

# Kimmeridgian (Late Jurassic) ostracods from Highway A16 (NW Switzerland): taxonomy, stratigraphy, ecology, and biogeography

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Received: 12 March 2013 / Accepted: 3 July 2013 / Published online: 16 November 2013  
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**Abstract** Ostracods are a common microfaunal element of the Kimmeridgian of the Jura Mountains in NW Switzerland. The stratigraphical subdivision within the Kimmeridgian can as clearly be inferred from ostracods as it is the case from the ammonite biozonation. This proves the utility of the ostracod biozonation, especially where ammonites are not available or rare. The ostracod-bearing layers of the sequence under study (middle part of the Reuchenette Formation = Banné Member, Courtedoux Member and Lower Virgula Marls) have been deposited in waters with highly brackish to marine salinities (high in the pliohaline range to—predominantly—brachyhaline according to the Venice System, Oertli 1964). From the base of the section (base of the Banné Member, high brachyhaline in average), salinities slowly decreased, with lowest salinities in the lower dinosaur track levels of Courtedoux Member (high pliohaline on average). They then increased again to higher salinities (high brachyhaline on average) above the upper dinosaur track levels of the Courtedoux Member and the Lower Virgula Marls (lowest *A. eudoxus* Zone). These trends perfectly correlate with the increased occurrence of ammonites above the upper dinosaur track levels. In terms of Kimmeridgian ostracod palaeobiogeography, the fauna of the NW Swiss

Jura Mountains described in this work is most similar to the Aquitan and Paris Basins, a little less to Northern Germany, and even less (with not even half of the species in common) to Southern Germany. The NW Swiss Jura Mountains still belong to a largely boreally influenced “Western and Central European subprovince”, whereas Southern Germany (though located more to the north) was subjected to an enhanced tethyan influence.

**Keywords** Ostracoda · Micropalaeontology · Biostratigraphy · Reuchenette Formation · Banné Member · Courtedoux Member · Swiss Jura Mountains

## Abbreviations

MJSN Musée jurassien des sciences naturelles, Porrentruy (Canton Jura, Switzerland)

## 1 Introduction

As a result of the construction of Highway A16 (“Transjurane”) in the Canton Jura (NW Switzerland), a new palaeontological survey project, the Palaeontology A16, was established in February 2000. This project, integrated in the “Section d’archéologie et paléontologie” of the “Office de la culture” of the “République et Canton du Jura”, is in charge of safeguarding and documenting the paleontological heritage prior to highway construction, and to make it accessible for scientific research (Hug et al. 2004; Marty et al. 2004; Ayer et al. 2005, 2006).

In Late Jurassic deposits, systematic excavations carried out between 2000 and 2011, have resulted in the discovery of several large-scale dinosaur tracksites (Marty 2008; Marty et al. 2003a, 2004, 2007, 2010), terrestrial wood

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Editorial Handling: C. Pirkenseer.

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remains (Philippe et al. 2010), numerous remains of marine vertebrates (Billon-Bruyat and Marty 2004; Billon-Bruyat 2005a, b; Billon-Bruyat et al. 2012), and a diverse marine invertebrate fauna (Marty et al. 2003b; Hicks 2006; Richardt 2006; Ayer et al. 2008; Waite et al. 2008). Moreover, in the course of these excavations and on highway construction sites and associated quarries, numerous sections were measured in detail and sampled for sedimentological (microfacies, geochemistry, clay mineralogy, stable isotopes, etc.) and micropalaeontological purposes.

Comment et al. (2011) have presented a composite reference section and two new members for the Kimmeridgian Reuchenette Formation of the Ajoie district. For this reference section, numerous new findings of ammonites provide a well-defined stratigraphical framework (Jank et al. 2006b; Comment 2012), which can further be refined by palynological data and the occurrence of microfossils such as foraminifers, charophytes, and ostracods. However, with a few exceptions (Oertli and Ziegler 1958; Oertli 1959, 1963), ostracod faunas from the Late Jurassic of the northwestern Swiss and French Jura Mountains were not studied in detail, due to the abundant ammonite faunas, which were preferentially and generally used for stratigraphical purposes (e.g. Hantzpergue 1975; Gygi 1995, 2000a, b, 2001, 2003). Nevertheless, ostracods are regarded useful in providing additional stratigraphic information and confirmation of previous age determinations (Colin and Lethiers 1988; Schudack and Schudack 2000, 2002) and especially as indicators for ecological changes (Oertli 1964; Neale 1988; Sames 2008).

Accordingly, the present contribution focuses on (1) the description and taxonomy of the ostracod fauna from the Kimmeridgian Reuchenette Formation; (2) the confirmation and—if possible—refinement of the ammonite biostratigraphy; (3) the reconstruction of the depositional environment and detection of salinity fluctuations; and (4) the palaeobiogeographic relationship of Kimmeridgian ostracods from the northwestern Jura Mountains with other European areas.

## 2 Geographical and geological setting

The studied material is from five excavation sites are located in the northwestern part of the Swiss Jura Mountains, on the future route of Highway A16, on a plateau between Courtedoux and Chevenez about 5 km to the west of Porrentruy, the provincial capital of the Ajoie district (Fig. 1). Today, all excavation sites are destroyed and/or obscured by the Highway A16.

The Ajoie district is located in the Tabular Jura Mountains, at the eastern end of the Rhine-Bresse transfer zone (Giamboni et al. 2004) and between the Folded Jura

Mountains to the South and east and the Upper Rhine Graben and Vosges Mountains to the north. In the Tabular Jura Mountains of the Ajoie district, mainly Mesozoic (Late Jurassic) sediments crop out. These form (sub-)horizontally layered rock formations, separated by narrow dislocation belts (Trümpy 1980; Jordan et al. 2008). Tectonic activities from the Eocene to the Pleistocene formed a broad complex of fractures and low amplitude faults (Giamboni et al. 2004; Ustaszewski et al. 2005; Brailard 2006).

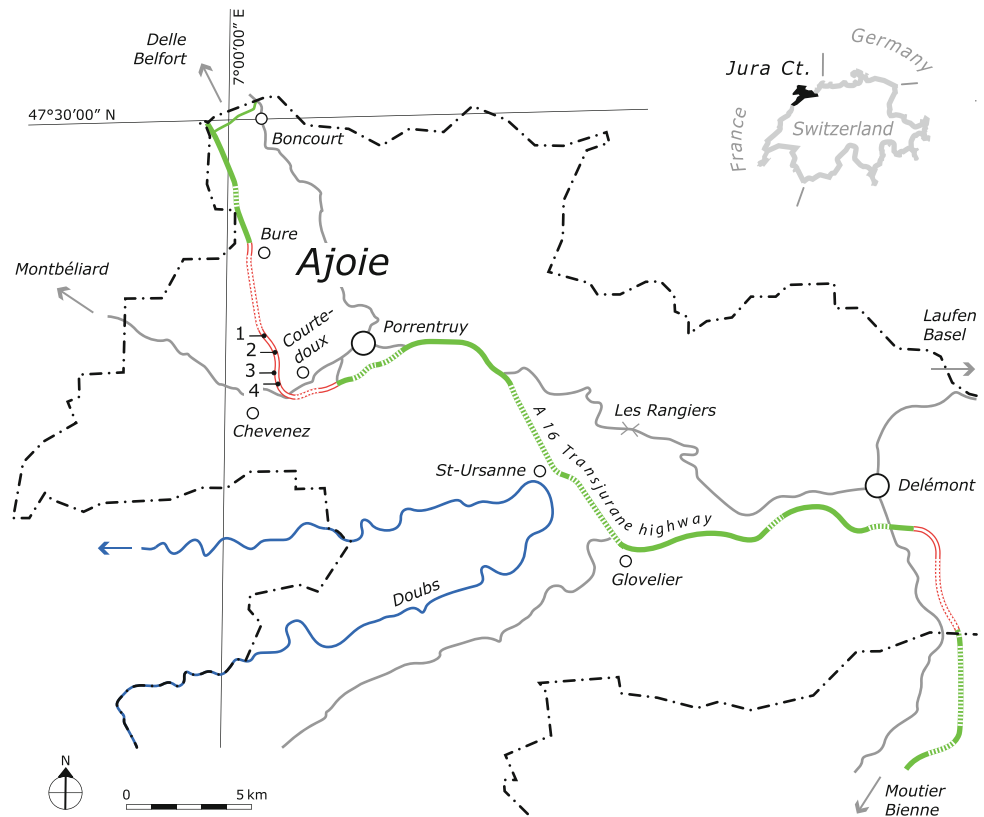
During the Late Jurassic, the study area was situated at the northern margin of the oceanic Ligurian Tethys (e.g. Gygi 1990; Thierry 2000; Stampfli and Borel 2002), as a large and structurally complex, epicontinental carbonate platform with palaeoenvironments including terrestrial areas, vast tidal flats, (internal and external) lagoons and barriers (e.g. Bläsi 1980; Mouchet 1998; Hillgärtner 1999; Hug 2003; Colombié and Strasser 2005; Colombié and Rameil 2007; Strasser 2007; Jordan et al. 2008; Marty 2008; Gygi 2012). Platform morphology was created by differential subsidence of tectonic blocks and by differential sediment accumulation (e.g. Pittet 1996; Allenbach 2001; Hug 2003; Wetzel et al. 2003). The Jura carbonate platform was situated at a palaeolatitude of around 30°N (Dercourt et al. 1994; Thierry et al. 2000), at the threshold between the Paris Basin to the northwest and the Tethyan Ocean to the south and thus, influenced by both the Tethyan and Boreal realms (Ziegler 1988; Meyer and Schmidt-Kaler 1989; Dercourt et al. 1994; Jank 2006a, c).

In central Europe, the climate during the latest Jurassic was semi-arid Mediterranean with strong seasonal differences between prolonged, warm, dry summers and relatively short, wet winters (Hallam 1985; Abbink et al. 2001; Rees et al. 2004). Orbitally-controlled high-frequency and low-amplitude (a few meters in range) sea-level changes were superimposed on the general second-order transgressive trend of the Late Jurassic (e.g. Hardenbol et al. 1998; Hallam 2001; Colombié and Rameil 2007; Strasser 2007).

