:

Presumed males

L: 1.05-1.24	H: 0.63-0.73	W: ~0.31

As given in the literature (various references):

Presumed males

L: 0.95-1.41	H: 0.60-0.91	W: ~0.50

Type locality and horizon: Chilcomb Down No. 1 Borehole, Hampshire, at 1710 ft., Hastings Group of the Wealden Supergroup, UK.

Lectotype: GSM Mik(M) 535001, formerly GSM 60682, as selected by Sylvester-Bradley (1949), Anderson collection, BGS Headquarters, Keyworth, UK.

Diagnosis: A variety of *C. (P.) setina* with elongated-rectangular carapace tapering towards posterior end, dorsal outline and margins moderately inclined. Anterior margin higher than posterior one. Elongated-ellipsoid in dorsal view, weakly tapering towards anterior end.

Description: Carapace Shape: Small to medium sized. Carapace shape in lateral view elongated-rectangular, well-rounded and slightly tapering to posterior end. Maximum length slightly below middle height, maximum height at 2/5 of length (at anterior cardinal angle), maximum width at or hardly behind middle length (anterior of 3/5 of length). LV>RV, LV slightly over-reaching RV along entire margin except for point and posterior part of rostrum, and alveolus. Overreach (excluding cyathus) most distinctive at anterodorsal margin, posterodorsal margin including posterior hinge margin, and ventral margin, additionally overreached by ventral ridge of LV. Overlap moderate at anterior and posterior margins, strong at ventral margin, weak at hinge margin area Pl. 7, Fig. 4).

Anterior margin broadly infracurvate with long straight dorsal part. Rostrum short, broad and strongly tapering, with bending angle of 45°, its point slightly overreaching the ventral margin of the smaller RV, but hardly ever reaching the ventral outline of the LV. Alveolus weakly developed, alveolar notch narrow and slightly incising in LV, somewhat stronger developed in RV. Alveolar furrow hardly present in both valves, triangular, very shallow and rather developed as a weak anteroventral lateral flattening, being ventrally delimited by a very weak alveolar ridge.

Posterior margin weakly infracurvate, slightly stronger in smaller RV, both distinctly narrower than anterior margin. LV's posterior margin ventrally passing into a narrow crescent cyathus, strongly obtuse and rounded, sometimes hardly visible in left lateral view.

Dorsal margin partly incised (hinge), dorsal outline of LV gently convex, nearly straight. RV usually less convex, straight in most cases. Dorsal margin and outline inclined in relation to the base line, with an angle of about 15°. Anterior cardinal angle rounded, obtuse but relatively well-marked, about 140-145°. Posterior cardinal angle well-rounded, gently passing into posterior margin and thus its apex being difficult to determine, about 150-155°. Hinge margin straight to slightly concave, about 1/3 of total carapace length, overreached by both cardinal angles.

Ventral margin straight to slightly concave; convex venter in larger LV feigned through weakly developed overreaching ventral ridge.

Carapace elongated-ellipsoid in dorsal view, gently tapering towards anterior end. Hinge margin weakly incised, forming a shallow furrow of moderate width. Sinuous appearing overlap in dorsal view due to convex overlap of LV over RV at the cardinal angles and flange of RV overlapping the LV along hinge margin. Strong ventral overlap, moderately convex.

Ventral view showing diffusely delimited weak ventral ridge in overlapping LV. In ventral view, a vague outline of the alveolar furrows and ridges is visible.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: Surface smooth with very few simple pores of 1-2μm diameter, barely to detect; about evenly scattered with a mean distance of about 70μm to each other.

2. Local ornamentation elements: None, absent.

Internal characters: Not observed or described. Sylvester-Bradley (1949, fig. 25) figures two sketches of internal views of *C. (P.) setina rectidorsata* (dealt with under this variety herein, see above).

Muscle scar pattern: As figured by Wolburg (1959, pl. 5, fig. 16 – refigured in Text-fig. 13 herein) for *Cypridea setina* (Anderson 1939).

Morphologic variation: Minor. Mostly concerning the more or less narrowly curved posterior outline (probably an ontogenetic effect, see below).

Ontogenetic variation: Few data available (see Pl. 7, Fig. 10). In comparison with the adults, the juveniles have a less higher posterior margin (hinge margin inclination more than 10°) which also seems to be less well-rounded in earlier instars, i.e., more distinctly infracurvate, and also show a smooth carapace surface (no ornamentation elements at all). In addition, the juvenile specimens tend have a less relative height (higher L/H-coefficient), being combined with higher values of the anterior (around 150°) and posterior cardinal angles as well as a lower angle of inclination of the straight dorsal part of the anterior margin (around or below 20°).

Dimorphism: Sexual dimorphism tentatively assumed herein. *Cypridea (Pseudocypridina) setina* var. *setina* is believed to be the male dimorph (see Section 6.2 also).

Discussion: Cypridea (P.) setina var. *setina* is the more common variant known thus far in North America (as given in the stratigraphic and geographic distribution below).

Cypridea inornata Peck 1941 in Peck (op. cit.) and Sohn (1979) are assigned to this variant because they perfectly match Anderson's (1939, pars; 1985, pl. 5, fig. 9, lectotype) specimens. One well preserved specimen from Peck's collection is figured here (Pl. 7, Fig. 2). Both specimens have been personally studied by the present author.

Cypridea setina ssp. 2 of Stoica (2007) is assigned to this variant because of its striking similarity in outline.

If *Cypridea (Pseudocypridina) setina* (Anderson 1939) and *Cypridea (Pseudocypridina) laevigata* (Dunker 1846) are

synonymized (refer to discussion of *Cypridea (P.) setina* above), this has consequences on the stratigraphic distribution of the species. In addition, the following variants (being regarded subspecies by F. W. Anderson in Anderson et al. 1967) of *C. (P.) laevigata* are believed to be synonymous to *C. (P.) setina* var. *setina* by the present author:

a) *Cypridea (Pseudocypridina) laevigata* var. *fairlightensis* Anderson 1967

b) *Cypridea (Pseudocypridina) laevigata* var. *laevigata* (Dunker 1846)

c) *Cypridea (Pseudocypridina) laevigata* var. *leonardi* Anderson 1967

d) *Cypridea (Pseudocypridina) laevigata* var. *wadhurstensis* Anderson 1967

Differential diagnosis: In contrast to *Cypridea (Pseudocypridina) setina* var. *setina*, *C. (P.) s.* var. *rectidorsata* is less elongate and more oblong (lower L/H-coefficient), barely shows an inclination of the dorsal margin and outline, the anterior and posterior margins are of about equal height, and thus not tapering towards posterior end. In dorsal view, it appears elongated-ovate, distinctly tapering towards anterior end.

As for the species *Cypridea (P.) setina* in general (see above), this variant is different from other species dealt with here in lacking any ornamentation elements.

Paleoecology: As for the genus.

Faunal association (see Text-fig. 11 also): In the Lakota Formation: with *Theriosynoecum fittoni* (Mantell 1944) [see Sames 2011a], *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979), *Cypridea? minuta* (Peck 1951), representatives of the family Darwinulidae Brady and Norman 1889 (*Alicenula?* sp.), and representatives of the Trapezoidellidae Sohn 1979: *Trapezoidella trapezoidalis* (Roth), *Limnocypridea? morrisonensis* (Roth 1933). As given in the literature (Sohn 1979, Lakota Formation), additionally associated with *Trapezoidella rothi* Sohn 1979. In the Cedar Mountain Formation: with *Cypridea* ex. gr. *alta* Wolburg 1959, *Cypridea (Longispinella) longispina* Peck 1941, *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* Loranger 1951, representatives of the family Darwinulidae Brady and Norman 1889 (*Alicenula?* sp.).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation, Lower Cretaceous, southern Black Hills Area (Text-fig. 2, locs. 1, 3 and 5), South Dakota, U.S.A. (this work)

+ Yellow Cat Member of the Cedar Mountain Formation, Lower Cretaceous, Text-fig. 2, loc. 10, Utah, U.S.A. (this work)

As for the occurrence in North America, the taxa *of Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939) were formerly designated and published under *Cypridea inornata* Peck 1941, *Pseudocypridina inornata* (Peck 1941) or *Cypridea*

(Pseudocypridina) inornata Peck 1941 from the following locations:

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, Calico Canyon south of Buffalo Gap [but NE of the town of Buffalo Gap!] in the SE1/4 sec. 24, T. 6 S., R. 6 E., Custer County, South Dakota, U.S.A. (Peck 1951 loc. 28, as equivalent to Peck and Craig 1962 and Craig 1961, loc. 184P [not Fall River County!])

+ Minnewaste Limestone Member of the Lakota Formation, Lower Cretaceous, partings in exposure of Skyline Drive, east of Hot Springs, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 29)

+ [Chilson Member of the] Lakota Formation, Lower Cretaceous, north side of Fall River Road 3.2. miles southeast of 1940 city limits Hot Springs, Fall River County, South Dakota, U.S.A. (Peck 1951, loc. 30 as equivalent to Peck and Craig's 1962 loc. D286 and Craig's 1961 loc. 435P; about loc. 3, Text-fig. 2 herein)

+ Lakota Formation [Chilson Member], Lower Cretaceous, Black Hills area, Sohn's (1979, fig. 2 therein) loc. 2, Lawrence County (about equivalent to loc. 7, Text-fig. 2 herein), and Sohn's (1979, fig. 2 therein) localities 13 to 18, Fall River County, South Dakota, U.S.A.

+ Cloverly Formation, Early Cretaceous, southeastern flank of Rawlins uplift, about 1/4 mile north of unimproved road bypassing Rawlins on the northeast, in the NW1/4 sec. 6, T. 21 N., R. 86 W., Rawlins quadrangle, Carbon County, Wyoming, U.S.A. (Peck and Craig 1962, loc. 954P)

+ Kootenai Formation, Lower Cretaceous, along the road 1 mile southwest of Griffin, about 14 miles southeast of Great Falls, T. 18 N., R. 4 E., Montana, U.S.A (Peck 1941, loc. 23)

Europe:

+ Lulworth to Battle faunicycles (cycles Nos. 34 to 40) of Anderson (1985) as equivalent to upper Purbeck Group (Durlston Formation) to Lower Wealden Supergroup (Ashdown and lowermost Wadhurst formations of the Hastings Group), that is *Cypridea propunctata* subzone of Horne (1995); upper Berriasian to lowermost Valanginian according to Hoedemaeker and Herngreen (2003)

+ lower 'Purbeck' of the southern Dobrudja, Romania, Zavoiana Member of the Amara Formation *Cypridea dunkeri* to *Cypridea granulosa* zone, Berriasian (Stoica 2007)

Questionable occurrence:

North America:

+ Lakota Formation [Chilson Member?], Lower Cretaceous, cut on railroad through a Lakota hodgeback just north of Sturgis, South Dakota, U.S.A. (Craig 1961, loc. 416P as also given in the locality catalog of Peck at the University of Missouri, Columbia)

Note: This sample comes from "a shale below the upper thick massive sandstone" (locality catalog Peck, as also given by Craig 1961, p. 8) being questionably equivalent to the mudstones sampled by the present author at localities 6, 8 and 9 (Text-fig. 2 herein) and believed to be equivalent to the Fuson

Member of the Lakota. Since Craig's (1961) material is not in Peck's collection, the species identification cannot be verified, and all the present author's samples from the same area and (tentatively) assumed same stratigraphic level do not contain any specimens of varieties of *Cypridea (P.) setina* nor the *Cypridea laevigata*-group.

Stratigraphic range in North America: Upper Berriasian to lower Valanginian as inferred from the English Purbeck/ Wealden) distribution in Europe; maximum distribution up to upper Valanginian (if synonymized with *Cypridea laevigata*).

Stratigraphic range outside North America: Europe (best data): Upper Berriasian to lower Valanginian. Up to upper Valanginian if *Cypridea (Pseudocypridina) setina* is synonymized with *Cypridea (Pseudocypridina) laevigata* (Dunker 1846), some variants of which are also very oblong and similar to *C. (P.) setina* var. *setina* (refer to discussion right above).

Cypridea alta-group

Remarks: This species group has been first defined by Wolburg (1959), who erected the new species *Cypridea alta* Wolburg 1959 and included the taxa *Cypridea alta alta* Wolburg 1959, *Cypridea alta formosa* Wolburg 1959 and *Cypridea alta wicki* Wolburg 1959. According to Wolburg (op. cit., p. 262), this group is characterized by a relatively high carapace [i.e., low L/H-coefficient], a distinct punctation, and a short but well-developed rostrum.

Additionally, representatives of this group are all strongly inequivalve, have a distinct but small, weakly obtuse-angled cyathus with a narrow basis, and bear a strong ventral ridge. Most conspicuous character is the strong ridge- or bulge-like overreach (dorsal ridge of Sames 2011c) of the larger valve (LV mostly) along the dorsal margin (e.g. Text-fig. 7/B), often covering the cardinal angles and being highest in the anterior part of the dorsal margin. For this reason, the name *Cypridea alta*-group (from Latin *altus* – high), although other species included (see below) might be considered more characteristic.

Based on the diagnostic characters, this group includes the following species in the present author's view (species in alphabetical order):
- *Cypridea alta alta* Wolburg 1959 (dorsal ridge weak)
- *Cypridea alta formosa* Wolburg 1959
- *Cypridea alta wicki* Wolburg 1959
- *Cypridea dolabrata angulata* (Martin 1940) syn. *Cypridea angulata* Martin 1940
- *Cypridea dolabrata dolabrata* (Anderson 1939)
- *Cypridea dolabrata kingsclerensis* Anderson 1971
- *Cypridea inaequalis* Wolburg 1959

Questionable (as found in the literature, to be further investigated):
- *Cypridea amisia* Wolburg 1959
- *Cypridea cymerata* Musacchio 1971 (inverse!)
- *Cypridea dromedarius* Krömmelbein 1962
- *Cypridea latiovata* Hou 1958 [*Cypridea (Cyamocypris) latiovata* therein]
- *Cypridea ludica* Musacchio 1971
- *Cypridea mundula* Lyubimova 1956
- *Cypridea triangula* Liu 1959 (with distinct alveolar ridge!)
- *Cypridea verrucosa* Jones 1878

- *Cypridea valdensis valdensis* (Sowerby 1836) as figured by
    Anderson (1985, pl. 8, fig. 18)
- *Cypridea zhijiangensis* Zhao 1978

Cypridea ex gr. *alta* described here (see below) has the strongest similarities to *Cypridea alta formosa* Wolburg 1959 syn. *Cypridea alta wicki* Wolburg 1959 (spines of the latter considered taxonomically insignificant, see Sames 2011c).

Stratigraphic range:

- *Cypridea alta* Wolburg 1959, "German Wealden", 'Wealden 3' and 'Wealden 4' (Wolburg 1959), upper Berriasian to lowermost Valanginian after Hoedemaeker and Herngreen (2003)

- *Cypridea dolabrata* (Anderson 1939), Scallop to Hythe faunicycles (cycle No. 29 to No. 46) of Anderson (1985), being middle/upper to lower Valanginian according to Hoedemaeker and Herngreen (2003)

- *Cypridea inaequalis* Wolburg 1959, "German Wealden", upper 'Wealden 2' to 'Wealden 3' (Wolburg 1959), middle Berriasian to upper Berriasian according to Hoedemaeker and Herngreen (2003)

Note: To the best knowledge and investigation of the present author, ostracods of the *Cypridea alta*-group as defined here, particularly showing the strong dorsal ridge and small cyathus in combination with being strongly inequivalve, generally occur in the lower part of the Lower Cretaceous (Berriasian to Valanginian; or older), mainly. Some exceptions, however, do occur: *Cypridea cymerata* Musacchio 1971, [upper?] Hauterivian-Barremian, and *Cypridea valdensis valdensis* (Sowerby 1836), (Valanginian) Hauterivian-Barremian, for example. Owing to the common uncertainties in the age determination of Lower Cretaceous nonmarine deposits, however, this matter has to be further investigated.

Cypridea ex gr. *alta* Wolburg 1959
Plate 8, Figures 1-6

?*Cypridea alta formosa* subsp. nov. – WOLBURG 1959, p. 264, pl. 3, figs. 2, 11, 12.
?*Cypridea alta wicki* subsp. nov. – WOLBURG 1959, p. 266, pl. 3, figs. 2, 11, 12.

Material: Eight carapaces, badly preserved, in part almost "steinkern" preservation.

USNM Numbers: USNM 544289-544293.

Dimensions (in mm): Overall length: 0.86-0.97

Own specimens (RV distinctly smaller):
    L: 0.86-0.97   H: 0.64-0.69   L: ~0.41

Type locality and horizon: Not applicable (yet). Only known from the upper Yellow Cat Member of the Cedar Mountain Formation at one locality (Text-fig. 2, loc. 10), north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A.

Holotype: Not applicable (yet).

Diagnosis: LV>RV, strongly inequivalve. Lateral outline, as given by the LV, inflated ovate, with large, strongly overreaching dorsal ridge in the LV. Small, well-developed cyathus, located distinctly anterior of posterior margin. Rostrum

well-defined, alveolus with short alveolar furrow and distinct alveolar ridge.

Remarks: The taxonomic status of this species is kept open for the reason that only few badly preserved specimens do exist this far. Better material is necessary. Though similarity to known taxa is strong, this could be a true new species. However, with such bad preservation a description of a new species cannot be justified.

Description: Carapace Shape: Small sized (<1mm). General outline, as defined by LV, inflated ovoid in lateral view, dorsal outline somewhat more prominent due to dorsal ridge. LV>RV, strongly inequivalve, outline of LV and RV strongly different. LV: Maximum length at mid-height, maximum height at mid-length. RV: Maximum length slightly below mid-height, maximum height at 2/5 length. Maximum width at about or slightly behind mid-length. Overlap of LV moderate to strong at all margins except hinge margin area. Very strong overreach of LV along hinge margin through dorsal ridge, strong overreach at ventral margin through ventral ridge.

Anterior margin of both valves weakly infracurvate, with a long straight dorsal part, inclined about 30°. Anterior margin ventrally passing into a well-defined rostrum, moderately (about 50°) bending backwards. Alveolar notch well-defined and moderately broad, somewhat less in RV, upwards continuing into a very narrow triangular groove behind the rostrum, separated from the main alveolar furrow by a strong, slightly undulated alveolar ridge. Alveolar furrow triangular and broad, but very short, reaching not higher than 1/4 of maximum height, and relatively shallow. Rostrum, alveolar furrow and alveolar ridge less developed in RV, but still recognizable.

Posterior margin nearly equicurvate, ventrally protruding into a well-developed, weakly obtuse-angled cyathus (circa 110°) in LV, being relatively narrow in its width along the outline.

Dorsal margin of LV strongly convex along hinge margin because of protruding dorsal ridge, anteriorly and posteriorly passing into the respective margins with a slightly concave, nearly straight curvature. LV's cardinal angles masked due to dorsal ridge, position of the anterior one between 1/5 and 2/5 of maximum length, anterior one not truly definable, but definitely located posterior of the dorsal ridge. Dorsal margin of RV straight to slightly convex, weakly inclined (circa 12°) towards posterior end. RV's anterior cardinal angle distinct, circa 140°, its angular point rounded, located between 1/5 and 2/5 of maximum length. Posterior cardinal angle of RV strongly rounded and thus, barely recognizable, circa 150°. Length of hinge margin about 2/5 of total carapace length.

Ventral margin of both valves straight to weakly convex. Moderately convex ventral margin feigned through presence of a well-developed and strongly overreaching ventral ridge at LV.

Carapace outline ellipsoidal in dorsal view, moderately tapering to both ends. Hinge incisure present, forming a moderately deep dorsal furrow with broad flanks; partially covered on the LV by a strong narrow, undulated ridge beginning at the position of the anterior cardinal angles and ending anteriorly of the posterior cardinal angle and dorsal furrow end. Position of dorsal furrow slightly oblique towards RV.

LV strongly convex overlapping the RV in ventral view. LV with moderately protruding, narrow ventral ridge, reaching from posterior alveolar region to anterior cyathus region.

Ornamentation: 1. Area-wide ornamentation elements: Because of weathering, the carapace surface is strongly degenerated and no reliable statement is possible. It is, however, covered with many pustulae that are considered to represent remains of internal (normal) pore fillings. In some specimens, a linear pattern in the ventrolateral and posterolateral regions can be recognized, running subparallel to the outer margins.

2. Local ornamentation elements: Not observed, perhaps due to preservation. No indication for strong elements (nodes, spines, tubercles), thus, the occurrence of these is very improbable. Most probably punctated, better preserved material necessary.

Internal characters: Not observed.

Muscle scar pattern: Not observed.

Morphologic variation: Minor. Most of the slight differences in outline and shape recognizable so far result from preservation and diagenesis (deformation of carapace).

Ontogenetic variation: Not observed.

Dimorphism: No dimorphism recognized.

Discussion: Although the specimens from the Cedar Mountain Formation are more or less badly preserved, most important characters are well-visible, i.e., lateral outline, rostrum, alveolus, cyathus, dorsal and ventral ridges, and the different valves. Owing to the striking similarity of the species described here to *Cypridea alta formosa* Wolburg 1959 syn. *Cypridea alta wicki* Wolburg 1959 (spines/tubercles or node like-tubercles of the latter considered taxonomically insignificant herein) in overall shape and characters, it is assigned to the *Cypridea alta*-group. However, since its surface characters are not visible anymore and, in particular, it bears a strong alveolar ridge, the presence of which has to be verified in the types of Wolburg's (1959) specimens it is not visible in Wolburg's (1959) figures, but in some figures of specimens assigned to *Cypridea alta* in other publications the species described here is not definitely assigned to *Cypridea alta*.

Differential Diagnosis: Cypridea ex gr. *alta* Wolburg distinctly differs from all other taxa described here in its outline, the presence of the strong dorsal ridge and in that it is strongly inequivalve.

The sole other species described here being moderately to strongly inequivalve (lesser than *C.* ex gr. *alta*) is *Cypridea (Longispinella) longispina* Peck 1941 syn. *C. (L.) asymmetrica* (Sohn 1979). The latter, however, differs from *Cypridea* ex gr. *alta* Wolburg 1959 in having a much larger alveolar furrow and no true dorsal ridge, but an overreach of the LV instead, which is a (hollow) protrusion of the dorsal part of the valve.

Paleoecology: As for the genus.

Faunal association (see Text-fig. 11 also): In the Yellow Cat Member of the Cedar Mountain Formation with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939), *Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949, *Cypridea (Longispinella) longispina*

Peck 1941 and *Cypridea* ex gr. *tuberculata* cf. *Cypridea tilleyi* Loranger 1951.

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

+ Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10)

Questionable occurrence: Not applicable (identic forms unknown thus far).

Stratigraphic range in North America: As deduced from the faunal association with *Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939): upper Berriasian to lower Valanginian, up to upper Valanginian if *Cypridea (P.) setina* (Anderson 1939) and *Cypridea laevigata* (Dunker 1846) are synonymized. As deduced from the striking similarity to *Cypridea alta formosa* Wolburg 1959 as occurring in the English Purbeck/Wealden: upper Berriasian to lowermost Valanginian.

Stratigraphic range outside North America: Not applicable.

Cypridea tuberculata-group

Remarks: Eponymous species is *Cypridea tuberculata* (Sowerby 1836). As defined herein, this morphogroup comprises of an inhomogenous combination of not necessarily closely related taxa of *Cypridea* with distinct and more or less strongly developed tuberculation (not to be confused with nodes, the smaller of which are sometimes called "granules", e.g. *Cypridea granulosa*, however, these are in fact swollen node-like tubercles, see definition in Sames 2011c). The tuberculation pattern is, in general, characterized by numerous paired tubercles (i.e., these are arranged oppositely to each other in both valves) that are of about equal size and more ore less evenly distributed on the valve's surface. Alternatively, there are more or less regular patterns of two horseshoe-shaped rows of tubercles covering the anterocentral, centroventral and posterocentral areas (cf. Text-fig. 3), thereby omitting the (central) area where the central muscle scar field is located, and opening towards dorsal margin (centrodorsal). The latter is complemented by anterolateral, ventrolateral and posterolateral tubercles that are irregularly distributed to a greater or lesser extend. In any case, and even if the central- and centrodorsal to dorsolateral regions are omitted, the remaining areas show a regular pattern. Single "erratic" tubercles of the same or smaller size can occur as well as single, central to subcentral larger spines.

Species with such typical tuberculate pattern (cf. also Anderson 1967, p. 239, fig. I/l) are pooled and defined as *Cypridea tuberculata*-group herein and considered to represent a phylogenetic lineage of *Cypridea tuberculata*, including its varieties. Other carapace characters as for *Cypridea tuberculata* are: Lateral outline suboblong, anterior cardinal angle somewhat prominent, rostrum relatively broad and short, alveolar furrow narrow and shallow but distinct and reaching up to 1/3 of height, with alveolar ridge(?), cyathus moderately developed and slightly obtuse thereby possibly including forms such as *Cypridea jonesi* Martin 1940 and *Cypridea aculeata aculeata* (Jones 1885), and *Cypridea comptonensis* Anderson 1967.

However, there are other representatives of *Cypridea* with strongly asymmetrically distributed tubercles and/or spines that

have to be excluded from the *Cypridea tuberculata*-group as defined herein. It is an almost purely descriptive group (except for potentially unrecognized taxa related to *Cypridea tuberculata*) that includes phylogenetically (most probably) not closely related taxa as well as potential ecophenotypes and/or juveniles of other groups. This includes varieties (subspecies) of *Cypridea aculeata* Jones 1885 as designated by Anderson (1967; except *Cypridea aculeata aculeata* Jones) as well as *Cypridea brendae* Anderson 1985, *Cypridea compta* Peck 1951, *Cypridea dequeenensis* Swain and Brown 1964, *Cypridea dunkeri carinata* Martin 1940, *Cypridea hispida* Anderson 1985, *Cypridea lasius* Anderson 1967, *Cypridea marina* Anderson 1967, *Cypridea melvillei* Anderson 1967, *Cypridea warlinghamensis* Anderson 1967, *Cypridea wyomingensis* (Jones 1893), for example. These species also differ in shape, development of rostrum and alveolus, and other characters from the *Cypridea tuberculata*-group.

Concerning tuberculate taxa of *Cypridea*, there is still a lot of taxonomic confusion needing detailed revision that is beyond the scope of this paper. Many more forms have to be included in such a review because many local ornamentation elements designated as "granules" and spines are in fact swollen tubercles, i.e., node-like tuberculi according to Sames (2011c).

Cypridea ex gr. *Cypridea tuberculata* (Sowerby 1836) cf. *Cypridea tilleyi* Loranger 1951
Plate 8, Figures 7-14

non*Cypridea tuberculata* (Sow.) var. *wyomingensis* nov. var. – JONES 1893, p. 386, pl. 15, figs. 5a-b, 6a-b.
non,v*Cypridea tuberculata* var. *gypsumensis* var. nov. – VANDERPOOL 1928, p. 103, pl. 13, figs. 9-12.
non*Cypridea wyomingensis* Jones – PECK 1941, p. 297, pl. 42, figs. 10-17.
non*Cypridea* cf. *C. wyomingensis* Jones – SWARTZ and SWAIN 1946, p. 372, pl. 52, figs. 19-22.
?*Cypridea tilleyi* sp. nov. – LORANGER 1951, p. 2363, pl. 3, fig. 1. – LORANGER 1954, p. 292, pl. 3, fig. 1.
non*Cypridea wyomingensis* Jones – LORANGER 1951, p. 2363, pl. 2, fig. 22. – LORANGER 1954, p. 293, pl. 2, fig. 22. – SWAIN and BROWN 1964, p. 16, pl. 4, fig. 10; pl. 5, figs. 1a-c, textfig. 4b.
non*Cypridea tuberculata langtonensis* Anderson – ANDERSON 1971, p. 88, pl. 13, fig. 4.
?*Cypridea australis* sp. nov. – MUSACCHIO 1971, p. 112, pl. 1, figs. 5, 6; pl. 2, figs. 6, 7; pl. 3, figs. 9, 10.
non*Cypridea (Cypridea) wyomingensis* Jones – SWAIN and BROWN 1972, p. 14, pl. 1, figs. 19-20; pl. 3, fig. 1.
vNew genus undescribed "*Cypridea*" sp. 1 – SOHN 1979, p. 18, pl. 7, figs. 8-12.

Material: Over 100 carapaces and few valves. Samples: BC5 04, BCB1?, BC8 04, Chilson Member of the Lakota Formation, Text-fig. 2, loc. 1. PS 2a, Yellow Cat Member of the Cedar Mountain Formation, Text-fig. 2, loc. 10.

USNM Numbers: USNM 544294-299.

Dimensions (in mm): Overall length: 0.83-0.92

Own specimens:
 L: 0.83-0.92   H: 0.57-0.63   W: ~0.39

As given in the literature (various references):
 L: ~0.90

Type locality and horizon: Not applicable yet.

Holotype: Not applicable. If this proves to be a new species, then to be designated from Sohn's (1979) or material of the present author (to be deposited at the USNM).

Diagnosis: Small sized tuberculate species of *Cypridea* with suboblong outline, well-developed rostrum only slightly bending backwards. Short but deeply incising alveolar furrow being ventrally delimited by a strong alveolar ridge. Well-developed, about right-angled cyathus with distinct limen, and prominent anterior cardinal angle. Surface strongly punctate with deep puncta. Typically bearing a pronounced subcentral robust spine on each valve, and two rows of tubercles in a horseshoe-shaped pattern opening towards dorsal margin.

Description: Carapace Shape: Small sized. General shape of carapace truncated pentagular, nearly oblong. Maximum length between 1/3 and mid-height, maximum height at anterior cardinal angle, between 1/5 and 2/5 of length, maximum width at 3/5 of length. LV>RV, moderately inequivalve. LV slightly overreaching the RV along entire margin; except for venter, where LV bears a ventral ridge that moderately overreaches the ventral margin. Overlap moderate at anterior, posterior and ventral margins, weak at dorsal margin.