## 3 Stratigraphical setting

In an area poor in natural outcrops, the construction of Highway A16 and associated excavations of the Palaeontology A16 Project have created unique opportunities to study both palaeontological and stratigraphical aspects. This has resulted in the compilation of a new, nearly complete composite reference section for the Ajoie district, ranging in age from the Mid Oxfordian to early Late Kimmeridgian. Numerous new findings of ammonites provide a well-defined stratigraphical frame (Jank et al. 2006b), and the Palaeontology A16 currently re-fines and

**Fig. 1** Geographical setting of the five studied sections on Highway A16, Canton Jura, NW Switzerland



re-defines the litho- and chronostratigraphy. Figure 2 provides an overview of the lithostratigraphy of the Upper Jurassic Reuchenette Formation (Thalmann 1966; Gygi 2000a, b) of NW Switzerland. The terminology currently used by the Palaeontology A16 are the Banné Member introduced by Gygi (2000a, b) and Vabenau and Courtedoux Members recently introduced by Comment et al. (2011), as well as the regional lithostratigraphical names (Lower) Virgula Marls and Coral Limestones introduced by Jank et al. (2006a, b) (Fig. 2). Within the Courtedoux Member (Nerinean Limestones sensu Jank et al. 2006a, b, c), three major track-bearing biolaminite intervals have been distinguished so far (Fig. 2) and are designated as the lower, intermediate, and upper (dinosaur track) levels (sensu Marty et al. 2007; Marty 2008).

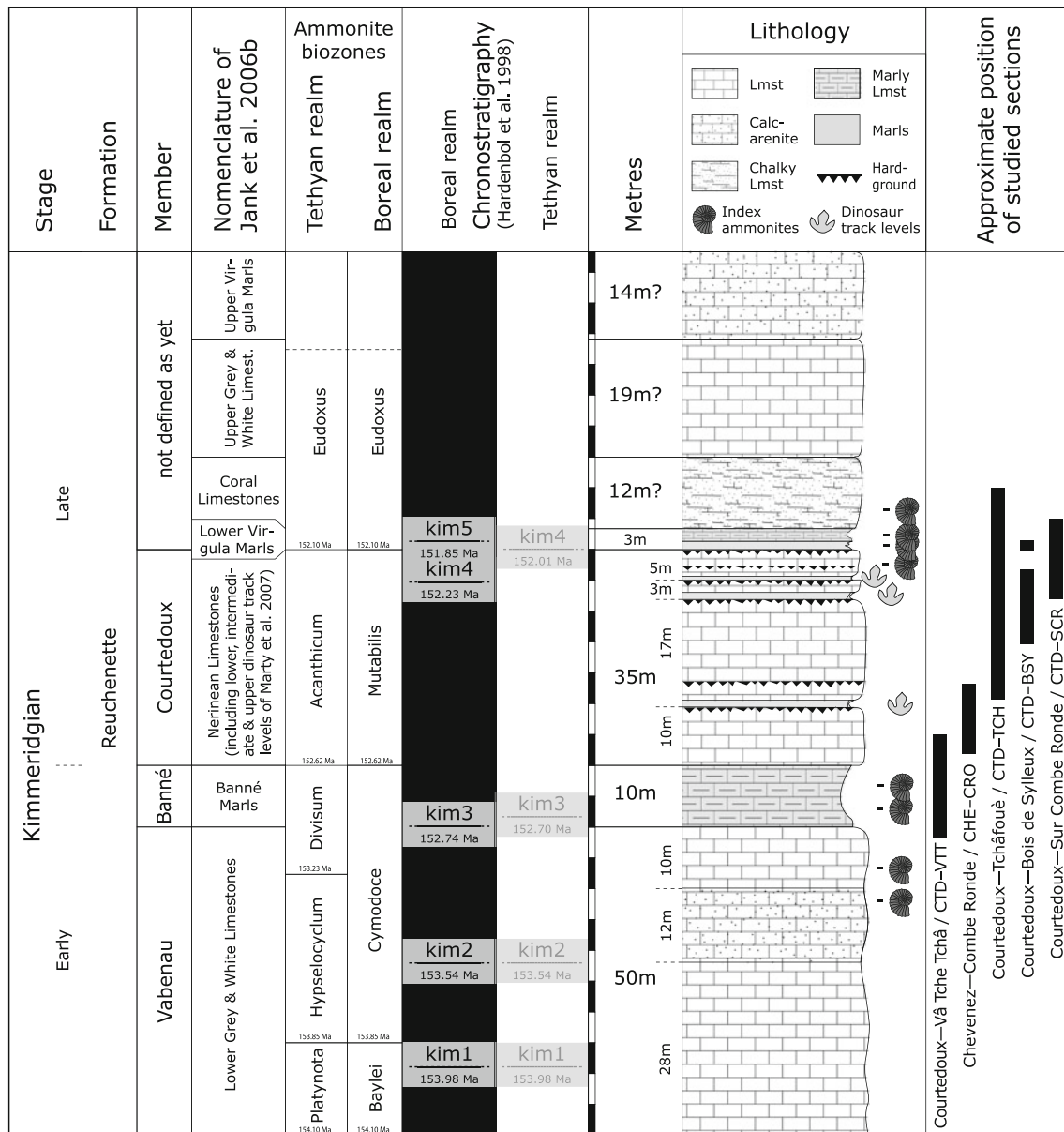
All five sections with ostracod samples are located in the middle part of the Reuchenette Formation, more precisely in the Banné and Courtedoux Members and the Lower Virgula Marls. Figure 3 shows the biostratigraphical position within the Kimmeridgian stage of each of the sections based on ammonites (Hantzpergue et al. 1997; Gygi 2001, 2003; Jank et al. 2006a, b, c), and also the stratigraphical ranges of ostracods (both locally and all over Europa in general). The study area is located in an intermediate position between boreal and tethyal faunal realms (Jank et al. 2006a, b), and in Fig. 3, the boreal ammonite zonation is used (see also Ogg et al. 2012 and Fig. 4 for a

summary). The studied sections range from the upper *Rasenia cymodoce* Zone (latest part of the Early Kimmeridgian) over the *Aulacostephanus mutabilis* Zone (early part of the Late Kimmeridgian) to the lowermost *Aulacostephanus eudoxus* Zone (base of the middle part of the Late Kimmeridgian).

#### 4 Material and methods

This investigation is based on 87 ostracod samples, recovered between 2000 and 2011 on five excavation sites (Figs. 1, 2). On each of the sites, a detailed cross-section was logged in order to precisely locate the samples within the sections, and also in order to correlate layers between different excavation sites.

All excavation sites of the Palaeontology A16 are named in a binominal way: first the community is indicated, followed by the name of the site, e.g. Chevenez—Combe Ronde is the Combe Ronde site on the parish area of Chevenez, and Courtedoux—Sur Combe Ronde is the Sur Combe Ronde tracksite on the parish area of Courtedoux. For each site an acronym is defined, which is composed of two times three capital letters, separated by a hyphen, e.g. CHE—CRO for the Chevenez—Combe Ronde site. This acronym is also used for the labelling of samples, e.g. CTD—SCR004-10 is sample number 10 of the year 2004 of



**Fig. 2** Stratigraphical setting of the Kimmeridgian sequence of the Ajoie region, Canton Jura, NW Switzerland. Sequence boundaries are after Hardenbol et al. (1998) Ammonite zones of the Oxfordian are after Gygi (2000a, b), and those of the Kimmeridgian after

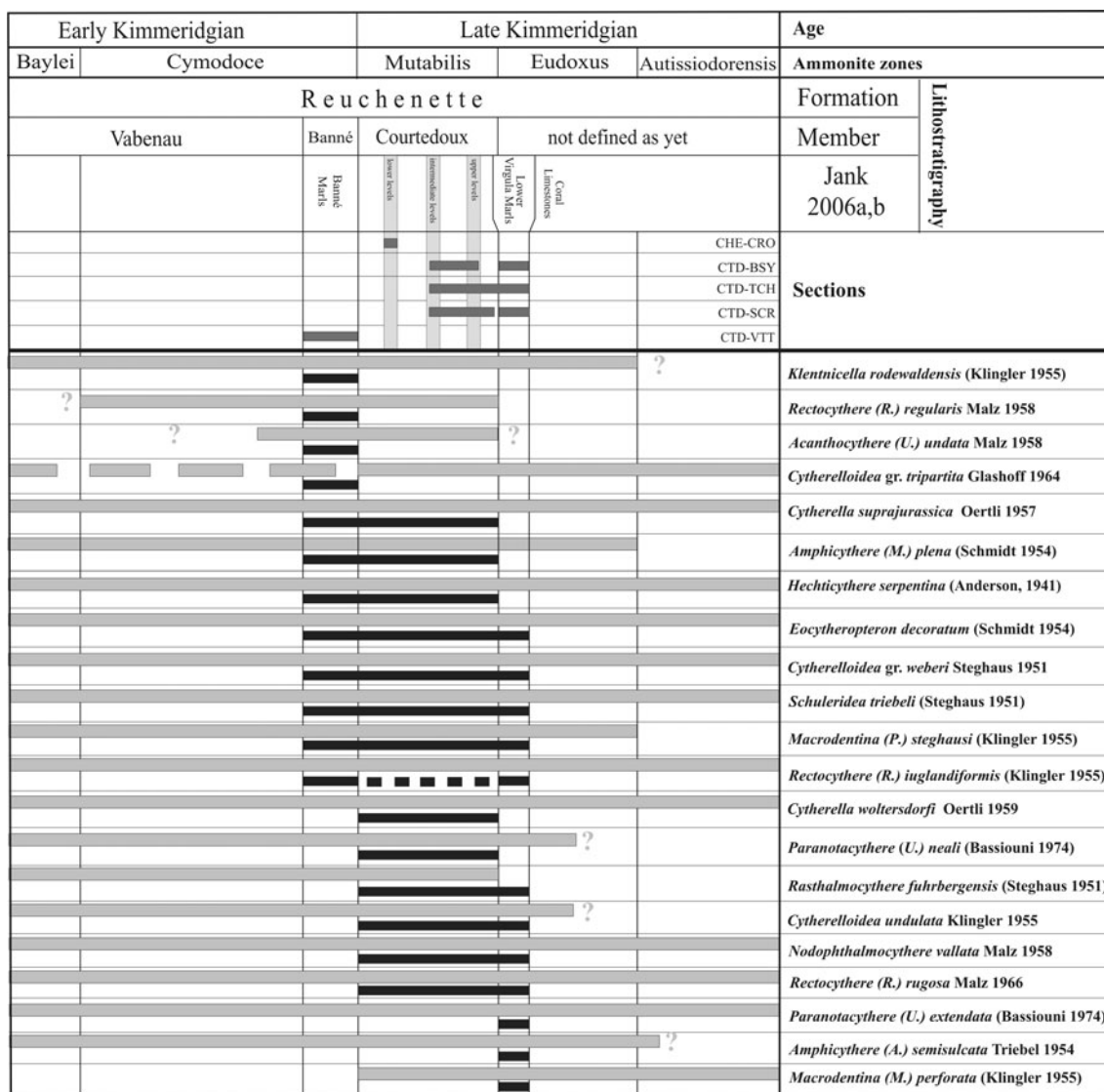
Hantzpergue et al. (1997). Note that the stratigraphic ranges of the five sections indicated on the right, refer to the entire sections logged in the field and not only to those parts of the sections containing ostracods, as indicated in Fig. 3

the Courtédoux—Sur Combe Ronde site. All studied material is deposited in the collection of the Palaeontology A16 (*Paléontologie A16*; PAL A16) of the Musée jurassien des sciences naturelles (MJSN, Natural History Museum of the Canton Jura) in Porrentruy, Canton Jura, Switzerland.