Anterior margin broad and slightly infracurvate to nearly equicurvate with short straight dorsal part, the latter being inclined with circa 35-40°. Rostrum broad and short, weakly tapering and with rounded point, slightly bending backwards with circa 20-25° and moderately overreaching the ventral margin while hardly reaching the LV's ventral outline. Alveolus well-developed. Rostrum separated from the ventral margin by a well incising but narrow alveolar notch. Alveolar furrow distinct and well-developed, somewhat less expressed in RV, triangular and short, deeply incised and reaching up to 1/3 of height, with small puncta. Alveolar furrow ventrally delimited by a strong alveolar ridge, which in the smaller RV separates the furrow into two parts, a very small part being below the ridge.

Posterior margin narrower than anterior one and slightly infracurvate, ventrally passing into a well-developed 'true' cyathus that reaches or even slightly overreaches the posterior margin as well as the ventral margin (not outline) of the LV. Cyathus broad, right-angled to weakly obtuse (90-110°), its apex slightly rounded.

Dorsal margin nearly straight, the cardinal angles slightly overreaching it, not coincident with dorsal outline, the latter being slightly convex. Both, dorsal outline and dorsal margin moderately inclined towards posterior end, with about 10-17°.

Anterior cardinal angle well-marked, distinctly protruding in LV and (somewhat less) in RV, 125-135°, weakly rounded. Posterior cardinal angle strongly rounded, 135-140°. Hinge margin length about half total carapace length.

Ventral margin gently convex to straight, ventral outline moderately convex through the well-developed overreaching ventral ridge of in the LV.

Dorsal view elongated-ovoid, slightly tapering towards anterior end. Hinge margin area strongly incised, forming a well-developed dorsal furrow of 80-100µm width, slight lateral offset towards RV, and flattended flanks. Dorsal suture about straight with slight lateral offset towards right valve.

Ventral view showing distinct ridge on the overlapping LV running parallel to its margin. Ventral part of LV weekly striated, 3-4 striae with a width of one punctum diameter; puncta in between them lined up. Overlap along venter gently convex.

Ornamentation: 1. Area-wide ornamentation elements/surface characters: Whole carapace distinctly punctate tending towards reticulation, with round to ovate deep puncta of about 10-15μm diameter in a relatively fine network, except for the areas of the point of rostrum and the cyathus, as well as anterior and posterior area of valve overlap. Dorsal furrow and ventral overlap area also punctate, but with more indistinct (shallower) puncta. Puncta in alveolus area much smaller (< 5μm), distorted (elongated) towards rostrum.

Many irregularly scattered normal pores of 1-3μm diameter and with a mean relative distance of about 30-35μm, always in between the puncta (i.e., surrounded by a group of 3 or 4 puncta).

2. Local ornamentation elements: One pair of large, robust central to centroventral or centrodorsal spines of up to circa 80μm length on each valve, always slightly posterior to mid-length, basal diameter 30-40μm. Spines in more or less opposite position to each other, weakly tapering and slightly bending backwards, point strongly rounded.

Several smaller (20-40μm), conic tubercles of about the same basal diameter (15-20μm) each, with a normal pore going through in center; mainly distributed in two rows around central area (with about 10 tubercles each), forming a horseshoe-shaped pattern opening towards centrodorsal/dorsolateral (central muscle scar) area, with some "erratic" tubercles in between or around it. All of about the same overall size. Some smaller additional tubercles anterolaterally and posterolaterally. The horseshoe-like pattern is often somewhat less recognizable in the RV. Normal pores in center of the tubercles of 1-3μm diameter, somewhat widened at emersion point (apex of tubercle) to 4-5μm.

A few smaller tubercles (5-10μm diameter) at the rostrum and in a row along most of the frontal part of anterior margin of the larger LV, but not on the overlapping part of this valve. Tubercles rarely overreach dorsal and posterior margins, but very often the anterior margin. Alveolus, cyathus, as well as ventral, dorsal (dorsal furrow) and posterior margin areas without tubercles.

Internal characters: Hinge lophodont (Pl. 8, Fig. 14). A straight and smooth ridge with widened sockets anteriorly and posteriorly in the LV fits into appropriate groove and teeth of the RV. Fused zone of inner lamella moderately broad, except for the lower third of height antero- and posteroventrally, where a crescent free part of is developed. Free inner margin only slightly concave, nearly straight, dipping about 30° towards middle of carapace, causing small semicircle-shaped vestibuli (Pl. 8, Fig. 12). Horizontal extension of free inner lamella at ventral margin: 2/5 of length anteriorly, 1/5 of length posteriorly. Striate crenulation occurring on introversive surface of inner lamella. Distinct and broad limen in cyathus area, being of about 10μm width and 40μm length.

Muscle scar pattern: Unknown.

Morphologic variation: As well as the position in relation to the valves, the relative position of the two central spines in relation to each other is subject to slight variation. In general, the LV spine is in a higher position, i.e., located hardly above mid-height, than the one of the RV, which is located scarcely below mid-height. Regarding horizontal position, either spine may lie slightly more anteriorly than the other.

As for the smaller tubercles, the general pattern (horseshoe-shaped) seems to be relatively stable with minor variations in presence or absence of single tubercles in different locations, particularly dorsolaterally. Only size and degree of expression of the tubercles vary.

Ontogenetic variation: Not observed.

Dimorphism: Not observed.

Discussion: Sohn (1979, p. 18) considered *Cypridea tuberculata* (Sowerby) var. *wyomingensis* Jones 1893 (i.e., *Cypridea (Cypridea) wyomingensis* Jones therein) as given in Swain and Brown (1972) to belong to his "New genus undescribed '*Cypridea*' sp. 1" but referable to another (probably new) species. Considering the diagnostic characters of the latter species rostrum and alveolus with alveolar ridge, true cyathus, dorsal furrow, ventral ridge it well fits into *Cypridea* and there is no justifiable reason to establish a new genus anymore.

Peck (1941) already had synonymized *Cypridea tuberculata* var. *wyomingensis* Jones with *Cypridea tuberculata* var. *gypsumensis* Vanderpool 1928 under *Cypridea wyomingensis* Jones 1893. Loranger (1951, 1954, the latter being a reprint of the former with some revisions) also reported and figured *Cypridea wyomingensis* Jones, as well as Swain and Brown (1964, 1972, see synonymies therein), and Swartz and Swain (1946, *Cypridea* cf. *C. wyomingensis*). However, apart from the taxonomically less significant local ornamentation elements and the similar area-wide ornamentation elements, all of these specimens considerably differ from *Cypridea* ex gr. *tuberculata* cf. *C. tilleyi* Loranger herein (some types were inspected by the author), in being much more elongate (having a higher L/H-ratio) and having a relatively narrow posterior margin, showing a shallow dorsolateral sulcus at 2/5 of length (above the central muscle scar field), having a less well-developed cyathus and alveolar furrow as well as a weakly developed ventral ridge and no prominent anterior cardinal angle. In addition, it is even questionably whether all of these specimens belong to one species; a detailed investigation is necessary. Altogether, the specimens included in *Cypridea (Cypridea) wyomingensis* Jones definitely belong to the *Cypridea tuberculata*-group, but have no closer relations to the species described here. Since Sohn (1979) potentially included *Cypridea (Cypridea) wyomingensis* Jones 1893 in his "New genus undescribed '*Cypridea*' sp. 1", the taxa included in the former are clearly excluded from *Cypridea* ex. gr. *tuberculata* cf. *C. tilleyi* in the synonymy list above.

Considering the shape, particularly the relatively narrow posterior margin, as well as the strong tuberculation, the representatives of *Cypridea (Cypridea) wyomingensis* Jones might be regarded as juveniles. Notwithstanding, the possibility that all or some of these species represent juvenile stages of *Cypridea* ex gr. *tuberculata* (or the other way round) seems rather impossible due to the fact that most of them have the same size or are even bigger than the latter.

Cypridea tilleyi Loranger 1951 resembles *Cypridea* ex gr. *tuberculata* in general shape and outline, valve overlap, tubercle pattern, punctation and the prominent anterior cardinal angle. However, the available description of *C. tilleyi* is short, Loranger (1951) only gives one scarcely moderate photograph of the holotype, and the taxon lacks the subcentral robust spine. Since the type material was not restudied and internal characters were not given by Loranger (op. cit.), a reliable attribution of the species described here to *Cypridea tilleyi* Loranger is impossible and remains arguable. Although this is highly speculative, it might also be considered and cannot be totally ruled out that *Cypridea tilleyi*, being a bit larger on average than the specimens from the Lakota Formation, represents adults of the latter, whereas these might be A-1 to A-2 instars then, showing stronger tuberculation as well as the main central spine (cf. Section 5.2, genus *Cypridea* under 'sexual dimorphism' for details and remarks/discussion under 'ornamentation' in Sames 2011c).

At first sight except for the subcentral spine the species described herein shows similarities to *Cypridea tuberculata langtonensis* Anderson 1971 (also as figured in Anderson 1985, pl. 5, fig. 5) in lateral outline, the development of the anterior cardinal angle and the cyathus. However, the alveolar furrow of the latter is longer and narrower and lacks an alveolar ridge, and, therefore, it is considered a different species.

The species described here also shows strong similarities to *Cypridea australis* Musacchio 1971 in outline, development of the rostrum, alveolus and cyathus, surface characters and tuberculation pattern, except that the latter is an inverse (not considered taxonomically significant here) form. For the reason that the original material has not been restudied, *C. australis* is slightly questionable included in the synonymy here.

Differential diagnosis: Cypridea ex gr. *tuberculata* (Sowerby 1836) cf. *Cypridea tilleyi* Loranger 1951 differs from the other species described here in its strong tuberculation with the characteristic horseshoe pattern, and its well-developed reticulation-like punctation with deep puncta.

Paleoecology: As for the genus.

Faunal association (see Text-fig. 11 also): In the Lakota Formation associated with *Theriosynoecum fittoni* (Mantell 1844) [potentially synonym to *Theriosynoecum alleni* (Pinto and Sanguinetti 1962) refer to Sames 2011a], *Cypridea (Longispinella) longispina* Peck 1941, *Cypridea (Pseudocypridina) piedmonti* (Roth 1933), *Cypridea (Pseudocypridina) piedmonti* var. *henrybelli* Sohn 1979, *Cypridea (Pseudocypridina) setina* var. *setina* Anderson (1939) and representatives of the Darwinuloidea, family Darwinulidae (*Alicenula?* sp.).

In the Cedar Mountain associated with *Cypridea (Longispinella) longispina* Peck 1941, *Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949, *Cypridea (Pseudocypridina) setina* var. *setina* Anderson (1939).

Stratigraphic and geographic distribution (Stratigraphic terms follow the most recent terminology available):

North America:

+ Chilson Member of the Lakota Formation, Lower Cretaceous, Buck Canyon, southern Black Hills area (Text-fig. 2, loc. 1), South Dakota, U.S.A. (this study)

+ Chilson Member of the Lakota Formation, Lower Cretaceous, Buck Canyon, unit 10 of Bell and Post (1971, p. 531) after Sohn (1979, loc. 17 as equivalent to loc. 1, Text-fig. 2, Buck Canyon herein), South Dakota, U.S.A.

+ Blairmore Group, Lower Cretaceous (late Aptian to Albian after Ross et al. 2005), Alberta, Canada, North America, as reported by Loranger (1951, 1954)

Questionable occurrence:

+ La Amarga Formation, Lower Cretaceous (Barremian?), Neuquén Province, Argentina (potential synonymy with *Cypridea australis* Musacchio 1971)

Stratigraphic range in North America: As documented this far and deduced from the faunal association with *Cypridea (Pseudocypridina) setina* mainly: upper Berriasian to (uppermost) Valanginian.

Theoretical maximum range as resulting from the range of *Cypridea tuberculata* (Sowerby 1863) in the English Purbeck/Wealden given by Anderson's (1985) Worth to Pluckley faunicycles (cycles Nos. 27 to 91), middle/upper Berriasian to middle Barremian according to Hoedemaeker and Herngreen (2003).

Stratigraphic range outside North America: Not directly applicable (taxonomic status). Range of *Cypridea tuberculata* (Sowerby 1863) in the English Purbeck/Wealden given by Anderson's (1985) Worth to Pluckley faunicycles (cycles Nos. 27 to 91), middle/upper Berriasian to middle Barremian according to Hoedemaeker and Herngreen (2003).

6. DISCUSSION AND SYNOPSIS

The high rate of endemicity in North American representatives of *Cypridea* (*sensu lato*) assumed in the past and hampering further application, has mainly been a taxonomic problem as well as the general perception of these and other contemporaneous North American nonmarine ostracods as being entirely endemic. Many of the reasons for these perceptions that have been identified and are discussed (in the taxonomic part here; and Sames 2011c) led to a strongly modified view on the taxonomy of *Cypridea* that has considerably implications, for representatives of *Cypridea* and their application possibilities in general, and the North American representatives in specific. Some additional topics emanating from this study and considered to be of interest or basis for further research are addressed in the following.

6.1 Reproductive modes and sexual dimorphism their significance for the taxonomy, evolution, distribution and ecology of *Cypridea*

The knowledge of dispersal and reproductive modes in nonmarine ostracods (representatives of the Cypridoidea, Cytheroidea and Darwinuloidea), as well as the worldwide distribution of Lower Cretaceous nonmarine ostracods has expanded considerably during the last 30 years. The Superfamily Cypridoidea, of which *Cypridea* is a representative, is of particular interest because its representatives are the most diverse in today's nonmarine waters and dominate the nonmarine faunas since Early Cretaceous times (e.g. Horne 2003 and references therein).

Most representatives of *Cypridea* have long been considered to reproduce entirely asexual. This assumption mostly derived from the fact that sexual dimorphism in *Cypridea* has rarely been reported or considered. Although there have been some reports of presumed sexual dimorphism in *Cypridea* ever since the first one of Hanai (1951; see Section 5.2.3 for overview and the discussion of sexual dimorphism in the genus *Cypridea*), the established and prevalent view of an entirely asexual (parthenogenetic) *Cypridea* lineage persisted till the 1990's (e.g. Whatley 1992). According to newer evidence, however, this view cannot be sustained anymore. Firstly, more recent findings in cypridoidean ostracods have lead to the conclusion that a "… lack of obvious sexual dimorphism of the fossilized shell does not necessarily mean lack of sexual reproduction" (Horne and Martens 1998, p. 557). Strong sexual dimorphism might be overlooked and misinterpreted in fossil ostracod material, like it has been in the case of *Cypridea (Longispinella) longispina* Peck 1941 (herein). However, weak sexual dimorphism (see Text-fig. 10 also) as apparent in the carapace morphology, like in many cypridoideans and darwinuloideans, may be easily overlooked as well. Secondly, according to the present state of knowledge there is no nonmarine ostracod superfamily or family that can be considered fully asexual; most show sexual or mixed reproduction in their taxa, and none of the Cypridoidea are brooders, i.e., none of these features brood care (Martens et al. 1998a). Recent discovery of living males of the darwinulid genus *Vestalenula* even calls into question that the family Darwinulidae is an ancient asexual group having reproduced asexually for over 200 million years (Smith et al. 2006). Thirdly, the high diversity and speciation rates of *Cypridea* and its allies are very much unlikely to have been achieved by an exclusively parthenogenetic lineage (Horne and Martens 1998, Martens 1998).

Therefore, according to Horne and Martens (1998), Martens (1998), Martens et al. (1998a) and results and conclusions concerning sexual dimorphism in *Cypridea* presented herein, mixed reproduction is the most likely reproductive mode in species of the genus *Cypridea* of the extinct cypridoid family Cyprideidae Martin 1940.

This hypothesis has considerable effects on the interpretation of morphologic variation (mainly shape, particularly as to lateral outline), taxonomy and diversity, distribution potential and distribution mechanisms, and evolution of representatives of the genus *Cypridea* Bosquet.

Modern research in ostracod genetic diversity and mixed reproduction (not only but -particularly in cypridoideans) lead to the awareness that the morphologic variation (shape, i.e., lateral outline mainly, and size in part) within one population may be considerable. Modern cypridoideans often show minor sexual dimorphism in their carapace shape but can show less morphologic variation between males and females of sexual populations than among parthenogenetic females (e.g. Horne and Martens 1998, Martens et al. 1998b). Species with mixed reproduction can comprise separated parthenogenetically and sexually (syngamically) reproducing populations, or bisexual populations (i.e., populations with mixed reproduction). With respect to polymorphism in representatives of *Cypridea*, Sylvester-Bradley (1976) was the first to discuss this subject, and he suggested an attribution to polyploidy after *inter*specific hybridization. According to recent findings, similar (strong) morphologic variability can be obtained by *intra*specific hy-

bridization (gene flow between sexual and asexual lineages and populations of one species). This leads to an "inclusive species concept" (Martens et al. 1998b) with large intraspecific genetic and morphologic variability (see Rossi et al. 2008, Schön et al. 2000, for recent studies on genetic diversity and mixed reproduction in the cypridoidean species *Eucypris virens*; for a detailed discussion of taxonomic problems in the context of reproductive modes, the reader is referred to Martens et al. 1998b; for an overview of the coherences of sexuality, asexuality, genetic diversity and possible routes to parthenogenesis in animals including ostracods see Simon et al. 2003, for example). Some implications of this modified perception for fossil cypridoidean ostracods are elucidated herein by example of *Cypridea (Pseudocypridina) setina* (Anderson 1939) (see next section below).

Thus, based on the fact of an assumed–and now well justifiable–mixed reproduction in *Cypridea* as presented here as well as new interpretations on the taxonomic significance of certain carapace characters, the taxonomy of the genus *Cypridea* is strongly modified in part (this paper) and will undergo considerable changes in the future, including all consequences for its diversity, biostratigraphy, paleobiogeography, and dispersal mechanisms.

Coming from the assumption that many taxa of *Cypridea* whether having been regarded species, subspecies or variants by different authors conceal sexual dimorphs, ontogenetic stages, ecophenotypes or morphologic variants deriving from intraspecific hybridization, it can be deduced that the species diversity in *Cypridea* has been, and still is, in general highly overestimated. According to the discussed concepts and by a speculative rough estimation, it seems possible that up to half or even two third of the taxa of *Cypridea* may well conceal the given intraspecific variations. This hypothesis of a much lower specific diversity, in turn, would affect the hypothesis of the (Middle) Jurassic-Cretaceous expansion of the Cypridoidea (e.g. Whatley 1992, Horne and Martens 1998) that is mainly represented by a global diversification of one lineage: the Cyprideidae Martin 1940 typified by its most important genus *Cypridea* (see Whatley 1990, fig. 1, simplified reproduced in Horne and Martens 1998, fig. 3). In his table 1, Whatley (1992) summarized the numerical distribution of nonmarine ostracod genera and species recorded from the Late Jurassic and Cretaceous and gave 698 cypridoidean (Cypridacea therein) species, 38 cytheroidean (Cytheracea therein) species and 14 darwinuloidean (Darwinulacea therein) species for the pre-Aptian Early Cretaceous ("Neocomian" therein). From these numbers, he (Whatley 1992) stated that the "… rise in the fortunes of the cyprids from the Kimmeridgian to the Neocomian [pre-Aptian Early Cretaceous] is nothing short of dramatic" (op. cit., p. 181) and interpreted that the nonmarine species of the pre-Aptian Early Cretaceous (overwhelmingly comprising of representatives of the Cyprideidae Martin, that is species of *Cypridea*, at that time) represented more than 70% of the total number of ostracod species (including marine ones) recorded for that interval. A much lower species diversity in *Cypridea*, however, would challenge Whatley's (1992) hypothesis of a dramatic rise in the fortunes of the Cypridoidea as well as require a strongly modified view on the Late Jurassic-Cretaceous evolution of the Cyprideidae in specific as well as the Cypridoidea in general. If the example given by Nye et al. (2008), who convincingly consider all five subspecies of *Cypridea clavata* Anderson 1939 plus *Cypridea bogdenensis*

Anderson 1967 (in Anderson et al 1967) and, questionably, *Cypridea insulae* Anderson 1967, is typical, then Anderson's (1939 et seqq.) *Cypridea* diversity would be exaggerated by a factor of up to five. This demonstrates that the diversity of *Cypridea* has most likely been, and still is, grossly overestimated.

A revised interpretation of the specific taxonomy in *Cypridea* also requires and facilitates different interpretations concerning the interrelations of reproductive modes, dispersal mechanisms and paleobiogeography. The (passive) dispersal of parthenogenetic females, or rather their eggs, is much easier (and faster) and allows a long-distance dispersion even across migration barriers while the supraregional dispersal of sexual populations and lineages is much more difficult. This leads to typical distribution patterns (e.g. Baltanás 1998), i.e., the asexuals are widespread while the sexuals have a restricted distribution. For an application and interpretation of such concepts to *Cypridea*, however, the temporal framework (many million years) has to be taken into consideration. Identification and analysis of fossil sexual, asexual or bisexual populations in *Cypridea* can, therefore, give new insights into dispersal mechanisms and patterns, faunal exchange, and evolutionary ecology of its representatives that, in turn, might lead to new options of application of these ostracods (e.g. paleoecology, paleoclimate, paleogeography).

With respect to the importance of resting eggs and parthenogenetic reproduction for the differential Late Mesozoic success of the Cyprideidae Martin 1940 (i.e., species of *Cypridea* mostly) and the global distribution and high diversity in it representatives, Horne and Martens (1998) challenged Whatley's (1990, 1992) hypothesis of these being the most important factors. Since representatives of other nonmarine ostracod lineages also possess resting eggs, this character "… cannot be held responsible for the differential success of the Cyprideidae, as compared to other cypridoidean lineages" (Horne and Martens 1998, p. 558). Also, as discussed above mixed reproduction is the most likely reproductive mode in *Cypridea*, not the entirely asexual (parthenogenetic) reproduction. Therefore, resting eggs and parthenogenesis are unlikely to have been the key factors. Horne and Martens (1998) favor the idea that the differential success of *Cypridea* and its allies is associated with their most characteristic carapace features: the rostrum and alveolus. However, since the functional significance of these features is not known, the specific reasons for the Late Mesozoic differential success of the Cyprideidae still remain to be identified.

6.2 Variability within one species, and its possible causal connection regarding reproductive modes, distribution and paleoenvironment: The *Cypridea (Pseudocypridina) setina*-case

Representatives of the *Cypridea (Pseudocypridina) setina* (Anderson 1939) are common within Purbeck/Wealden like deposits of Europe and North America and a good index group for the Late Berriasian-Valanginian nonmarine Early Cretaceous of the northern hemisphere. Among other representatives of *Cypridea*, these are easily to identify because this is the only group with a smooth carapace surface and completely lacking any ornamentation elements. The morphologic variation within this group is, therefore, almost exclusively expressed in the lateral and dorsal outlines (so far, only sparse data of internal characters are available). For the synonymy and detailed information, the reader is referred to the taxonomic section

(Section 5.2.3). Many subspecies (18, considered varieties herein) have been described from Europe, the majority of these by Anderson (1939, 1962, 1971, 1985, Anderson et al. 1967) from the English Purbeck/ Wealden. However, many of these are stratigraphically co-occurring, some even belonging to the same fossil population (i.e., deriving from the same layer).

The English case, as based on Anderson's (1985) data, is particularly interesting because of the outstanding documentation and biostratigraphic resolution. With respect to the most likely reproductive mode in *Cypridea* (mixed reproduction) and based on assumed sexual dimorphism in *Cypridea (P.) setina* as presented here, new interpretations of the causes of morphologic variability, dispersal and distribution of this species' variants can be made.

Whether the hypothesis presented herein, i.e., that *Cypridea (P.) setina* var. *rectidorsata* is the (sexual? or asexual?) female and *C. (P.) s.* var. *setina* the male dimorph, is correct or if it is the other way round, the fact is that few variants of this species have been described from Europe outside England, and only two variants are known from North America thus far.

This matter is in need of further investigation and different hypothesis can and should be tested by geometric morphometrics and by inclusion of internal features into the analysis wherever possible. Several matters are in need of clarification:

1) Which variants can be assigned to the different morphs: sexual males and females and parthenogenetic females.

2) Did bisexual populations firstly evolve in England and were the asexually (parthenogenetically) reproducing females, potentially deriving from these, the first to invade the North American continent (and were they followed by males?)?

3) With respect to the impression of a very high diversity of *Cypridea (P.) setina* in England, this might be a problem of Anderson's (1939, 1962, 1971, 1985, Anderson et al. 1967) taxonomy in combination with the excellent documentation (more data) in England. According to modern insights in genetics and reproductive mechanisms (see e.g. Simon et al. 2003 for overview), Anderson's (1939, 1962, 1971, 1985, Anderson et al. 1967) subtaxa of *Cypridea setina* could well fit into possible morphologic variation ranges of single populations of recent nonmarine ostracods (Cypridoidea) with mixed reproduction (pers. comm. Valeria Rossi, Parma, 2008). Taking this into account, it has to be reassessed whether the much lower diversity documented in other areas of Europe and other continents is due to a really existent lesser diversity (fewer morphotypes) in these areas, or due to lesser data available (insufficient documentation and taxonomic treatment) or incomplete stratigraphic record outside England. As for North America, the documentation of Early Cretaceous nonmarine ostracods to date can at best be designated moderate, irrespective of the previous work.

4) Parthenogenetic lineages can only evolve from sexual ones (e.g. Simon et al. 2003), that is to say, the earliest populations should have had lesser morphologic variability (which is the case in England, e.g. Anderson 1985) and sexual dimorphism should be observable (if apparent in the carapace).

6.3 Some notes and ideas on trends in the evolution of some lineages of *Cypridea*

As elucidated in Section 5.4.1, Wolburg developed and applied the morphogroup concept to the biostratigraphy of the "NW German Wealden". Herein, morphogroups are successfully applied for taxonomic and biostratigraphic purposes. Application of the morphogroup concept also requires the consideration of morphologic trends in the evolution of the concerning taxa through time. Although a comprehensive analysis of these trends in *Cypridea* is hitherto lacking and cannot be given here, some observations and ideas resulting from the author's recent works in North America are elucidated in the following to provide a basis and some perspectives for future works.

Analyzing the morphologic development in *Cypridea* during Late Jurassic to Early Cretaceous times, several trends become apparent that are, or may become, stratigraphically useful. Conclusions must remain tentative at the moment since the detailed stratigraphy of most Purbeck/Wealden-like deposits of the world, including North America, is still inaccurate and under discussion and much more taxonomic research on a global scale is necessary. However, though possibly not universally valid and whether taking *Praecypridea* (Sames et al. 2010b) into consideration as member of an ancestral lineage of *Cypridea* or not, the following morphologic trends have been recognized, for example:

1) Many more ancient (circa Kimmeridgian to Valanginian-Hauterivian) forms of *Cypridea* often possess a prominent, rounded-rectangular to pointed cyathus-like protrusion that may or may not distinctly overreach the posterior margin, while most younger forms have a 'true' cyathus. The cyathus is in most cases not as strongly developed as the cyathus-like protrusion, i.e., not as distinct as the latter, more strongly rounded and not overreaching the posterior margin. *Cypridea nitidula* Peck 1951 and *Cypridea (Longispinella) longispina* (Sohn 1979) described herein show a distinct cyathus-like protrusion, in *Cypridea obesa* Peck 1951 it is developed to a lesser degree. Representatives of the *Cypridea laevigata*-group and of *Cypridea (Pseudocypridina)* in general, have a true cyathus, which is crescent and narrow.

2) Many Late Jurassic-lowermost Cretaceous *Cypridea*-species show a strong degree of inequality of the valves. This feature, however, seems to be limited to certain lineages of *Cypridea*. Among the species described here, *Cypridea (Longispinella) longispina* (Sohn 1979) and *Cypridea* ex gr. *alta* Wolburg 1959 are strongly inequivalve. Most of the younger (post-Valanginian-Hauterivian) forms are less than moderately inequivalve, or subequivalve.

3) The development of dorsolateral sulci in some (one or several?) lineages of *Cypridea* (see discussion of a *Cypridea-Bisulcocypridea* lineage in Section 5.2.1 also) seems to be a relatively late acquisition (the known stratigraphic distribution of *Bisulcocypridea* Sohn is Late Cretaceous-Early Paleogene) in the evolution of *Cypridea* Bosquet 1852 to *Bisulcocypridea* Sohn 1969. New data on *Cypridea? minuta* (Peck 1951) from North America presented herein point to a pre-Barremian first appearance of sulcate taxa.

However, these are only trends that cannot be applicated to all groups or lineages of *Cypridea*. Much more data and research is necessary to test these hypotheses. The early pre-uppermost

Tithonian evolution of *Cypridea* is not yet well known. Sames et al. (2010b) introduced the new genus *Praecypridea*, the taxaa of which they consider to represent members of the ancestral lineage of *Cypridea* Bosquet, with North and South American, European and West African representatives. A successive evolutionary lineage from the former to the latter has not been documented so far. The oldest representatives of 'true' *Cypridea* have been reported from the Kimmeridgian of the Tendaguru Formation (Tanzania, East Africa) by Schudack and Schudack (2002) and Sames (2008). With respect to Europe, the oldest known species of *Cypridea* derive from the Lower Tithonian of the Île d'Oléron (Island of Oleron, Bay of Biscay, France, J.-P. Colin, Cestas, France, pers. comm. 2006).

It seems likely that the oldest true representatives of *Cypridea* are older than Kimmeridgian-Early Tithonian. These early representatives are already strongly different, some are smooth (Sames 2002) others punctated (Schudack and Schudack 2002), and they distinctly differ in outline, development of rostrum and alveolus as well as the cyathus-like protrusion. Several lineages seem to have been established in the Early Tithonian already and further differentiated in the latest Tithonian to Berriasian. As the example of *Cypridea (Pseudocypridina)* shows, which can be exemplified on *Cypridea (P.) setina* and *C. (P.) piedmonti* here, "younger morphotypes", being subequivalve and having a true (and weakly developed), cyathus already existed during the Berriasian.

Based on the most recent data, the evolution of *Cypridea* Bosquet 1852 (Kimmeridgian to Early Eocene) spanned some 100 Ma (cf. Gradstein et al. 2004) and its representatives are known from all continents except Antarctica and Australia. Taking such a long period of time into consideration in the context with mixed reproduction and different dispersal modes and the development of the earth during that time, it is not surprising that cypridean evolution took different directions in different areas of the world.