All ostracods were recovered from clay- and marlstone samples, which were systematically sampled, and subjected to a standard screen-washing procedure. Microfossils were picked by the Palaeontology A16, and mainly found in fractions larger than 0.14 and 0.25 mm. All SEM photographs were taken with a ZEISS SUPRA<sup>TM</sup> 40 VP Ultra

Scanning Electron Microscope at the Fachrichtung Paläontologie, Institut für Geologische Wissenschaften, FU Berlin.

Concerning salinity tolerances, the classification of brackish waters follows the Venice System according to Oertli (1964). The particular information about the genera derives from diagrams mainly after Sohn (1951), Oertli et al. (1961), Neale (1964) and Anderson (1971), compiled by Weiss (1995). Methods of biostratigraphic and palaeoecologic analyses are described in the relative chapters.



**Fig. 3** General stratigraphic ranges of the ostracod species in the sections under study (*black lines*) and supra-regional stratigraphical ranges of these species in neighbouring European areas (*grey lines*). Sequence boundaries are after Hardenbol et al. (1998), ammonite zones of the Oxfordian after Gygi (2000a, b), and ammonite zones of

the Kimmeridgian after Hantzpergue et al. (1997). Note that the stratigraphic ranges of the five sections only refer to those parts of the sections containing ostracods. (1) Courtedoux—Vâ Tche Tchâ; (2) Courtedoux—Bois de Sylleux; (3) Courtedoux—Combe Ronde & Tchâfouè; (4) Courtedoux—Sur Combe Ronde

**5 Systematic palaeontology**

Twenty-one species (1 species in open nomenclature) belonging to 13 genera were identified and they are listed in Figs. 5, 6, 7, 8, 9 and illustrated in Figs. 10, 11, 12. Generally, the descriptions of the identified species are not exhaustive, as none of them is new. More detailed comments are given for only those taxa, which need systematic revision or where peculiar, additional information is required. All further characteristics are explained under “remarks”.

The stratigraphical range of Late Jurassic ostracods in Europe is compiled after Schudack (1994, 2004) and Schudack and Schudack (2000). Figure 3 only provides the

stratigraphical ranges of species with assured determinations at the species level. For a few species in open nomenclature (cf. and others), the nominate species is taken as the stratigraphical reference. In order to provide the most comprehensive information possible, we have added “cf.”—species to the nominate species in cases of unsecure (due to bad preservation) specific assignment in several cases, which does not mean we believe these might be different species.

- Subclass Ostracoda Latreille 1802
- Order Müller 1894
- Suborder Sars 1866

Age	Biozones Zeiss (2003)		Lithostratigraphy of the Swiss Jura Mountains (after Gygi 2000a,b, Jank et al. 2006a,b, Comment et al. 2011)		Caesar (2012)		Ostracod zones NW Germany (modified from Schudack 1994)	Southern Germany (as used by Schudack & Schudack 2000)				
	submedi- terran	sub- boreal			Lithostratigraphy	Klingler et al. (1962)		Ammonite Zones				
Late Kimmeridgian	Beckeri	Autissiodorensis	Reuchenette Formation	non défini	Ober-Kimmeridge	jwo1	Zone 15	Late	Beckeri			
	Eudoxus	Eudoxus		Coral Limestones		Eudoxus				jwm3	Zone 14	Eudoxus
	Acanthicum	Mutabilis		Courtedoux Mb.		Mutabilis				jwm2		
	Divisum	Cymodoce		Banné Mb.		Cymodoce				jwm1	Zone 12	Divisum
Early Kimmeridgian	Hypselocyclum	Cymodoce	Vabernau Mb.	Lower Grey and White Limestones	Unter-Kimmeridge	Baylei	Zone 11	Early	Hypselocyclum			
	Baylei									Zone 10	Baylei	
	Zone 9									Zone 8	Zone 7	
	Zone 8									Zone 7		
	Zone 7											
	Humeralis-Schichten									jwu6		
		Süntel-Formation		Mittel-Kimmeridge								

Fig. 4 Chrono- and lithostratigraphic correlation, as well as ammonite and ostracod biozones of the Kimmeridgian in Germany and Switzerland

Family Sars 1866

Genus *Cytherella* Jones 1849

*Cytherella suprajurassica* Oertli 1957 (Fig. 10a)

*Localities and samples.* Section CTD-VTT, samples 006-1506 to 1507, 006-1510 to 1512, 006-1514 to 1517, 006-520, 006-1523 to 1524, 006-1526 to 1528, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD-TCH, samples 006-1166, 006-1169, 006-1173, 004-1219, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian to early Late Kimmeridgian, *R. cymodoce* Zone to *A. mutabilis* Zone.

*Stratigraphic range in Europe.* Oxfordian (Oertli 1957) to Late Kimmeridgian (*sensu gallico*) (*Aulacostephanus autissiodorensis* Zone, Ioannides et al. 1988).

*Cytherella cf. suprajurassica* Oertli 1957

*Localities and samples.* Section CTD-VTT, sample 006-1522, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.





Chevenez–Combe Ronde CHE-CRO					Salinity		
Age	Ammonite Zone	Formation	Member	Layer		Sample	
Late Kimmeridgian	Mutabilis	Reuchenette	Courtedoux Member			no ostracods identifiable	
				550	CRO003-35		
				546	CRO004-308		
				545	CRO004-315		
				544	CRO004-313		
				542-543	CRO004-280		
				535-540	CRO004-300		
					CRO004-298		
				528-530	CRO004-283		
				525	CRO004-294		
				520	CRO004-285		
				510-515	CRO004-289		
				505-508	CRO004-240		■
				502	CRO004-303		
				501	CRO004-319		■

**Fig. 6** Identified ostracod species in the various layers of section CHE–CRO and the resulting “average” salinity changes within the lower dinosaur track levels of the Courtedoux Member of the Reuchenette Formation (salinities according to the Venice System, Oertli 1964)

*Stratigraphic range in the study area.* Late Early Kimmeridgian, *R. cymodoce* Zone.

*Cytherella woltersdorfi* Oertli 1959 (Fig. 10b)

*Localities and samples.* Section CTD–TCH, sample 005-935, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in Europe.* Oxfordian to Late Kimmeridgian (Schudack and Schudack 2000), Oxfordian of the Swiss Jura Mountains (Oertli 1959).

*Cytherella* sp. (Fig. 10c)

*Localities and samples.* Section CTD–TCH, samples 006-1159, 006-1161, 006-1164 to 1166, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

Genus *Cytherelloidea* Alexander 1929

*Remarks.* The problem of the “Formenkreis” of the species *Cytherelloidea weberi/paraweberi/tripartita* and *recticostata* is discussed in detail by Schudack (1994, 2004) and Schudack and Schudack (2000). The classification used in this paper is based on Schudack and Schudack (2000).

*Cytherelloidea* gr. *weberi* Steghaus 1951 (Fig. 10d, e)

*Localities and samples.* Section CTD–VTT, samples 006-1506, 006-1511 to 1512, 006-1515, 006-1517, 006-1520, 006-1523 to 1527, 003-346, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD–TCH, sample 005-940, Lower Virgula Marls, early Late Kimmeridgian, *A. eudoxus* Zone, samples 006-1159 to 1163, 006-1169 to 1171, 004-1219 to 1220, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Early to early Late Kimmeridgian, *R. cymodoce* Zone to *A. eudoxus* Zone.

*Stratigraphic range in Europe.* Late Oxfordian (Oertli 1957) to Kimmeridgian (*A. mutabilis* Zone and *A. eudoxus* Zone in England, Wilkinson 1983), Tithonian, “Lower Portlandian” (Kilenyi 1978).

*Cytherelloidea* gr. *tripartita* Glashoff 1964 (Fig. 10f)

*Localities and samples.* Section CTD–VTT, sample 006-1513, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in Europe.* Late Kimmeridgian (*Aspidoceras acanthicum* Zone to *Hybonoticeras beckeri* Zone of Southern Germany, Schudack and Schudack 2000), Middle Kimmeridge Member of Eastern Germany (approximately *A. mutabilis* Zone, Schudack 2004), Late Oxfordian of Switzerland (Oertli 1959) and NW Germany (Glashoff 1964).

*Cytherelloidea undulata* Klingler 1955 (Fig. 10g–i)

*Remarks.* *Cytherelloidea undulata* appears with a variety of ornamentations. Forms with an apparently coarse undulation (Fig. 10g) are as well represented as forms with a more subtle ornamentation pattern (see also Oertli 1959: 18), usually diagnostic for this species (Fig. 10h). In addition there are individuals, where the ornamentation is dissolved to small knob-like crests (Fig. 10i). There is only insufficient material available, thus it is not possible to decide whether it is possible or required to separate a new species. We preliminarily regard it as a variability of the “normal” species.







Subfamily Palaeocytherideinae Mandelstam 1960  
 Tribus Hechticytherini Gründel 1974  
 Genus *Hechticythere* Gründel 1974

***Hechticythere serpentina* (Anderson 1941)** (Fig. 10j, k)

*Remarks.* We follow Wilkinson and Whatley (2009), who regard *Hechticythere serpentina* (Anderson 1941) and *Hechticythere sigmoidea* (Steghaus 1951) to be synonymous, enclosing the variability of both forms. This was already assumed by Barker (1966), but dissented by Malz (1966).

*Localities and samples.* Section CTD–VTT, samples 006-1516, 003-296, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD–TCH, samples 005-935, 006-1159, 006-1161, 006-1163, 006-1169 to 1170, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian to early Late Kimmeridgian, *R. cymodoce* Zone to *A. mutabilis* Zone.

*Stratigraphic range in Europe.* Early Kimmeridgian (e.g. Oertli 1963, Dépêche 1985) to Tithonian (Oertli 1963, Kilenyi 1969: *Pavlovia rotunda* Zone).

***Hechticythere cf. serpentina* (Anderson 1941)** (Fig. 10m)

*Localities and samples.* Section CTD–TCH, sample 004-1219, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

***Hechticythere sp.*** (Fig. 10n)

*Localities and samples.* Section CTD–TCH, samples 004-1219, 006-1162, 006-1164, 005-966, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

Tribus Palaeocytherideinae Lyubimova 1955

Genus *Klenticella* Pokorny 1973

***Klenticella rodewaldensis* (Klingler 1955)** (Fig. 10o)

*Localities and samples.* Section CTD–VTT, samples 006-1506, 006-1512, 006-1520, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in Europe.* Late Oxfordian (Stinder 1991), questionably to the mid Late Kimmeridgian (*A. eudoxus* Zone, Oertli 1959); Kilenyi (1978): *Ringsteadia pseudocordata* to *Pictonia baylei* zones, Middle Kimmeridgian Member of NW-Germany (Glashoff 1964; Klingler et al. 1962).

***Klenticella cf. rodewaldensis* (Klingler 1955)**

*Localities and samples.* Section CTD–VTT, sample 006-1522, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian, *R. cymodoce* Zone.

Family Cytherideidae Sars 1925

Subfamily Cytherideinae Sars 1925

Genus *Nodophthalmocythere* Malz 1958

***Nodophthalmocythere vallata* Malz 1958** (Fig. 10p)

*Localities and samples.* Section CTD–SCR, sample 002-1186, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone. Section CTD–TCH, sample 005-938, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; samples 006-1168, 006-1170, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

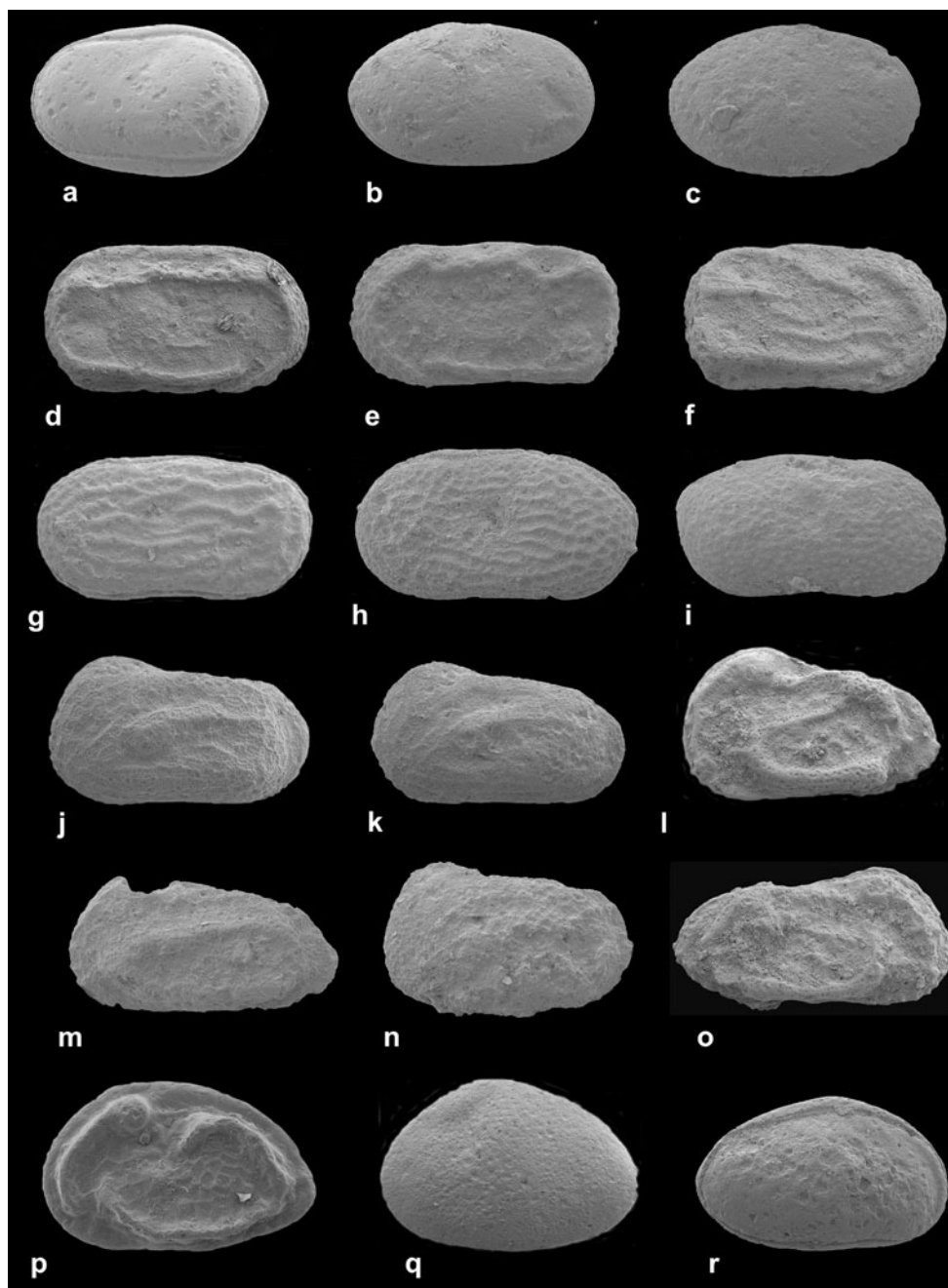
*Stratigraphic range in the study area.* Late Kimmeridgian, *A. mutabilis* Zone to *A. eudoxus* Zone.

*Stratigraphic range in Europe.* Early Kimmeridgian to Late Kimmeridgian, *P. baylei* Zone to *A. autissiodorensis* Zone (Schudack 1994).

Genus *Schuleridea* Swartz & Swain 1946

***Schuleridea triebeli* (Steghaus 1951)** (Fig. 10q, r)

*Localities and samples.* Section CTD–SCR, samples 002-1186, 002-1135, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone. Section CTD–VTT, samples 006-1506 to 1508 006-1511 to 1512, 006-1515 to 1517, 006-1520, 006-1523 to 1528, 003-346, 003-334, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD–TCH, samples, 005-935, 005-968, 006-1160 to 1161, 006-1166, 006-1169, 006-1171, 004-1219, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone; samples 005-39, 005-936, 005-941, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone. Section CTD–BSY, samples 009-259, 009-263 to 265, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; samples 009-1091, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.



*Stratigraphic range in the study area.* Late Early Kimmeridgian to mid Late Kimmeridgian, *R. cymodoce* Zone to *A. eudoxus* Zone.

*Stratigraphic range in Europe.* Late Oxfordian (e.g. Klingler et al. 1962; Oertli 1957, 1959, Swiss Jura Mountains) to Tithonian (Christensen 1968), occasionally having a maximum of occurrence in the early Late Kimmeridgian *A. mutabilis* Zone (Klingler et al. 1962).

Family Cytheruridae Müller 1894

Subfamily Cytherurinae Müller 1894

Genus *Eocytheropteron* Alexander 1933

***Eocytheropteron decoratum* (Schmidt 1954)** (Fig. 11a, b)

*Localities and samples.* Section CTD-VTT, samples 006-1517, 006-1520, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD-TCH, sample 005-939, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; samples 006-1164, 006-1167 to 1168,

◀ **Fig. 10 a** *Cytherella suprajurassica* Oertli 1957, sample TCH006-1166, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 653 µm, carapace from the left. **b** *Cytherella woltersdorfi* Oertli 1959, sample TCH005-935, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 718 µm, right valve. **c** *Cytherella* sp., sample TCH 006-1164, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 543 µm, right valve. **d** *Cytherelloidea* gr. *weberi* Steghaus 1951, sample VTT006-1506, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 537 µm, right valve. **e** *Cytherelloidea* gr. *weberi* Steghaus 1951, sample TCH006-1163, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 557 µm, left valve. **f** *Cytherelloidea* gr. *tripartita* Glashoff 1964, sample VTT006-1512, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 592 µm, µm, carapace from the right. **g** *Cytherelloidea undulata* Klingler 1955, sample TCH006-1161, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 695 µm, carapace from the right. **h** *Cytherelloidea undulata* Klingler 1955, sample TCH006-1170, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 693 µm, carapace from the left. **i** *Cytherelloidea undulata* Klingler 1955, more punctate variety, sample TCH004-1219, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 783 µm, carapace from the right. **j** *Hechticythere serpentina* (Anderson, 1941), sample TCH006-1159, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 722 µm, left valve. **k** *Hechticythere serpentina* (Anderson, 1941), sample VTT006-1516, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 813 µm, left valve. **l** *Klentnicella rodewaldensis* (Klingler 1955), sample VTT006-1506, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 625 µm, left valve. **m** *Hechticythere* cf. *serpentina* (Anderson, 1941), sample TCH004-1219, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 656 µm, left valve. **n** *Hechticythere* sp., sample TCH004-1219, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 756 µm, left valve. **o** *Klentnicella rodewaldensis* (Klingler 1955), sample VTT 006-1512, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 594 µm, right valve. **p** *Nodophthalmocythere vallata* Malz 1958, sample TCH005-938, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 514 µm, carapace from the left. **q** *Schuleridea triebeli* (Steghaus 1951), sample BSY009-259, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length 663 µm, left valve of a female. **r** *Schuleridea triebeli* (Steghaus 1951), sample TCH006-1166, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length 616 µm, right valve of a male

006-1170, Courtedoux Member, early Late Kimmeridgian, *A. eudoxus* Zone. Section CTD–BSY, samples 009-261 to 262, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

Stratigraphic range in the study area: Late Early Kimmeridgian to mid Late Kimmeridgian, *R. cymodoce* Zone to *A. eudoxus* Zone.