Neither climatic changes nor the flooding of the Western Interior foreland basin caused by major area-wide marine transgressions starting in Middle Albian times and leading to the Cretaceous "Western Interior Seaway" (e.g. Kauffman and Caldwell 1993, Miall et al. 2008) have eliminated all representatives of *Cypridea* (or *Bisulcocypridea*) in North America (see Swain 1999 and references therein). However, Maastrichtian species of *Cypridea* and *Bisulcocypridea* reported by Brouwers and De Deckker (1993) from northern Alaska more likely have been immigrated from Asia.

Lower Cretaceous nonmarine deposits of the North American Western Interior foreland basin play an important role in the documentation of the evolution and dispersion of *Cypridea* and *Bisulcocypridea*, particularly on the northern hemisphere and in relation to European and Asian faunas, and in relation to South America. In turn, new findings in this regard allow, amongst other things, the biostratigraphic application of taxa of *Cypridea* in North America and are capable of improving the Early Cretaceous chronostratigraphy of the Western Interior foreland basin.

6.4 General stratigraphic considerations for the nonmarine Lower Cretaceous of the Western Interior foreland basin

The specific stratigraphic implications of this taxonomic review and that of representatives of *Theriosynoecum* (Sames 2011a) for the North American Western Interior foreland basin have been published (Sames et al. 2010a) or are in preparation to be

published elsewhere. Sames et al. (2010a) gave a comprehensive overview of the stratigraphy and age determination (chronostratigraphy and geochronology) of the basin, associated problems and perspectives, and a synopsis of the most important implications of a higher maximum age (Late Berriasian to Valanginian) of some of the basin's Lower Cretaceous formations as based on ostracod correlations. These derive from ongoing taxonomic revisions, of which Sames (2011a, c) and the paper at hand are parts of.

At this point, a short overview and synopsis of some important aspects related to the North American taxa of *Cypridea* shall be given.

Peck (1956, 1959) combined the Late Jurassic to Paleocene nonmarine ostracod fauna (representatives of *Theriosynoecum*, all the latter allocated to the genus *Metacypris* by Peck, and *Cypridea* mainly) and charophyte flora of the U.S.A. (Rocky Mountain area, Western Interior foreland basin, mainly Wyoming, South Dakota, Montana, Idaho and Utah) into four assemblages:

a) the (Late) Jurassic "Morrison assemblage",

b) the Early Cretaceous "Gannett-Cloverly assemblage" (Gannett Group: Ephraim Formation, Peterson Limestone, Bechler Formation and Draney limestone; and the Cloverly Formation of Wyoming; pre-Albian Lower Cretaceous according to Peck 1956, Aptian according to Peck 1959),

c) the Early Cretaceous "Bear River assemblage" (Albian according to Peck 1956, 1959; Bear River Formation of Wyoming),

d) and the Paleocene "Hoback-Flagstaff assemblage" (after the Hoback Formation of Wyoming and the Flagstaff Formation of Utah, including other correlatables, see Peck 1959).

In his first publication (Peck 1956, fig. 23) still had included a representative of *Cypridea*, i.e., *Cypridea (Pseudocypridina) piedmonti*, in his "Morrison assemblage". Sohn (1958), however, had demonstrated that the rocks from which Roth (1933) or Harper and Sutton (1935) had described ostracods from the Black Hills area (South Dakota), were actually from the Lakota Formation and not the Morrison Formation as given by these authors. Consequently, Peck (1959) removed representatives of *Cypridea* from his "Morrison assemblage"; he also changed the name of his "Gannett-Cloverly assemblage" (Peck 1956) to "Gannett-Cedar Mountain assemblage" (Peck 1959) and supplemented all of his four assemblages with additional ostracod and charophyte taxa. To the current state of knowledge, the Morrison Formation is entirely devoid of true representatives of *Cypridea* Bosquet. Schudack (1995, 1996, Schudack in Schudack et al. 1998) was the first to systematically deal with and describe ostracods and charophytes from the Morrison Formation. *Cypridea acuticyatha* Schudack 1998 (in Schudack et al. 1998) and as given in Schudack (1995, 1996) is considered not to be a true *Cypridea* but rather an ancestral form belonging to a different genus and has currently been chosen by Sames et al. (2010b) as the type species for a new genus: *Praecypridea* Sames, Whatley and Schudack 2010(b).

Peck's (1956, 1959) assemblages require extensive revision, and his age determinations are outdated (see Sames et al. 2010a). In addition, a complete taxonomic revision of all of Peck's taxa and

material is still pending (but will be partially difficult since the whereabouts of most of the material is unknown).

Based on the literature (Harper and Sutton 1935, Peck 1941 et seqq., Peck and Craig 1962, Roth 1933, Sohn 1958, 1979, Schudack 1995, 1996, Schudack et al. 1998) as well as results from the Lakota and Cedar Mountain formations presented here and in Sames (2011a), the Early Cretaceous nonmarine ostracod faunas of North America can be divided into at least three informal successive assemblages, perhaps even more but this remains subject to upcoming publications and studies. These exclude the assemblages of the Upper Jurassic (to Berriasian?, see Sames et al. 2010a) Morrison Formation, which are characterized by distinct species of *Theriosynoecum* Branson 1936, representatives of *Cetacella* and *Timiriasevia*, and the absence of representatives of *Cypridea* Bosquet (cf. Sohn 1958). In contrast to the assumptions of Schudack (in Schudack et al. 1998) and according to the results of the author's ongoing research, the Early Cretaceous nonmarine ostracod faunas have no taxa in common with the Morrison Formation at species level.

The Early Cretaceous informal ostracod faunas of the Western Interior foreland basin comprise:

1) a "Fauna A" of the early Lower Cretaceous (upper? Berriasian-Valanginian), besides the common occurrence of *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) laeli* Sohn 1979 characterized by representatives of the *Cypridea laevigata*-group, the *Cypridea alta*-group and representatives of *Cypridea nitidula* Peck 1941,

2) a "Fauna B" of the middle Lower Cretaceous (middle/upper? Valanginian, Hauterivian to lower/middle? Barremian) that is most probably further differentiable and which, besides comprising *Cypridea (Pseudocypridina) piedmonti* (Roth 1933) syn. *C. (P.) laeli* Sohn 1979, is mainly characterized by *Cypridea (Pseudocypridina) laeli* Sohn 1979 and *Theriosynoecum pahasapensis* (Roth 1933).

3) a "Fauna C" of the upper (middle?/upper Barremian to middle Albian, questionably Cenomanian) that is only partially according to Peck's (1956, 1959) "Bear River assemblage" (revision required), and comprises *Cypridea? anomala* (Peck 1941), *Cypridea compta* Peck 1941, *Theriosynoecum persulcata* (Peck 1941), and *Theriosynoecum angularis* (Peck 1941) (see Sames 2011a also).

With regard to the ostracods of the Lakota Formation of the Black Hills area, to the present state of knowledge the Lakota–even its upper parts (Fuson Member or informal L2 and L3 interval of Way et al. 1998) in the eastern Black Hills–only comprises of faunal elements that belong to the informal "faunas A and B", and has no faunal elements in common with Peck's (1956, 1959) "Bear River assemblage". Therefore, the entire Lakota Formation is considered distinctly older than Middle?/Late Barremian–Aptian (see also Sames et al. 2010a). Ostracod-bearing samples from the Yellow Cat Member of the Cedar Mountain Formation (Utah) mostly comprise elements of "Fauna A".

7. CONCLUSIONS

The detailed taxonomic revision of the genus *Cypridea* Bosquet with emphasis on some North American Early Cretaceous species resulted in considerable progress concerning the taxonomy, paleoecology, paleogeography and evolution of the genus and

some subgenera as well as selected representatives, and a breakthrough in the perception of their biostratigraphic utility in North America.

The high rate of (even total) endemicity widely assumed for the Early Cretaceous North American representatives of *Cypridea* in the past has been highly overestimated, as well as the species diversity within this genus. The main reason for these views is here identified as having been basically a taxonomic problem. In most cases, overestimation or wrong interpretation of local ornamentation elements (in the sense of Sames 2011c), outline, or the too regional view on the faunas led to the erection and retention of numerous new species names, some subgenera or even few different genera in North America (as well as other continents). In addition, the taxonomic confusion also derives from the factually existing strong variability within *Cypridea* that is difficult to deal with and could not be explained for a lineage having been previously believed to reproduce exclusively parthenogenetic by many authors. Now that more and more sexual dimorphs have been presumed, the hypothesis of a mixed reproduction can be supported well. Based thereupon, the high morphologic variability and different paleogeographic distribution patterns become much better explainable (geographic parthenogenesis).

The conducted comprehensive "classic" morphologic analyses and descriptions including a revised definition of the (in-)significance of certain carapace characters, detailed and standardized descriptions as well as new insights in ostracod biology and reproduction, facilitate a modified and new perception of the taxonomy of the representatives of the fossil genus *Cypridea*. First steps towards identification and better differentiation between taxonomically significant and insignificant (ecophenotypic, ontogenetic, intraspecific variation) carapace characters have been achieved. That facilitates a more effective choice and application of additional methods, such as geometric morphometrics, for example, in that it is possible to focus on significant characters as base data to measure depending on the hypothesis to test.

As can be demonstrated, a biostratigraphic application of representatives of *Cypridea* and an improvement of the age determi-

nation of nonmarine Lower Cretaceous formations of the North American Western Interior foreland basin is possible. With respect to the maximum age of these formations that has been under discussion for the entire 20th century and remains controversial to date, first biostratigraphic applications are promising (Sames et al. 2010a). New results strongly suggest that the maximum age of some of these formations (Lakota Formation, South Dakota, and Cedar Mountain Formation, Utah) is Late Berriasian to Valanginian, and therefore much higher than most published lines of evidence have given in the past (Barremian or Aptian-Albian, respectively). These results can have considerable impact on the geology and paleontology (chronostratigraphic framework) of the basin (Sames et al. 2010a).

In addition to the revision of *Cypridea*, a different and updated systematics of the family Cyprideidae Martin 1940 is proposed (see Table 1). Within the scope of further research in the evolution and distribution of the *Cypridea-Bisulcocypridea* lineage in time and space as well as the diverse application of its representatives, the Lower Cretaceous formations of the North American Western Interior foreland basin provide an important resource of information

8. ACKNOWLEDGMENTS

PLATE 1
Scale bar: 100μm; specimens to scale (except Figs. 3, 7, 8, 11, 12). SD: South Dakota.

Cypridea nitidula Peck 1941

Note: Greyish stains on the specimens are caused by glue covering of material from Peck's collection; small needles are splints from the cardboard microcells. The latter were not removed for the reason not to damage the fragile original material.

1 Right lateral view of adult carapace, weathered anteriorly but weak alveolar notch in larger LV well visible, punctation well-defined, cyathus-like protrusion broken off. Specimen in Peck's collection, Peck's locality 82P (Draney Limestone(Sub-?)Formation?), specimen figured in Peck 1959, pl. 2, fig. 18, and Peck and Craig 1962, pl. 2, fig. 2).

2 Right lateral view of adult carapace, ventrolaterally partially covered with glue and sediment, punctation well-developed, antero- and posterolateral small tubercles visible as well as cyathus-like protrusion in the LV (see Text-fig. 3 of this plate for magnification). Specimen in Peck's collection, Peck's locality 82P (Draney Limestone(Sub-?)Formation?).

3 Magnification of figure 2 of this plate, right lateral view posteroventral area with the true (undeformed) shape (attached sediment retouched) of the cyathus-like protrusion; partially covered with sediment and glue.

4 Left lateral view of weathered (corroded through processing?) carapace, slightly compressed and deformed, with sediment particles in centroventral area, cyathus-like protrusion clearly visible, punctation faint. Specimen from Peck's Collection, Peck's locality 280P, Bear River Formation at Thomas Fork Creek, Lincoln County, Wyoming, U.S.A., USNM 544208.

5 Left lateral view of weathered (corroded through processing?) carapace, slightly deformed, with stub (basis) of massive posterocentral spine that is broken away, cyathus-like protrusion clearly visible, punctation faint. Specimen from Peck's Collection, Peck's locality 280P, Bear River Formation at Thomas Fork Creek, Lincoln County, Wyoming, U.S.A., USNM 544209.

6 Right ventrolateral view of weathered (corroded through processing?) carapace, cyathus-like protrusion of RV well visible, anteroventral region damaged. Specimen from Peck's Collection, Peck's locality 280P, Bear River Formation at Thomas Fork Creek, Lincoln County, Wyoming, U.S.A., USNM 544210.

7 Left lateral view of posteroventral area with LV's cyathus-like protrusion. Magnification of Fig. 4 of this plate, USNM 544208.

8 Right lateral view of posteroventral area with cyathus-like protrusion in the RV and LV (slightly shifted in relation to each other). Magnification of Fig. 6 of this plate, USNM 544210.

Cypridea obesa Peck 1951

9 Left lateral view of adult carapace, punctation and faint alveolar notch well visible. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Angell Ranch – Cheyenne River, SD, U.S.A. (Text-fig. 2, loc. 5), USNM 544211.

10 Right lateral view of adult carapace, dipped to the left, posteroventral part of LV with cyathus broken apart, ventral overreach and ventral ridge of LV visible as well as faint rostrum and alveolar notch of RV. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Angell Ranch – Cheyenne River, SD, U.S.A. (Text-fig. 2, loc. 5), USNM 544212.

11 Left lateral view of anteroventral region with faintly visible rostrum and alveolar notch. Magnification of Fig. 9 of this plate, USNM 544211.

12 Right lateral view of anteroventral region with faintly visible rostrum, alveolar notch and furrow. Magnification of Fig. 15 of this plate.

13 Ventral view of adult carapace, anterior end to the right, potentially a female dimorph, anterior end to the right, adult carapace, with weak rostrum visible at right end. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Angell Ranch - Cheyenne River, SD, U.S.A. (Text-fig. 2, loc. 5).

14 Dorsal view of carapace, anterior end to the right, male dimorph? or A-1? preadult, narrow dorsal furrow and anterior and posterior overlap of larger LV well visible. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Angell Ranch – Cheyenne River, SD, U.S.A. (Text-fig. 2, loc. 5).