Stratigraphic range in Europe. Oxfordian to Kimmeridgian of the Swiss Jura Mountains (Oertli 1959), Early Tithonian of the Paris Basin, France (Oertli 1963).

***Eocytheropteron* cf. *decoratum* (Schmidt 1954) (Fig. 11c)**

*Localities and samples.* Section CTD–BSY, sample 009-261, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Mid Late Kimmeridgian, *A. eudoxus* Zone.

***Eocytheropteron* sp. (Fig. 11d)**

*Localities and samples.* Section CTD–TCH, samples 005-940, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; samples 006-1162, 005-966, 005-968, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

***Eocytheropteron?* sp. (Figs. 11e, 12o)**

*Remarks.* Due to the habit we regard this specimen to belong to *Eocytheropteron*, but as there are no inner valve structures visible on any of the studied specimens, it is not possible to validate this, particularly as the ornamentation pattern is not common for any species of the genus.

*Localities and samples.* Section CTD–TCH, samples 006-1162, 004-1220, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone. Section CHE–CRO, samples 004-240, 004-319, lower (dinosaur track-bearing) levels of the Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

Genus *Paranotacythere* Bassiouni 1974

Subgenus *Paranotacythere (Unicosta)* Bassiouni 1974

***Paranotacythere (Unicosta) extendata* (Bassiouni 1974) (Fig. 11f)**

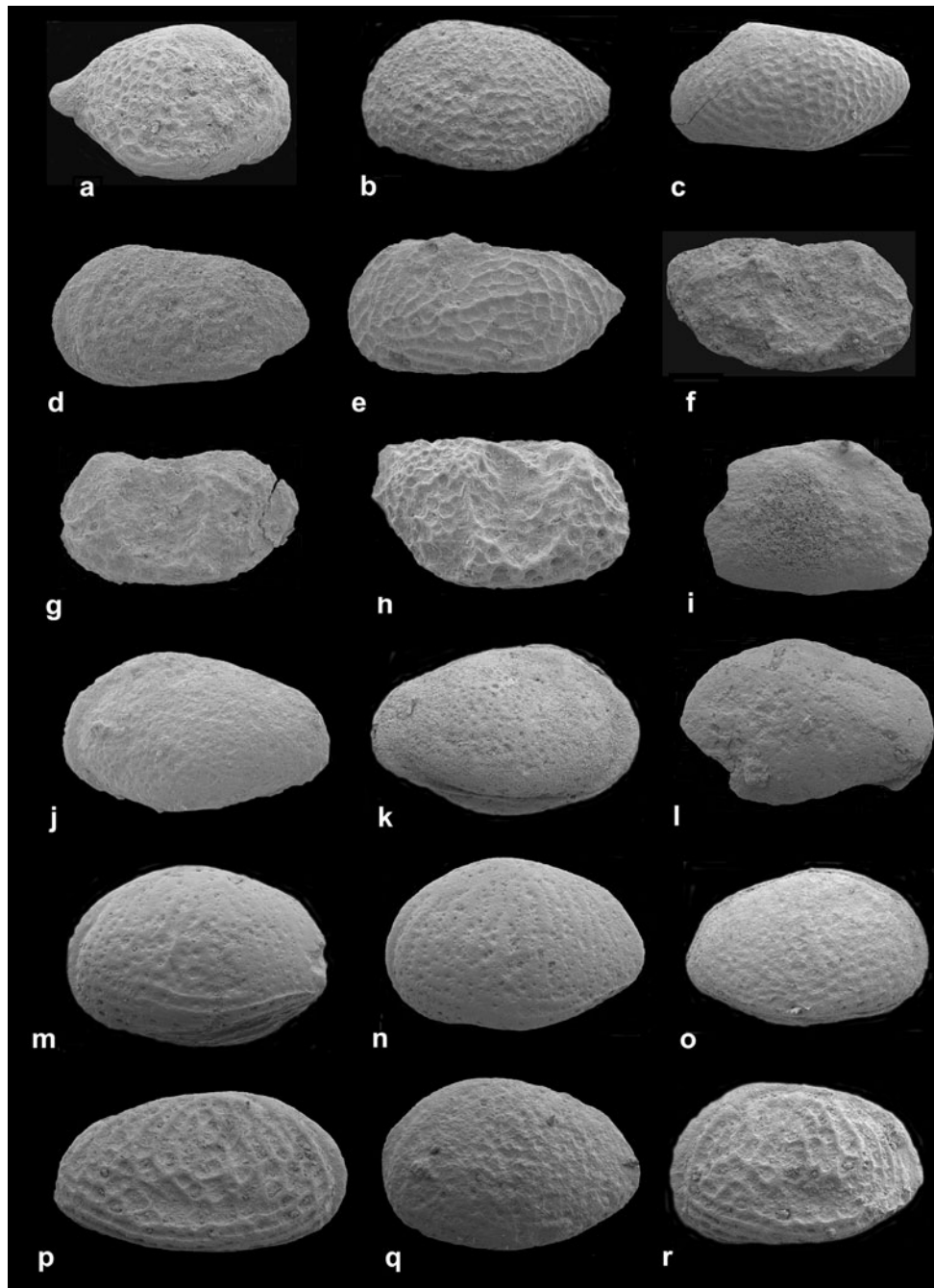
*Remarks.* We agree with Bassiouni (1974) who assigned those specimens which Oertli (1957, 1963) regarded to belong to the species *Paranotacythere (Unicosta) interrupta* (Triebel 1941) to the species *P. (U.) extendata* (Bassiouni 1974). Besides the size (which is disputable), the differences refer to the absence of any ridges or any cone-like pores in *P. (U.) interrupta*, thus the classification to *P. (U.) extendata* seems to be warranted.

*Localities and samples.* Section CTD–SCR, sample SCR 002-1186, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone. Section CTD–TCH, sample 005-939, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in Europe.* Oxfordian to Early Tithonian (Schudack 1994).





***Paranotacythere (Unicosta) cf. extendata* (Bassiouni 1974) (Fig. 11g)**

*Localities and samples.* Section CTD–TCH, sample 006-1162, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

***Paranotacythere (Unicosta) neali* (Bassiouni 1974) (Fig. 11h)**

*Remarks.* We agree with Bassiouni (1974), who assigned those specimens which Oertli (1959) regarded to belong to the species *Paranotacythere (Unicosta) rimosa* to the species *P. (U.) cf. neali* (Bassiouni 1974).



◀ **Fig. 11 a** *Eocytheropteron decoratum* (Schmidt 1954), sample VTT006-1517, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 533 µm, right valve **b** *Eocytheropteron decoratum* (Schmidt 1954), sample BSY009-261, Lower Virgula Marls, Late Kimmeridgian, to *A. eudoxus* Zone, length: 431 µm, left valve. **c** *Eocytheropteron* cf. *decoratum* (Schmidt 1954), sample BSY009-261, Courtedoux Member to Lower Virgula Marls, Late Kimmeridgian, *A. mutabilis* to *A. eudoxus* Zone, length: 480 µm, left valve of a ?male, partially broken. **d** *Eocytheropteron* sp., sample TCH005-940, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 394 µm, left valve. **e** *Eocytheropteron* ? sp., sample TCH006-1162, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 481 µm, left valve. **f** *Paranotacythere (Unicosta) extendata* (Bassiouni 1974), sample SCR002-1186, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 578 µm, right valve. **g** *Paranotacythere (Unicosta)* cf. *extendata* (Bassiouni 1974), sample TCH006-1162, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 442 µm, left valve. **h** *Paranotacythere (Unicosta) neali* (Bassiouni 1974), sample TCH006-1170, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 428 µm, right valve. **i** *Amphicythere (Amphicythere)* cf. *semisulcata* Triebel 1954, sample SCR002-1135, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 524 µm, anterior part of a right valve. **j** *Amphicythere (Merocythere) plena* (Schmidt 1954), sample TCH006-1163, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 714 µm, carapace from the left. **k** *Amphicythere (Merocythere) plena* (Schmidt 1954), sample VTT006-1523, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 656 µm, carapace from the right. **l** *Amphicythere (Merocythere)* cf. *plena* (Schmidt 1954), sample VTT003-296, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 594 µm, carapace from the left. **m** *Macrodentina (Macrodentina) perforata* Klingler 1955, Probe BSY009-263, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 605 µm, left valve. **n** *Macrodentina (Macrodentina) perforata* Klingler 1955, sample BSY009-265 Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 644 µm, left valve. **o** *Macrodentina (Macrodentina) cf. perforata* Klingler 1955, Probe TCH005-39, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 555 µm, left valve. **p** *Macrodentina (Polydentina) steghausi* (Klingler 1955) evolving to *Macrodentina (Polydentina) wicheri* (Steghaus 1951), sample SCR002-1186, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 599 µm, right valve. **q** *Macrodentina (Polydentina) cf. steghausi* (Klingler 1955) evolving to *Macrodentina (Polydentina) cf. wicheri* (Steghaus 1951), sample SCR002-1135, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 551 µm, left valve. **r** *Macrodentina (Polydentina) steghausi* (Klingler 1955), sample BSY009-263, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 595 µm, left valve of a female

*Localities and samples.* Section CTD–TCH, sample 006-1170, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in Europe.* Early and Mid Kimmeridgian of the Swiss Jura Mountains, Lower Kimmeridgian of England and the Kimmeridgian of Lower Saxony, Germany (all data from Bassiouni 1974).

Family Progonocytheridae Sylvester-Bradley 1948  
Subfamily Progonocytherinae Sylvester-Bradley 1948  
Genus Progonocytherinae Sylvester-Bradley 1948  
Subgenus *Acanthocythere (Unodentina)* Malz (1958)

***Acanthocythere (Unodentina) undata* Malz 1958**  
(Fig. 12n)

*Remarks.* The single specimen from the CTD–VTT section shows the wavelike ribs as diagnostic features. Differing from those illustrated in Malz (1958), these ribs are ornamented with little knobs which are string-like oriented along those crests. The knobs are regarded to be diagenetic structures.

*Localities and samples.* Section CTD–VTT, sample 003-334, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in Europe.* Upper part of the Lower Kimmeridgian of Vernon1 borehole (Oertli 1957), corresponding to the *A. mutabilis* Zone to lower *A. pseudomutabilis* (*A. eudoxus*) Zone. According to Malz (1958), the first appearance datum (FAD) of the species is situated in the *R. cymodoce* Zone, or eventually at the transition to the *A. mutabilis* Zone.

Genus *Amphicythere* Triebel 1954  
Subgenus *Amphicythere (Amphicythere)* Oertli 1957

***Amphicythere (Amphicythere) cf. semisulcata* Triebel 1954** (Fig. 11i)

*Remarks.* Only one single fragment, showing all characteristic features of the species.

*Localities and samples.* Section CTD–SCR, sample 002-1135, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

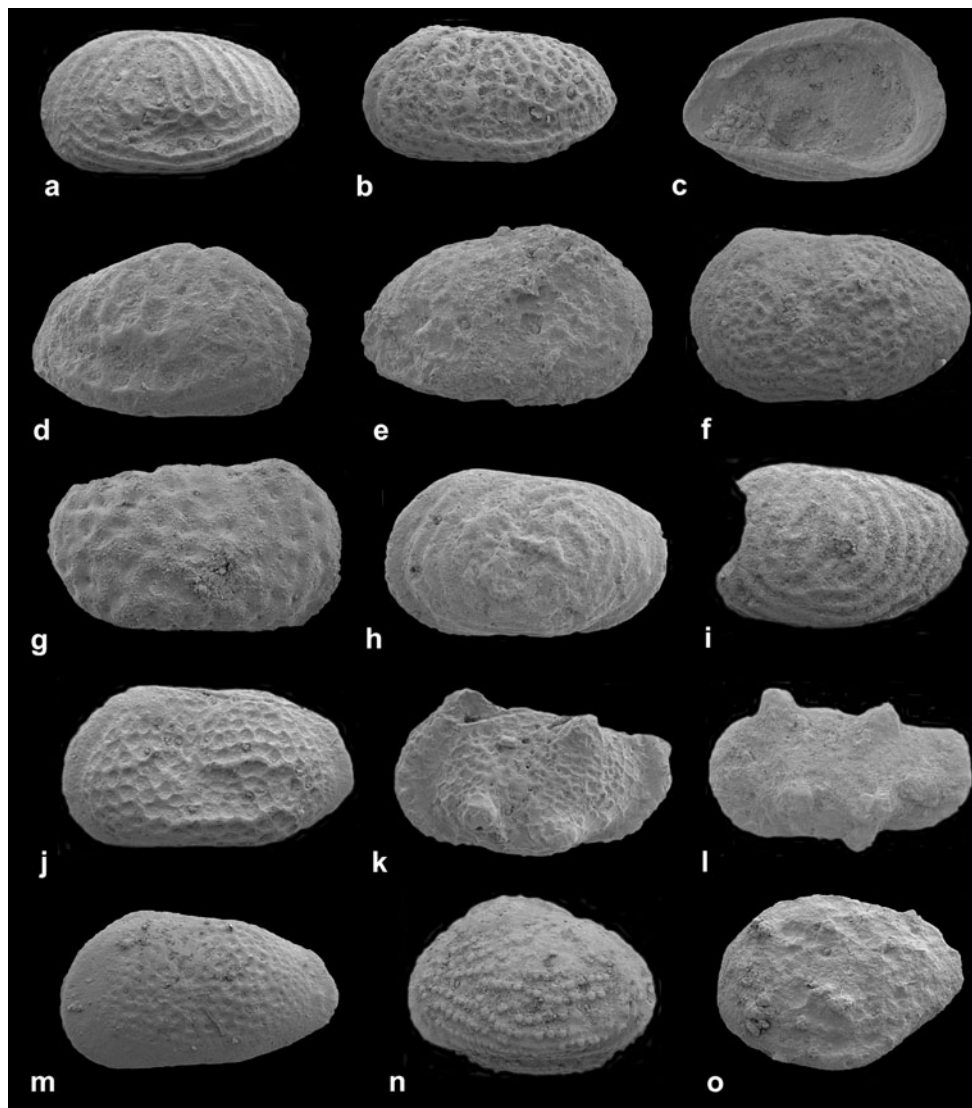
*Stratigraphic range in the study area.* Mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in Europe (n nominate species).* Early Kimmeridgian to Late Kimmeridgian (Schudack 1994).

Subgenus *Amphicythere (Merocythere)* Oertli 1957

***Amphicythere (Merocythere) plena* (Schmidt 1954)**  
(Fig. 11j-k)

*Localities and samples.* Section CTD–VTT, samples 006-1506 to 1507, 006-1509 to 1510, 006-1512 to 1516, 006-1519 to 1520, 006-1523 to 1528, 003-334, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD–TCH, samples 006-1159, 006-1163,



**Fig. 12** **a** *Macrodentina* (*Polydentina*) *steghausi* (Klingler 1955), sample BSY009-265, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 599  $\mu\text{m}$ , left valve of a male. **b** *Macrodentina* (*Polydentina*) *steghausi* (Klingler 1955), sample VTT006-1506, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 618  $\mu\text{m}$ , left valve. **c** *Macrodentina* (*Polydentina*) *steghausi* (Klingler 1955), sample TCH005-937, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 554  $\mu\text{m}$ , left valve from inside. **d** *Macrodentina* cf. (*Polydentina*) *steghausi* (Klingler 1955), sample TCH005-935 Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 568  $\mu\text{m}$ , right valve. **e** *Macrodentina* sp., sample TCH006-1168 Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 483  $\mu\text{m}$ , right valve. **f** *Rectocythere* (*Rectocythere*) *regularis* Malz (1958) sample VTT006-1506, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 481  $\mu\text{m}$ , left valve. **g** *Rectocythere* (*Rectocythere*) cf. *rugosa* Malz 1966, sample TCH005-939, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 531  $\mu\text{m}$ , right valve. **h** *Rectocythere* (*Rectocythere*) *iuglandiformis* (Klingler 1955), sample TCH005-941, Lower Virgula

Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 531  $\mu\text{m}$ , left valve. **i** *Rectocythere* (*Rectocythere*) *iuglandiformis* (Klingler 1955), sample VTT003-296, Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 421  $\mu\text{m}$ , broken part of a left valve. **j** *Rectocythere* sp., sample BSY009-264, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone, length: 507  $\mu\text{m}$ , left valve. **k** *Rasthalmocythere fuhrbergensis* (Steghaus 1951), sample TCH006-1159, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 722  $\mu\text{m}$ , left valve. **l** *Rasthalmocythere* cf. *fuhrbergensis* (Steghaus 1951), sample TCH004-1219, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 674  $\mu\text{m}$ , left valve. **m** Gen. et sp. indet. 1, sample SCR002-1186, length: 457  $\mu\text{m}$ , left valve. **n** *Acanthocythere* (*Unodentina*) *undata* Malz 1958, sample VTT-003-334; Banné Member, Early Kimmeridgian, *R. cymodoce* Zone, length: 568  $\mu\text{m}$ , carapace from the left. **o** *Eocytheropteron* ? sp., sample CHE-CRO 004-319; lower dinosaur track levels of the Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone, length: 413  $\mu\text{m}$ , left valve

006-1172, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian (*R. cymodoce* Zone) to early Late Kimmeridgian (*A. mutabilis* Zone).

*Stratigraphic range in Europe.* Late Oxfordian (Glashoff 1964, uppermost Korallenoolith) to Upper Kimmeridgian *A. pseudomutabilis* (*A. eudoxus*) Zone (Oertli 1957).

***Amphicythere (Merocythere) cf. plena* (Schmidt 1954)** (Fig. 11l)

*Localities and samples.* Section CTD-VTT, samples 006-1521 to 1522, 003-296, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian, *R. cymodoce* Zone.

***Amphicythere* sp.**

*Localities and samples.* Section CTD-TCH, sample 005-966, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone. Section CTD-VTT, sample 003-280, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian (*R. cymodoce* Zone) to early Late Kimmeridgian (*A. mutabilis* Zone).

Genus *Macrodentina* Martin 1940

Subgenus *Macrodentina (Macrodentina)* Martin 1940

***Macrodentina (Macrodentina) perforata* (Klingler 1955)** (Fig. 11m, n)

*Localities and samples.* Section CTD-SCR, samples 002-1186, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone. Section CTD-TCH, samples 005-936 to 938, 005-940, 005-942, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone. Section CTD-BSY, samples 009-261 to 265, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in Europe.* Late Kimmeridgian to Early Tithonian (Schudack 1994).

***Macrodentina (Macrodentina) cf. perforata* Klingler 1955** (Fig. 11o)

*Localities and samples.* Section CTD-TCH, sample 005-39, 005-938, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Mid Late Kimmeridgian, *A. eudoxus* Zone.

Subgenus *Macrodentina (Polydentina)* Malz 1958

***Macrodentina (P.) steghausi* (Klingler 1955)** (Figs. 11r, 12a–c)

*Localities and samples.* Section CTD-VTT, samples 006-1506, 006-1508 to 1512, 006-1515, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD-TCH, samples 005-39, 005-936 to 937, 005-939 to 942, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; samples 006-1160 to 1161, 006-1163, 004-1220, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone. Section CTD-BSY, samples 009-259, 009-261 to 265, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian to mid Late Kimmeridgian, *R. cymodoce* Zone to *A. eudoxus* Zone.

*Stratigraphic range in Europe.* Early Kimmeridgian (above the basal Kimmeridgian, e.g. Ainsworth et al. 1989) to mid Late Kimmeridgian (*A. eudoxus* Zone, e.g. Ioannides et al. 1988, Wilkinson 1983). After Klingler et al. (1962) occasionally very numerous in the Middle and lower Upper Kimmeridge Members of Northwestern Germany (*A. mutabilis* Zone and *A. eudoxus* Zone).