15 Right lateral view of well preserved adult carapace, partially covered with glue and organic crystals of some sort, elongate puncta forming ventral rows well visible. Specimen in the Peck collection, labeled to have been figured in Peck and Craig (1962, pl. 2, fig. 5, locality 658P therein), Cloverly Formation northwest of Lander, Fremont County, Wyoming, U.S.A.
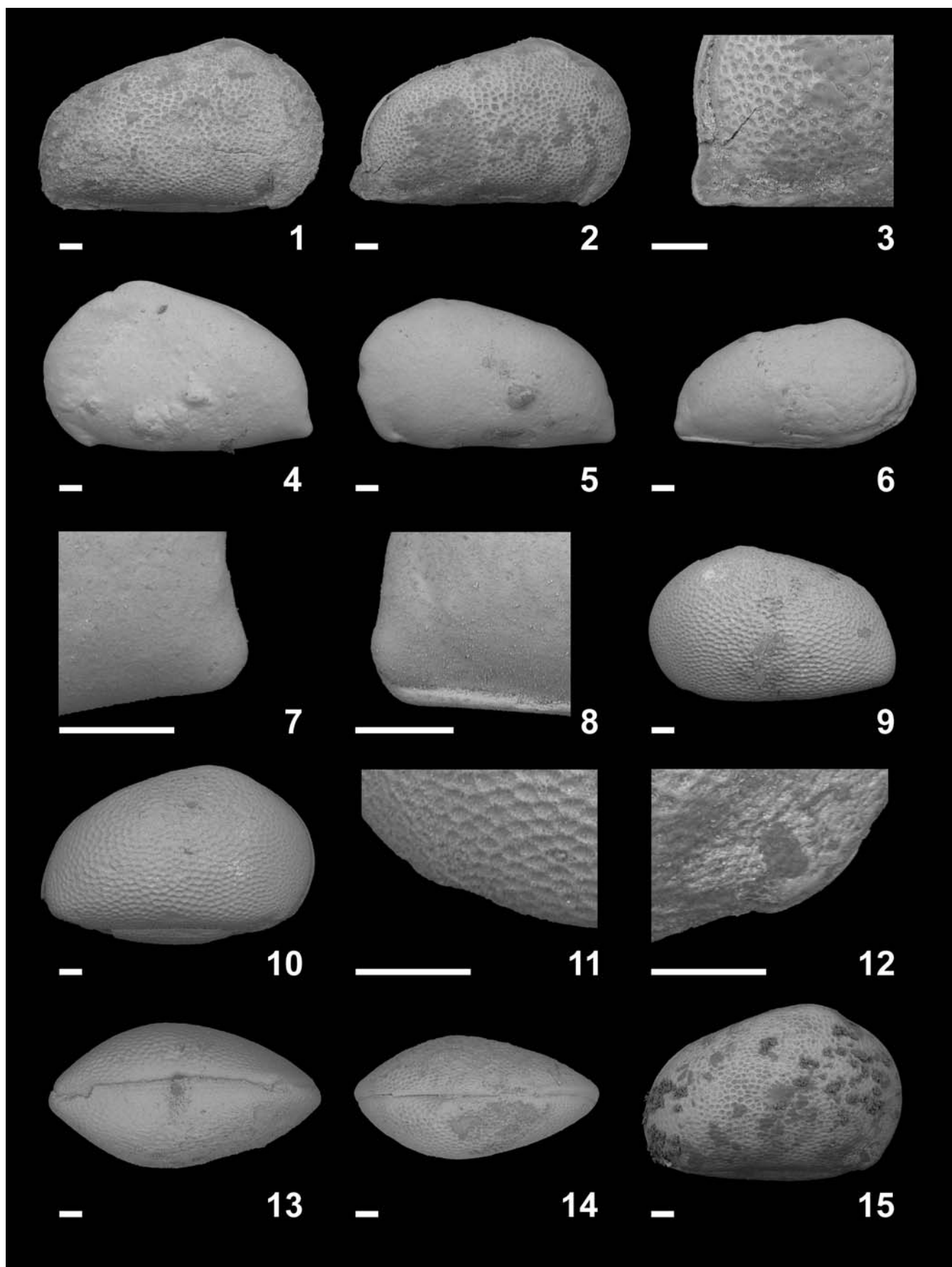
PLATE 2
Scale bar: 100μm; specimens to scale (except Figs. 3, 15). SD: South Dakota.

Cypridea? minuta **(Peck 1951)**

1 Left lateral view of well preserved (male?) carapace, slightly compressed at mid-length in vertical direction. Alveolar furrow, dorsolateral sulcus and reticulation-like punctation well visible, cyathus in larger RV broken off, outline retouched (large sediment particles overreaching dorsally removed). Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544215.

2 Left lateral view of well preserved (female?) carapace, with some sediment remains and edged cavities of sediment grains. Overreach of larger LV, dorsolateral sulcus and punctation pattern well visible; posteroventral area of RV broken off. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544216.

3 Left lateral view of anteroventral region with rostrum, alveolus, normal pores and small tubercles at the anterior margin. Magnification of Fig. 2 of this plate, USNM 544216.

4 Dorsal view of moderately preserved carapace, anterior end to the left, presumed male (slender), dorsolateral region of right valve compressed. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544217.

5 Ventral view of carapace, anterior end to the left, moderately to well-preserved, alveolar furrow well visible, inflated posteriorly. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544218.

6 Dorsal view of moderately to badly preserved adult carapace, anterior end to the right, typical lateral constriction at mid-length, strongly inflated dorsally. Sample ARCR Chz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Text-fig. 2, loc. 5), USNM 544219.

7 Left lateral view of strongly altered, badly preserved ("steinkern") carapace with slight imprints of the central muscle scar field, anterior mandibular scar well visible (arrow), alveolar notch and alveolar furrow. Sample ARCR Chz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Text-fig. 2, loc. 5), USNM 544220.

8 Left lateral view of badly preserved carapace, sediment attached posteroventrally and posterodorsally, RV>LV overlap apparent. Sample ARCR Chz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Text-fig. 2, loc. 5), USNM 544221.

9 Left lateral view of badly preserved carapace, preadult (A-2?) specimen, dorsolateral sulcus slightly visible as well as alveolar notch. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P of Peck, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544222.

10 Left ventrolateral view of badly preserved adult (or preadult A-1?) carapace, RV attached to another ostracod valve, female? specimen (posterolaterally inflated), RV>LV overlap distinctly visible, with dorsolateral sulcus. Posteroventral area showing no sign of a cyathus. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P of Peck, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544223.

11 Right lateral view of badly preserved adult carapace, with edged cavities of sediment grains, female? specimen (posterolaterally inflated), rostrum and alveolar furrow visible. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544224.

12 Left lateral view of a badly preserved carapace with much sediment attached to it, female? specimen. Specimen from the Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P of Peck, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A., USNM 544225.

13 Left lateral view of adult male? (slender) carapace, covered with recrystallized glue, RV>LV overlap apparent, punctation still visible. Specimen figured in Peck and Craig (1962, pl. 1, fig. 7 therein), Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P of Peck, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

14 Left lateral view of adult male? (slender) carapace, covered with recrystallized glue, RV>LV overlap apparent. Specimen (like specimen in Fig. 13 of this plate) labeled as having been figured in Peck and Craig (1962), but looking different from the drawing therein. Peck collection, Minnewaste Limestone Member of the Lakota Formation, locality 439P of Peck, Skyline Drive east of Hot Springs, Fall River County, SD, U.S.A.

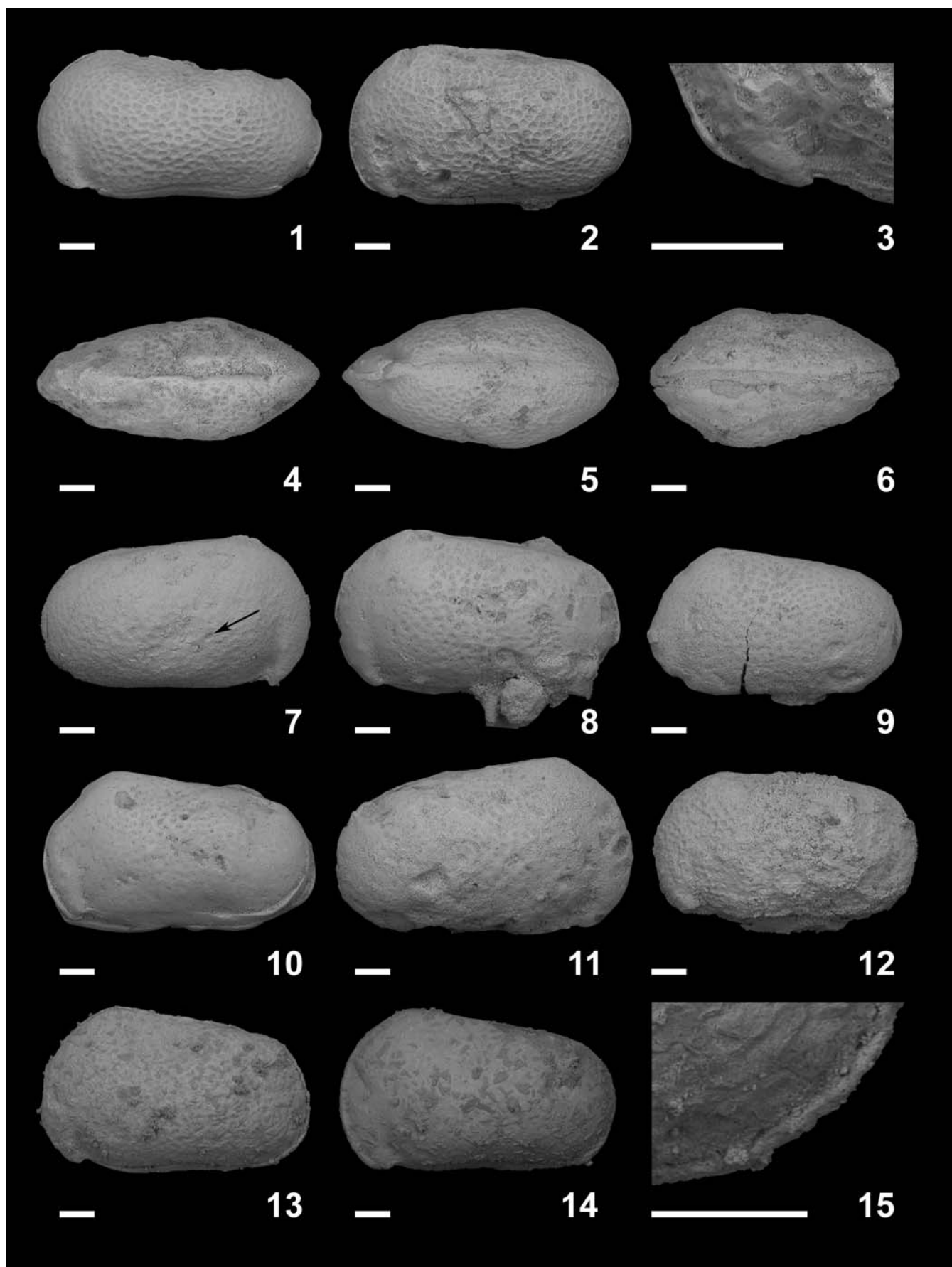15 Left lateral view of posteroventral region, no cyathus cognizable. Magnification of Fig. 13 of this plate.

PLATE 3
Scale bar: 100µm; specimens to scale (except Figs. 13-15). SD: South Dakota, UT: Utah.

Cypridea (Longispinella) longispina **Peck 1941 syn.** *C. (L.) asymmetrica* **(Sohn 1979)**

1   Left lateral view of adult carapace of presumed female, rostrum point and spine broken off, Anterocentral perpendicular ridge and sulcus of LV well visible (see also Fig. 14 of this plate for magnification). Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544226.

2   Right lateral view of adult carapace of presumed female, point of rostrum and spine broken off, specimen partially covered with dirt. Strong overreach of LV and lateral pores visible. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544227.

3   RV, lateral view of moderately presumed female valve, point of rostrum and spine broken away. Different shape of RV clearly visible, as well as the alveolar ridge and the small cyathus-like protrusion in the RV. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544228.

4   Left lateral view of presumed female carapace, point of rostrum and spine broken off, moderately preserved and in part diagenetically altered. Surface characters not visible anymore, alveolar ridge, alveolar furrow and cyathus distinct. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544229.

5   Dorsal view, anterior end to the left, adult carapace of presumed female, posterior part somewhat covered with sediment. Spine well visible as well as anterocentral ridge and sulcus on the LV only. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544230.

6   Ventral view of adult carapace of presumed female, anterior end to the left, posterior end somewhat covered with sediment. Spines and anterocentral ridge and sulcus on the LV only well visible as well as strong ventral overlap of LV, the deeply incising alveolar furrow (even along the alveolar ridge) and the strong alveolar ridge on both valves. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544231.

7   RV, lateral view of presumed female valve, point of rostrum broken off, spine partially covered with sediment. Valve moderately preserved. Different shape of RV clearly visible, as well as the alveolar ridge and the small cyathus-like protrusion in the RV. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544232.

8   Right lateral view of adult carapace of presumed female dimorph, diagenetically altered, posterior region partially damaged, dark stains are impressions of sediment grains. Cyathus-like protrusion in both valves. Sample SBCR Lah3Tp, Lakota Formation, Stage Barn Canyon Road, SD, U.S.A., (Text-fig. 2, loc. 8), USNM 544233.

9   Right dorsolateral view (specimen inclined to the left), adult carapace of presumed female. Strong perpendicular anterocentral ridge, well-developed spine and strongly developed surface characters. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544234.

10 Right lateral view, adult carapace of presumed male. Areas appearing dark are covered with glue. Spine and cyathus of left valve broken off. Specimen in the collection of I. G. Sohn, assemblage slide USNM 242984, Chilson Member of the Lakota Formation, Fall River Canyon (locality 12 in Sohn 1979), SD, U.S.A. (about Text-fig. 2, loc. 3 here).

11 Left lateral view, strongly diagenetically altered and partly deformed adult carapace of presumed male. Dorsally und laterally compressed, anterodorsal part of outline and anterolateral area atypical through deformation of carapace. Anterocentral ridge visible, spine small and mostly broken off. Dark areas covered with glue. Specimen in the collection of I. G. Sohn, assemblage slide USNM 242984, Chilson Member of the Lakota Formation, Fall River Canyon (locality 12 in Sohn 1979), SD, U.S.A. (about Text-fig. 2, loc. 3 herein).

12 Left lateral view, adult carapace of presumed male, partially vertically compressed and slightly deformed. Areas appearing dark covered with glue. Surface characters and anterocentral ridge and sulcus developed, no spine. Specimen in the collection of I. G. Sohn, assemblage slide USNM 242984, Chilson Member of the Lakota Formation, Fall River Canyon (locality 12 in Sohn 1979), SD, U.S.A. (about Text-fig. 2, loc. 3 here).

13 Magnification of a section of specimen 1 of this plate, USNM 544226. Basal part of spine (broken off), surface characters and lateral pores.

14 Magnification of a section of specimen 1 of this plate, USNM 544226. Alveolar furrow, alveolar ridge and perpendicular anterocentral ridge and sulcus of the LV (only).