***Macrodentina (P.) cf. steghausi* (Klingler 1955)** (Fig. 12d)

*Localities and samples.* Section CTD-VTT, samples 006-1518 to 1519, 006-1522, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD-TCH, sample 005-935, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian to early Late Kimmeridgian, *R. cymodoce* Zone to *A. mutabilis* Zone.

*Remarks.* Both sections CTD-SCR and CTD-TCH yielded *Macrodentina* specimens in which the ventrolateral ridge is not pronounced, especially in the ventero-posterior region. Such forms could relate to *Macrodentina (Polydentina) wicheri* (Steghaus 1951) in which the ventrolateral ridge is less prominent or absent. These specimens are assigned to *M. (P.) steghausi* (Klingler 1955) here, and specified separately, being aware of the fact that this classification is arguable. They are listed separately below to distinguish them from other specimens assigned to *M. steghausi*.

***Macrodentina (P.) steghausi* (Klingler 1955)** (Fig. 11p)  
**Evolving to *Macrodentina (Polydentina) wicheri* (Steghaus 1951)**



*Localities and samples.* Section CTD–SCR, samples 002-1186, 002-1135, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; sample 002-1867, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Kimmeridgian, *A. mutabilis* Zone to *A. eudoxus* Zone.

***Macrodentina (P.) cf. steghausi* (Klingler 1955) (Fig. 11q) Evolving to *Macrodentina (Polydentina) cf. wicheri* (Steghaus 1951)**

*Localities and samples.* Section CTD–SCR, samples 002-1135, 002-1186, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; sample 002-1866, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Kimmeridgian, *A. mutabilis* Zone to *A. eudoxus* Zone.

***Macrodentina* sp.** (Fig. 12e)

*Localities and samples.* Section CTD–VTT, sample 006-1521, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD–TCH, samples 004-1219, 005-968, 006-1166 to 1173 Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian to mid Late Kimmeridgian, *R. cymodoce* Zone to *A. mutabilis* Zone.

Genus *Rectocythere* (Malz 1958)

Subgenus *Rectocythere (Rectocythere)* Christensen & Kilenyi (1970)

***Rectocythere (Rectocythere) regularis* Malz (1958) (Fig. 12f)**

*Localities and samples.* Section CTD–VTT, samples 006-1506, 006-1509, 006-1512, 006-1515, 006-1517, 006-1520, 006-1526 to 1527, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian, *R. cymodoce* Zone.

*Stratigraphic range in Europe.* Late Early Kimmeridgian, *R. cymodoce* Zone (Malz 1958) to early Late Kimmeridgian, *A. mutabilis* Zone (Dépêche 1985).

***Rectocythere (Rectocythere) cf. rugosa* Malz 1966 (Fig. 12g)**

*Remarks.* The posterodorsal/anteroventral bulge is only distinct whereas the coarse reticulation is characteristic for the species.

*Localities and samples.* Section CTD–TCH, sample 005-939, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; sample 005-968, Courtedoux Member, Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Kimmeridgian, *A. mutabilis* Zone to *A. eudoxus* Zone.

*Stratigraphic range in Europe (nominata species).* Late Kimmeridgian to Tithonian (Schudack 1994).

***Rectocythere (Rectocythere) iuglandiformis* (Klingler 1955) (Fig. 12h, i)**

*Localities and samples.* Section CTD–VTT, sample 003-296, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD–TCH, sample 005-941, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian *R. cymodoce* Zone to Late Kimmeridgian *A. eudoxus* Zone, questionable already *A. mutabilis* Zone.

*Stratigraphic range in Europe.* Early Kimmeridgian (*P. baylei* Zone, Dépêche 1985) to Late Kimmeridgian (Malz 1958).

***Rectocythere* sp.** (Fig. 12j)

*Remarks.* These individuals are assigned to *Rectocythere* due to the shape of their carapace, especially the appearance of the dorsal and posterior margins. The ornamentation and development of the small and characteristic ridges resemble *Rectocythere horrida* (Wilkinson 1983).

*Localities and samples.* Section CTD–BSY, samples 009-262, 009-264, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Mid Late Kimmeridgian, *A. eudoxus* Zone.

Family Trachyleberididae Sylvester-Bradley 1948

Subfamily Exophthalmocytherini Gründel 1966

Tribus Parexophthalmocytherini Gründel 1976

Genus *Rasthalmocythere* Gründel 1976

***Rasthalmocythere fuhrbergensis* (Steghaus 1951) (Fig. 12k)**

*Localities and samples.* Section CTD–TCH, sample 005-941, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone; sample 006-1159, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Late Kimmeridgian, *A. mutabilis* Zone to *A. eudoxus* Zone.

*Stratigraphic range in Europe.* Generally known in the Early and Late Kimmeridgian (*P. baylei* Zone to *A. mutabilis* Zone), after Cox et al. (1987) first occurrence already in the Late Oxfordian of England.

***Rasthalmocythere* cf. *fuhrbergensis* (Steghaus 1951)** (Fig. 12l)

*Localities and samples.* Section CTD–TCH, sample 004-1219, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone.

*Stratigraphic range in the study area.* Early Late Kimmeridgian, *A. mutabilis* Zone.

**Gen. et sp. indet. 1** (Fig. 12m)

*Remarks.* This species in open nomenclature originates from several samples in almost all sections. Internal valve structures such as muscle scars or hinges are not evident due to the bad preservation of the material and/or the existence of closed carapaces only. The specimens show close relationships to *Hekistocythere* Bate 1969. Similar forms were observed in the Middle Kimmeridge Member of Eastern Germany (Schudack 2004).

*Localities and samples.* Section CTD–SCR, sample 002-1186, Lower Virgula Marls, Late Kimmeridgian, *A. eudoxus* Zone. Section CTD–VTT, samples 006-1512, 006-1515, 006-1517, 006-1520, 006-1526 to 1527, Banné Member, late Early Kimmeridgian, *R. cymodoce* Zone. Section CTD–TCH, samples 004-1220, 006-1170 to 1171, Courtedoux Member, early Late Kimmeridgian, *A. mutabilis* Zone. Section CTD–BSY, sample 009-263, Lower Virgula Marls, mid Late Kimmeridgian, *A. eudoxus* Zone.

*Stratigraphic range in the study area.* Late Early Kimmeridgian to mid Late Kimmeridgian, *R. cymodoce* Zone to *A. eudoxus* Zone.

## 6 Discussion

### 6.1 Biostratigraphy

In the 21 ostracod species from 13 genera (+1 species in open nomenclature) were identified in the five studied sections (see Fig. 3), which are all located in the middle part of the Reuchenette Formation (Banné and Cortedoux Members, Lower Virgula Marls).

The chronostratigraphy used in this paper is “*sensu gallico*” which means that the term “Kimmeridgian” does not include the boreal *Pectinatites elegans* to *Virgatopavlovia fittoni* ammonite biozones (=upper part of the

“Kimmeridgian” *sensu anglico* = “Bolonian”, see Ogg et al. 2012).

The biostratigraphical framework of the studied sections is largely known due to the discovery of ammonites (Jank et al. 2006b; Marty et al. 2007; Comment et al. 2011). The ostracods presented in this paper have been studied in order to support these relative datations. With respect to the boreal ammonite zones (see e.g. Ogg et al. 2012) used in this study, the ostracod-bearing parts of the sections represent more or less the middle part of the Kimmeridgian (*sensu gallico*), corresponding to the uppermost part of the *R. cymodoce* Zone (Banné Member = late Early Kimmeridgian), the entire *A. mutabilis* Zone (Courtedoux Member = early Late Kimmeridgian) and the lowermost part of the *A. eudoxus* Zone (Lower Virgula Marls = mid Late Kimmeridgian) (Figs. 3, 4).

In comparison with the well-established ostracod biozonation of NW Germany (Schudack 1994), the studied succession represents the equivalent of zones 12 (Banné Member and lowermost Courtedoux Member), 13 (middle and major part of the Courtedoux Member) and 14 (uppermost Courtedoux Member and Lower Virgula Marls, see Fig. 4). There are only very few discrepancies between the first or last occurrences of the species in both areas (NW Switzerland and NW Germany).

In this study, four (out of the 21) ostracod species (*Klentnicella rodewaldensis*, *Rectocythere regularis*, *Acanthocythere undulata*, *Cytherelloidea* gr. *tripartita*) are exclusive to the uppermost *R. cymodoce* Zone (late Early Kimmeridgian), whereas three species (*Cytherella suprajurassica*, *Amphicythere plena* and *Hechticythere serpentina*) range from the *R. cymodoce* Zone into the *A. mutabilis* Zone (early Late Kimmeridgian) and five species (*Eocytheropteron decoratum*, *Cytherelloidea* gr. *weberi*, *Schuleridea triebeli*, *Macrodentina steghausi*, *Rectocythere iuglandiformis*) into the lowermost *A. eudoxus* Zone (mid Late Kimmeridgian). Nine species (*Cytherella waltersdorfi*, *Paranotocythere neali*, *Rasthalmocythere fuhrbergensis*, *Cytherelloidea undulata*, *Nodophthalmocythere vallata*, *Rectocythere* cf. *rugosa*, *Paranotocythere extendata*, *Amphicythere* cf. *semisulcata*, *Macrodentina perforata*) are exclusive to the *A. mutabilis* Zone and the lowermost *A. eudoxus* Zone, the latter three even to the lowermost *A. eudoxus* Zone.

Apart from the occurrence of *R. fuhrbergensis* in the lowermost *A. eudoxus* Zone, the observed stratigraphical ranges of the ostracods do not contradict the ammonite biozonation of the studied sections. However, they do not permit a more refined stratigraphical subdivision, which is explained by the fact that the stratigraphical ranges of these species (all over Europe) are in all cases much longer than those of the index ammonite species (*R. cymodoce*, *A. mutabilis*, *A. eudoxus*, etc.).

Nevertheless, we observe the trend that several species providing geologically older FADs and LADs preferably occur lower in the sections (at least statistically), and vice versa (see Fig. 3). This is considered a confirmation of the principal usability of these ostracods for biostratigraphical purposes, though not as precise as it is possible with ammonites (assuming that the stratigraphically most valuable ammonite species are available).