15 Magnification of specimen 2 of this plate, USNM 544227. Basal part of spine (broken off) with clearly visible normal pore in its center.
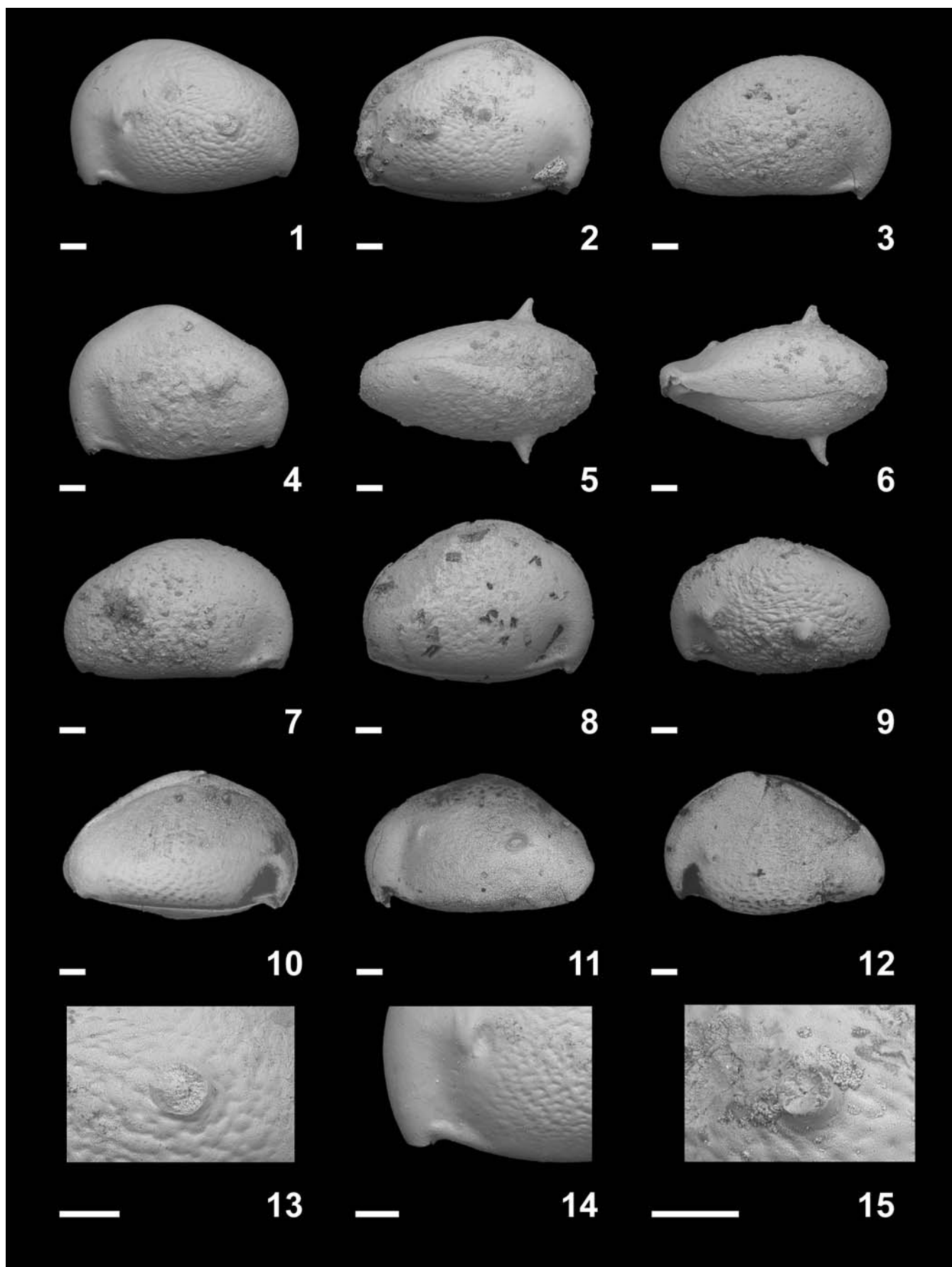
PLATE 4
Scale bar: 100μm; specimens to scale (except Figs. 13-15). SD: South Dakota, UT: Utah.

Cypridea (Pseudocypridina) piedmonti **Sohn 1979**

1 LV, lateral view of adult, slightly compressed laterally and partially covered with sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544235.

2 Right lateral view of adult carapace, dorsolaterally slightly weathered. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544236.

3 LV, internal view, preadult? (A-2?) valve, partially filled with sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544237.

4 Dorsal view of adult carapace showing incised hinge margin, anterior end to the left, posteriorly slightly covered with sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544238.

5 Ventral view, anterior end to the right, adult carapace (with wax stain) showing convex overlap of the LV. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544239.

6 Right lateral view of carapace (view from slightly ventrolateral), adult, specimen in Sohn's collection, specimen No. USNM 242939, loc. 8 of Sohn (1979, fig. 2 therein), Chilson[?] Member of the Lakota For-

mation, eastern Black Hills, SD, U.S.A. (close to Text-fig. 2, loc. 8 herein).

7 Right lateral view of preadult (A-1) carapace, with faint striation anteroventrally and posterodorsally due to slightly sheared sediment. Sample BCB1, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544240.

8-12 Right lateral views, series of photos showing deformation by lateral compression of adult carapaces and resulting changes in carapace outline. Sample HSDC3, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2). 8. USNM 544241, 9. USNM 544242, 10. USNM 544243, 11. USNM 544244, 12. USNM 544245.

13 LV, internal view of rostrum, magnification of specimen 1 of this plate, USNM 544235.

14 Rostrum, lateral view, anteroventral region of carapace with rostrum, rostral part of right valve partially missing and thus showing part of the internal view of the left valve's rostral region. Sample HSDC3, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2).

15 Cyathus, internal view of LV, partially covered with sediment. Sample HSDC3, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2).
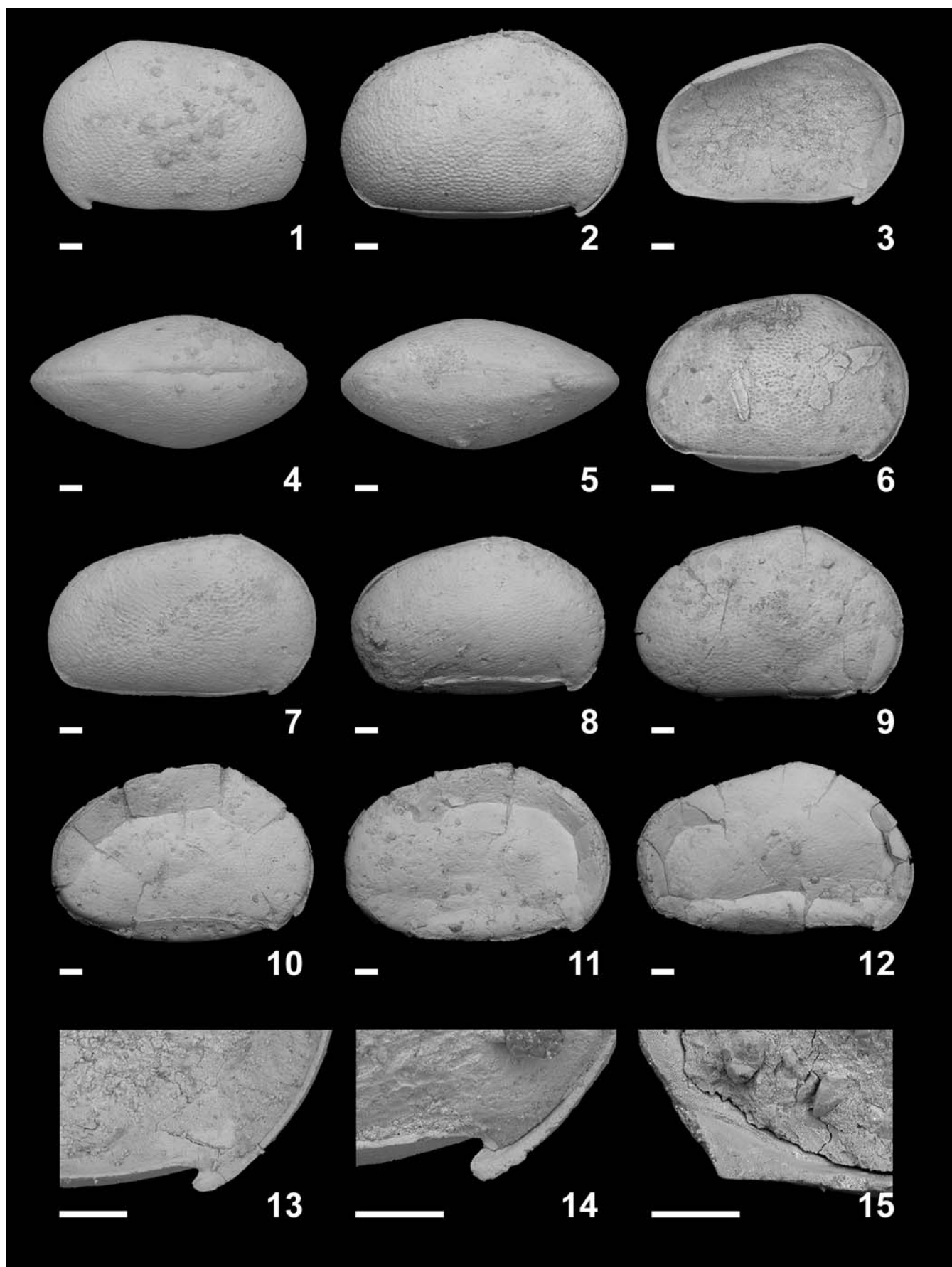
PLATE 5
Scale bar: 100µm; specimens to scale. SD: South Dakota

Cypridea (Pseudocypridina) piedmonti **var.** *henrybelli* **Sohn 1979**

1 LV, lateral view, adult presumed female valve with slight cracks and moderate anterolateral node. Sample HSDC1, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2), USNM 544246.

2 LV, lateral view, adult presumed female valve, damages anterodorsally, with strong anterolateral and moderate posterolateral node. Sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2), USNM 544247.

3 LV, lateral view, adult valve, presumed male. Strong anterolateral and moderate posterolateral nodes. Sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2), USNM 544248.

4 Right lateral view of adult carapace, without nodes, ventral overreach of LV distinct. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544249.

5 Right lateral view of adult carapace, with small but strongly developed anterolateral and posterolateral nodes. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544250.

6 RV, internal view of adult carapace, partially filled with sediment. Sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2), USNM 544251.

7-12 Dorsal views, series of photos showing prograding development of noding: 7. starting with a very weakly developed anterior node in the LV only (anterior end to the right, presumed male, sample HSDC3), USNM 544252; 8. then followed by a stronger anterior left node and a weak posterior left node (anterior end to the right, presumed female, sample HSDC3), USNM 544253; 9. next stage with relatively strong anterior and posterior nodes in the LV and a barely noticeable anterior node in the RV (anterior end to the left, sample BCE*), USNM 544254; 10. stage with four nodes, those in the LV larger than in the RV (anterior end to the left, sample BCE*), USNM 544255; 11. specimen with four strong nodes, those of the LV much stronger developed (anterior end to the left, presumed male, sample HSDC4), USNM 544256; 12. specimen with four very strong nodes of about the same size, except the anterior left one still being the largest (anterior end to the left, presumed female, sample HSDC4), USNM 544257. Sample BCE*: Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1). Samples HSDC3 and HSDC4: Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2).

13 LV, lateral view of adult valve, presumed male, rostrum broken apart, antero- and posterolateral nodes broken/deformed, sample BCB2, Lakota Formation, Buck Canyon, SD U.S.A. (Text-fig. 2, loc. 1), USNM 544258.

14 LV, lateral view of adult valve, strongly damaged and partially weathered. Anterolateral node broken on top and showing its hollow interior. Sample BCB2, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544259.

15 LV, internal view of adult valve, partially filled with sediment, rostrum missing, sample HSDC4, Chilson Member of the Lakota Formation, Horse Sanctuary – Devil's Canyon, SD, U.S.A. (Text-fig. 2, loc. 2), USNM 544260.
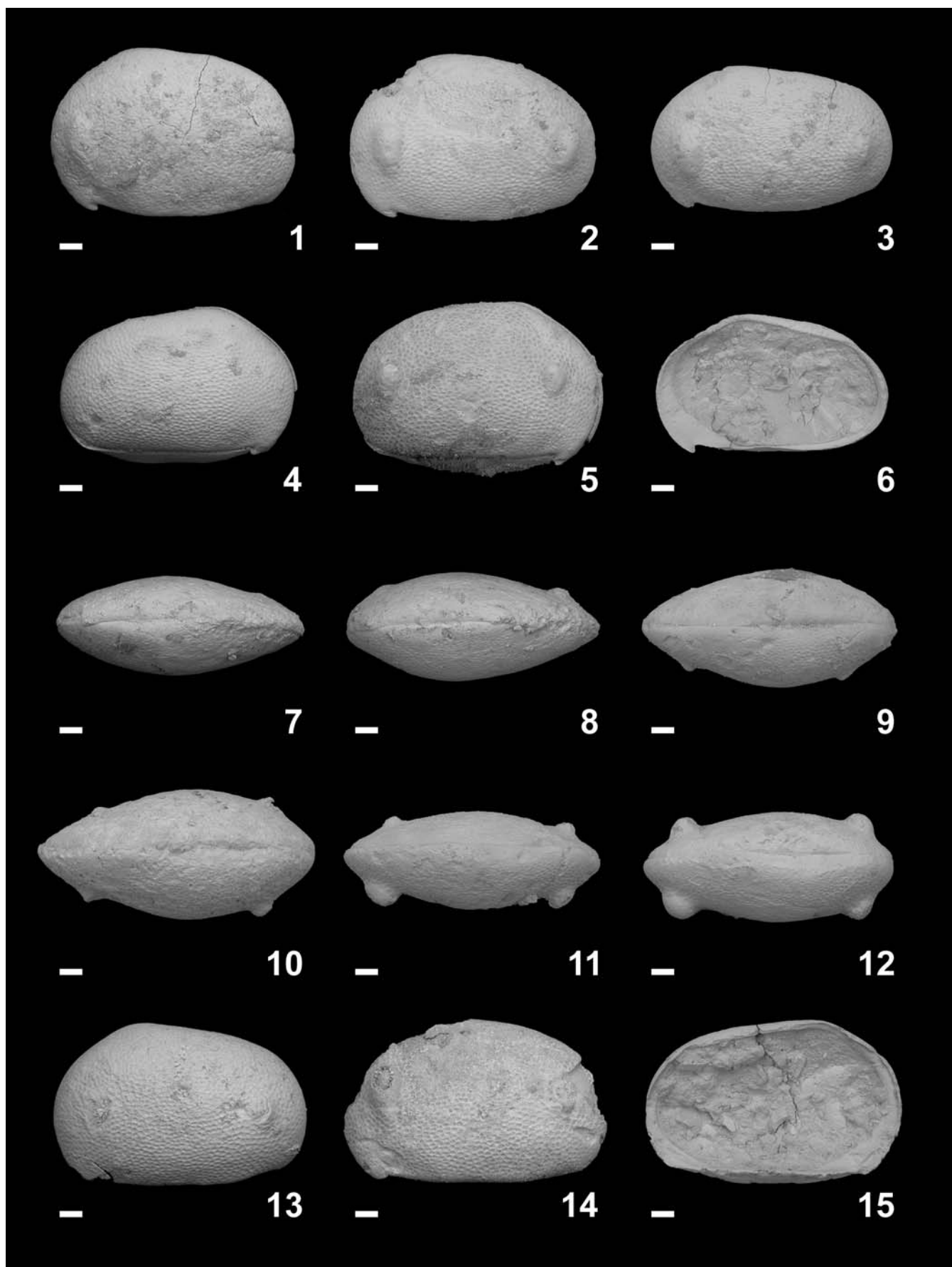
PLATE 6

Scale bar: 100μm; specimens to scale (except Figs. 4, 5, 15). SD: South Dakota.

Cypridea (Pseudocypridina) laeli **Sohn 1979 cf.** *C. (P.)* *moneta* **Kneuper-Haack 1966**

1 LV, lateral view of adult (female?) valve, with cracks but nearly true outline, lateral normal pores visible, carinate rostrum. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Text-fig. 2, loc. 9), USNM 544261.