On the basis of ostracods alone (compare with Fig. 3), and without the available stratigraphic information from ammonites, the Banné Member would have been correlated with the upper *R. cymodoce* Zone and/or *A. mutabilis* Zone (but in any case older than *A. eudoxus* Zone), the Courtedoux Member with the *A. mutabilis* Zone (but in any case younger than the *R. cymodoce* Zone and older than the *A. eudoxus* Zone), and the Lower Virgula Marls with the *A. mutabilis* Zone and/or lower *A. eudoxus* Zone (but in any case younger than the *R. cymodoce* Zone and older than the *A. autissiodorensis* Zone).

## 6.2 Palaeoecology (salinity)

Ostracods, as a group, provide a large variety of ecological tolerances, i.e., they are living in various aquatic environments from the deep sea up to humid terrestrial freshwater biotopes. Thus, they are considered to be optimal index fossils for palaeoecological analyses (temperature, salinity, water depth, trophic level etc.) of sedimentary sequences (De Dekker et al. 1988). Among the various ecological parameters which can be deciphered, ostracods (here: genera) are mostly used as proxies for palaeosalinity. Based upon estimations and calculations of several authors (mainly Sohn 1951; Oertli et al. 1961; Neale 1964; Anderson 1971, all compiled by Weiss 1995), ranges of salinity tolerances of most Late Jurassic genera are meanwhile known (or better: assumed) quite well and can be used for such analyses.

For the various genera, we have used the following “main” (i.e. without very insecure boundary conditions) salinity tolerances as working hypotheses (in alphabetical order): *Amphicythere* 15–40 ‰, *Cytherella* 15–40 ‰, *Cytherelloidea* 15–40 ‰, *Eocytheropteron* 5–30 ‰, *Hechticythere* 10–30 ‰, *Klentnicella* 10–30 ‰, *Macrodentina* 5–30 ‰, *Nodophthalmocythere* 30–40 ‰, *Paranotacythere* 30–40 ‰, *Rasthalmocythere* 10–30 ‰, *Rectocythere* 30–40 ‰, *Schuleridea* 5–30 ‰ (*Acanthocythere* not used here).

Based upon these salinity ranges and using the Venice System according to Oertli (1964) for the classification of brackish waters, we have calculated the average (mean) salinities for each of the ostracod-bearing layers in the five sections under study. For this purpose, we have added the average salinities (i.e., the median between the lowest and

the highest tolerated salinities in ‰) for all genera existing in given samples of a single layer and then divided the sum by the number of genera. The resulting number is regarded as the “average salinity” of a layer, and considered to enable the most objective “salinity curves” for each of the five sections.

According to these calculations (but only applying to the ostracod-bearing layers), the lowermost part of the sequence under study provides the highest salinity. All samples from the CTD–VTT section (Fig. 5, Banné Member of the late Early Kimmeridgian, see also Figs. 2 and 3 for the stratigraphical position of each section) provide average salinities between 23 and 28 ‰, reflecting clearly brachyhaline waters. The Banné Member seems to become a little more brackish in its upper part, which is in agreement with the fact that ammonites were only found in the lower half of the Banné Member (Jank et al. 2006b; Comment 2012), and that the invertebrate fauna (mainly bivalves and gastropods) is more diverse in its lower part.

Most of the samples from the section CHE–CRO from the lower part of the Courtedoux Member have unfortunately yielded no ostracods (Fig. 6). Only in two samples, ostracod associations point to an average salinity of around 16–18 ‰ (highly pliohaline, and thus a little more brackish than the underlying Banné Member). This corresponds well with the fact that these samples are from tidal-flat biolaminites with dinosaur tracks (lower dinosaur track levels of the Courtedoux Member) (Marty 2008).

Section CTD–TCH (Courtedoux Member and Lower Virgula Marls, representing the early Late Kimmeridgian) has yielded a large number of ostracod-bearing samples, pointing to somewhat higher (as compared to the lower dinosaur track levels of the Courtedoux Member) salinities mostly within the brachyhaline zone (Fig. 7). A slight trend leads from average salinities around 20–25 ‰ in the basal part of the section (=intermediate dinosaur track levels of the Courtedoux Member) to higher average salinities of 25–30 ‰ in its upper part (=upper dinosaur track levels of the Courtedoux Member and Lower Virgula Marls of the *A. eudoxus* Zone). Again, this trend of slightly increasing salinities is paralleled by more frequent ammonite occurrences above the upper dinosaur track levels of the Courtedoux Member. Actually, no ammonites at all have as yet been found between the lower Banné Member and the upper dinosaur track levels of the Courtedoux Member.

The other two sections (CTD–SCR, Fig. 8, and CTD–BSY, Fig. 9, both stratigraphically in a position similar to section CTD–TCH, Fig. 7) have supplied a lower number of ostracod-bearing samples, but interestingly both also show a clear trend from lower average salinities (around 18–20 ‰) in their lower parts (still *A. mutabilis* Zone) to slightly higher average salinities (around 23–25 ‰) in their upper parts (lowermost *A. eudoxus* Zone). This again



complies with section CTD–TCH (Fig. 7) and the increasing occurrence of ammonites (Fig. 2).

### 6.3 Palaeobiogeography

In a comprehensive analysis of the biogeography of the Late Jurassic ostracoda of northwestern and Central Europe, applying various similarity indices to calculations of the relationships between 15 separate areas, Schudack and Schudack (1995, 1997, see also Schudack 1999) have demonstrated the biogeographic diversification from a relatively uniform Oxfordian to the separation into two subprovinces in the Kimmeridgian, and then the differentiation into four subprovinces in the Tithonian. This differentiation correlates with a number of factors such as climate change and differentiation, eustatic sea-level changes, physical-palaeogeographic developments (barriers and marine corridors), and a change in the ocean current systems.

In the Kimmeridgian “*sensu gallico*” (as a whole, not furthermore subdivided), two subprovinces developed: A northwestern fauna (North Sea area and England), called “subboreal” by Schudack and Schudack (1995), and a rather uniform central and western European fauna (including the Swiss Jura) in the area from France over Germany up to Poland.

The French and Swiss Jura is one of the 15 separate areas compared by Schudack and Schudack (1995, 1997), and the then known 16 ostracod species increased to 21 herein. There is a strong relationship to the Aquitan and Paris Basins, to the Lorraine, and to Northern Germany (strong enough to be considered part of the same biogeographic subprovince), but interestingly not to the geographically nearer areas of Southern Germany (Schudack and Schudack 1995, 1997). The latter is supposed to be due to strong facies differences which are more important than the geographical vicinity of both areas (see maps in Ziegler 1988).

The present paper now demonstrates quite a larger number of species in the Swiss Kimmeridgian (21 instead of formerly only 16) and also a stronger faunal relationship to Southern Germany than formerly known. Nevertheless, this relationship (with 9 common species) is still smaller than with Northern Germany (with 18 common species). All Swiss species common with Southern Germany also exist in Northern Germany (except for *C. gr. tripartita*, a species group comprising some taxonomic inconsistency, see taxonomic part), but not vice versa. On the other hand, only 2 of the Swiss species (*R. regularis* and *A. undata*) are not known from Germany (North or South), but—like most of the other Swiss species—from the Paris Basin and the Lorraine (Schudack and Schudack 1995).

In summary, Kimmeridgian ostracoda from the NW Swiss Jura Mountains can still (and even more than 10–20 years ago) be considered part of the largely boreally-influenced Central/Western European subprovince, with strongest relationships to the Aquitan and Paris Basins and—a little less—to Northern Germany (NE and NW). Faunal relationships with Southern Germany (subjected to a stronger tethyan influence than the deposits of the NW Swiss Jura Mountains, Schudack and Schudack 2000) are only half as strong when compared with Northern Germany. This is all due to facies differences rather than to mere geographical distances. Even more “tethyan” ostracod faunas are dominant in areas such as Southeastern France (Schudack and Schudack 1995, 1997).

## 7 Concluding remarks

1. Ostracods are a common microfaunal element of the Kimmeridgian of the Jura Mountains in NW Switzerland.
2. The stratigraphical subdivision within the Kimmeridgian can as clearly be inferred from ostracods as it is the case from the ammonite biozonation. This proves the utility of the ostracod biozonation, especially where ammonites are not available or rare.
3. The ostracod-bearing layers of the sequence under study (middle part of the Reuchenette Formation = Banné Member, Courtedoux Member and Lower Virgula Marls, Fig. 2) have been deposited in waters with highly brackish to marine salinities (highly pliohaline to—mostly—brachyhaline according to the Venice System, Oertli 1964). From the base of the section (base of the Banné Member, high brachyhaline in average), salinities are slowly decreasing, with lowest salinities in the lower dinosaur track levels of Courtedoux Member (high pliohaline in average), and then again increasing up to higher salinities (high brachyhaline in average) in the upper dinosaur track levels of the Courtedoux Member and the Lower Virgula Marls (lowermost *A. eudoxus* Zone). These trends perfectly correlate with the increased occurrence of ammonites above the upper dinosaur track levels.
4. In terms of Kimmeridgian ostracod palaeobiogeography, the NW Swiss Jura Mountains are most similar to the Aquitan and Paris Basins, a little less to Northern Germany, and even less (with not even half of the species in common) when compared with Southern Germany. The Swiss Jura Mountains still belongs to a largely boreally influenced “Western and Central European subprovince”, whereas Southern Germany (though located more to the north) provides an enhanced tethyan influence.

**Acknowledgments** This work results from collaboration between the Palaeontology A16 (Office de la culture, Canton du Jura, Switzerland) and the department of palaeontology of the Freie Universität Berlin (Germany). We are grateful to both institutions for enabling us to accomplish this work. The Palaeontology A16 is funded by the Swiss Federal Roads Authority (FEDRO 95 %) and the Canton Jura (RCJU 5 %). We also acknowledge the technical staff of the Palaeontology A16 for their careful work during the screen-washing of the samples and their patience whilst picking the ostracods studied here. Thanks also go to technical drawers of the Palaeontology A16 for their help with some of the Figures. The authors also acknowledge the invaluable reviews by Ekaterina Tesakova and Ian Wilkinson.

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