2 RV, lateral view of adult (female?) valve, broken. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544262.

3 Dorsal view of adult (female?) carapace, anterior end to the left. With strong crack in center. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544263.

4 LV, lateral view, anteroventral region with carinate rostrum in LV. Sample EBF 04b2, Fuson Member of the Lakota Formation, East of Belle Fourche Road, SD, U.S.A. (Text-fig. 2, loc. 7), USNM 544261.

5 RV, lateral view, magnification of specimen 2 of this plate, anteroventral region with carinate rostrum in RV. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544262.

6 RV, internal view of preadult (A-1?, female?) valve, mostly filled with broken parts of LV. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544264.

7 LV, lateral view of adult (male?) valve, lateral pores visible, with very weak tubercles posterolaterally. Alveolus masked by sediment behind it, carinate rostrum, ventral ridge. Sample SBCR Lag3*, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544265.

8 RV, lateral view of adult valve, broken/laterally compressed, rostral keel not visible. Sample SBCR Lag3*, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544266.

9 RV, lateral view of adult (male?) valve, rostral keel not visible. Sample SBCRClay v1254 (=SBCR LAg3* here), Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544267.

10 RV, lateral view of preadult (A-2?) valve, with moderate punctation being somewhat stronger than in adults of the same sample. Sample SBCRClay v1254 (=SBCR LAg3* here), Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544268.

11 Right ventrolateral view, internal mold of adult carapace with typical outline following that of the RV. Sample SBCR LAg2, Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544269.

12 Left lateral view, internal mould of preadult (A-2?) carapace, laterally compressed. Sample SBCRClay v1254 (=SBCR LAg3* here), Fuson Member of the Lakota Formation, Stage Barn Canyon Road, SD, U.S.A. (Text-fig. 2, loc. 8), USNM 544270.

13 LV, internal view of adult (female?) carapace, partially filled with sediment, with carinate rostrum. Deep incision of the hinge margin visible. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Text-fig. 2, loc. 9), USNM 544271.

14 RV, internal view of adult valve, posterior end broken apart, muscle scars visible in part. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Text-fig. 2, loc. 9), USNM 544272.

15 RV, internal view, magnification of specimen 14 of this plate, rostrum in RV. Sample REKO 04, Fuson Member of the Lakota Formation, Boxelder Creek, SD, U.S.A. (Text-fig. 2, loc. 9), USNM 544273.
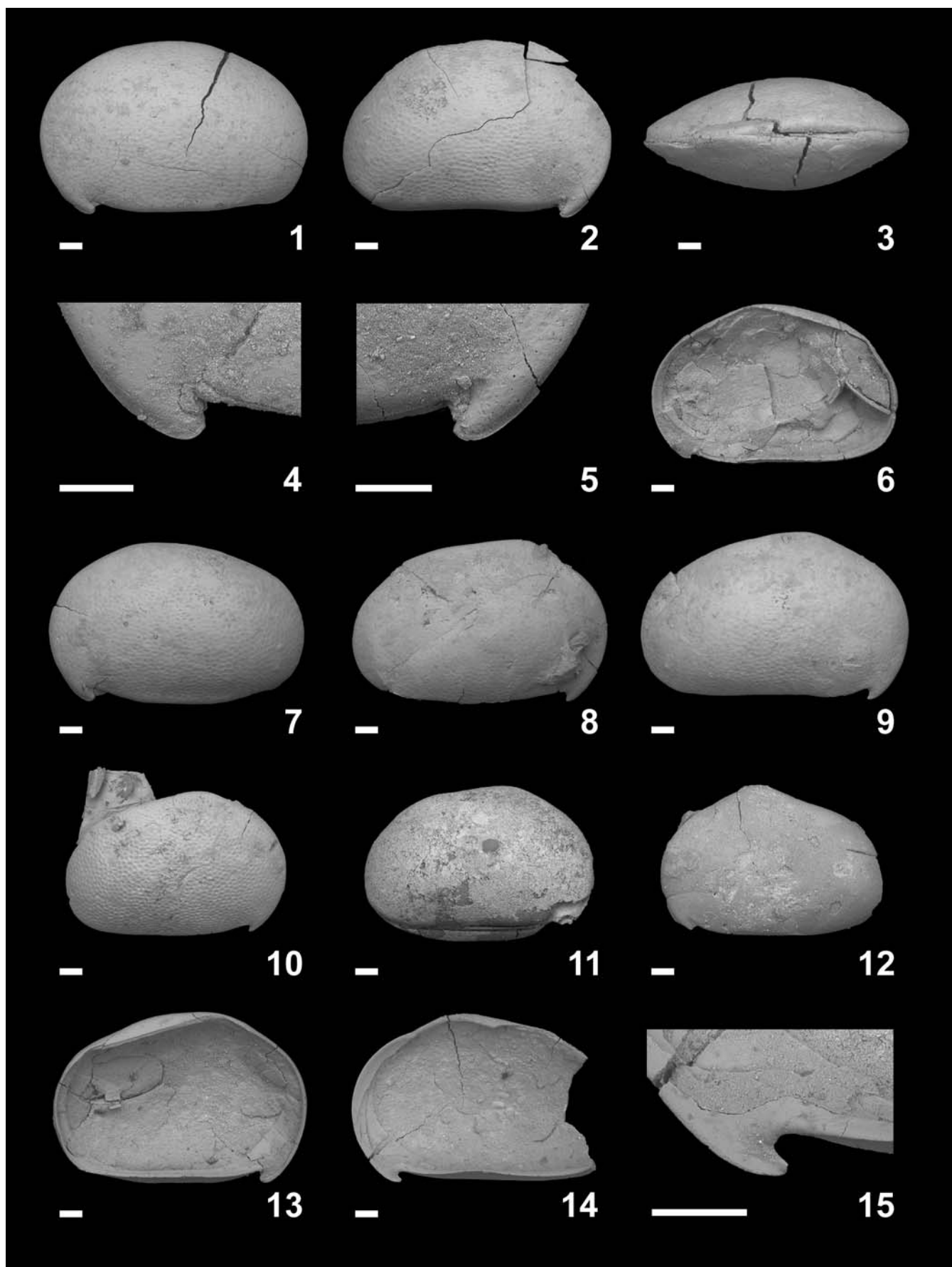
PLATE 7
Scale bar: 100μm; specimens to scale. SD: South Dakota, UT: Utah.

***Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939)**

1 Left lateral view of adult carapace, point of rostrum not complete. Sample BCE, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544274.

2 Right lateral view, complete adult(?) carapace, cyathus and parts of rostrum of LV missing, specimen from the collection of R. E. Peck at the University of Missouri, Columbia (MO). Lower Lakota Formation (Chilson Member), USGS locality D 432 (cf. Peck and Craig 1962, p. 41), SW section of Flint Hill quadrangle, Fall River County, Black Hills, SD (collected by Henry Bell III. and E. V. Post), USNM 544275.

3 Right lateral view of complete adult carapace, weathered, cyathus and rostrum of LV broken apart. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544276.

4 Ventral view, anterior end to the left, upper valve = LV, point of rostrum and posteroventral part of LV broken away. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544277.

5 Dorsal view of preadult (A-1?) carapace, anterior end to the right, upper valve = LV. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544278.

6 Dorsal view of adult (female?) carapace, anterior end to the right. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544279.

7 Left lateral view of adult carapace, strongly weathered, point of rostrum broken away. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544280.

8 Right lateral view of adult carapace, weathered, cyathus present, point of LV's rostrum broken away. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544281.

***Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949**

9 Right lateral view of adult carapace, point of rostrum and cyathus broken away, specimen from the collection of R.E. Peck at the University of Missouri, Columbia (MO). Peck's locality 184-P, Minnewaste Limestone Member of the Lakota Formation, Calico Canyon north of the town of Buffalo Gap, Custer County, SD, U.S.A., USNM 544282.

10 Right lateral view of juvenile (A-2/A-3?) carapace, strongly weathered, ventral part of LV missing. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Text-fig. 2, loc. 5), USNM 544283.

***Cypridea (Pseudocypridina) setina* var. *setina* (Anderson 1939)**

11 RV, lateral view of preadult (A-1?) carapace, posterior marginal part of LV missing. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544284.

12 eft lateral view of strongly weathered adult carapace. Sample FRCA, basal Chilson Member of the Lakota Formation, Fall River Canyon, SD, U.S.A. (Text-fig. 2, loc. 3), USNM 544285.

***Cypridea (Pseudocypridina) setina* var. *rectidorsata* Sylvester-Bradley 1949**

13 Dorsal view of badly weathered adult specimen and steinkern in part, anterior end to the left. Internal imprint of hinge area visible, slightly inclined to the right. Sample ARCR CHz1, uppermost Chilson Member of the Lakota Formation right below Minnewaste Limestone Member, Fall River County, SD, U.S.A. (Text-fig. 2, loc. 5), USNM 544286.

14 Left lateral view of weathered adult species with central parts of its valve missing, partial steinkern. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544287.

15 Left lateral view of weathered and slightly (horizontally) compressed specimen, rostrum broken off but alveolar ridge well visible. Sample PS 1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544288.
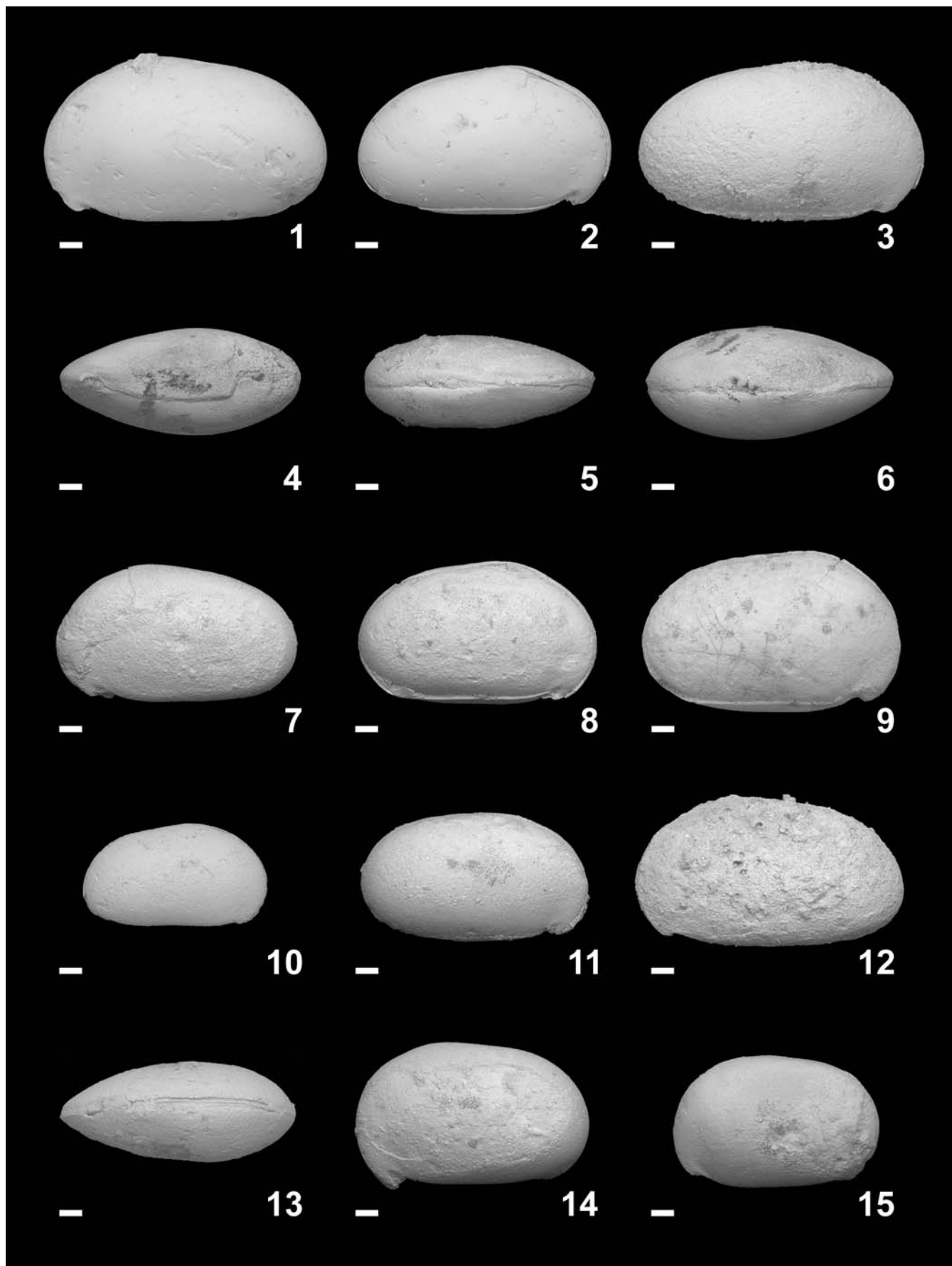
PLATE 8
Scale bar: 100µm; specimens to scale (except Figs. 4, 13, 14). SD: South Dakota, UT: Utah.

Cypridea ex gr. *alta* Wolburg 1959

1 Left lateral view of adult carapace, weathered, point of rostrum broken, alveolar ridge well visible. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544289.

2 Right lateral view of adult carapace, weathered, rostrum broken apart, strong dorsal overreach (dorsal ridge) of larger LV clearly visible, faint indication of alveolar ridge in RV. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544290.

3 Dorsal view of adult carapace, anterior end to the right, weathered, with some wax stains, showing sinuous dorsal ridge in the LV and strong anterior overlap. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544291.

4 Left lateral view, anteroventral region with rostrum and alveolus with alveolar ridge. Magnification of specimen 1 of this plate, USNM 544289.

5 Left lateral view of deformed and strongly weathered carapace. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544292.

6 Right lateral view of adult carapace, strongly weathered, rostrum, and cyathus broken apart. Sample PS1a-70, Yellow Cat Member of the Cedar Mountain Formation, north of Moab, east-northeast of the Ringtail Mine, UT, U.S.A. (Text-fig. 2, loc. 10), USNM 544293.

Cypridea ex gr. *tuberculata* c.f. *C. tilleyi* Loranger 1951

7 Left lateral view of adult? carapace, slightly dipped to the left, spined with dominant central spine and alveolar ridge. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544294.

8 Right lateral view of adult? carapace, partially covered with sediment, showing overlap and overreach of LV over RV. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544295.

9 Left lateral view of adult? valve, prominent anterior cardinal angle visible, partially covered with sediment. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544296.

10 Dorsal view of adult? carapace, anterior end to the left. Slightly dipped to the right, showing broad dorsal furrow. Sample BC504, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544297.

11 Ventral view of adult? carapace, anterior end to the left. Strong overlap of LV visible. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544298.

12 LV, internal view of adult? carapace, partially filled with sediment, posterior limen visible. Sample BC5 04, Chilson Member of the Lakota Formation, Buck Canyon, SD, U.S.A. (Text-fig. 2, loc. 1), USNM 544299.

13 Left lateral view of anteroventral region. Magnification of Fig. 7 of this plate, USNM 544294. Rostrum with minor tubercles, alveolar ridge and alveolar furrow (with puncta!), and several normal pores well visible.

14 LV, internal view of hinge. Magnification of Fig. 12 of this plate, USNM 544299. Elongate sockets and broad median ridge, all elements smooth.