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INTRODUCTION

The Hippuritida NEWELL, 1965 (rudist bivalves) evolved from the Late Jurassic–Cretaceous to characterize the only prolonged episode of Earth history when bivalves dominated tropical and subtropical shallow-marine environments otherwise occupied by coral and calcareous algae as major carbonate producers (GILI, MASSE, & SKELTON, 1995; SCOTT, 1995; SKELTON, 2000, 2003a; STEUBER, 2000). They diversified into a wide range of shell morphologies as reflected in a large number of taxa (approximately 1500 species in more than 160 genera). Much progress in refining the stratigraphic ranges of the Hippuritida has been made since the last compilation in the Treatise on Invertebrate Paleontology (COX & others, 1969), as new methods of stratigraphy have been applied to the group, allowing for a better understanding of the dynamics of their evolution in relation to late Mesozoic global paleoenvironmental change.

Range charts of genera and species of the Hippuritida have been compiled previously for individual regions of the Mediterranean (e.g., POLŠAK, BAUER, & SLIŠKOVIĆ, 1982; BILOTTE, 1985; CESTARI & SARTORIO, 1995; MASSE, 1996, 2003; PHILIP, 1998a) and the U.S. Gulf Coast and Caribbean (e.g., COOGAN, 1977; SCOTT, 2010; SCOTT & FILKORN, 2007; MITCHELL, 2013a, 2014). Earlier examples of calibrating ranges of rudist bivalves to the global stratigraphic charts included only relatively few taxa (MASSE, 1998; PHILIP, 1998b) and/or differ substantially from the ranges compiled here (PHILIP, 1998b; SKELTON, 2003b).

Biozonations based on rudist bivalves were more recently established for the Barremian–Albian of the U.S. Gulf Coast (SCOTT & FILKORN, 2007), and for the Late Cretaceous of the central-eastern Mediterranean and the Arabian Plate based on numerical ages derived from strontium-isotope (Sr-isotope) stratigraphy (STEUBER & SCHLÜTER, 2012).

The current range charts include all currently (as of July 2014) accepted genera of the Hippuritida (SKELTON, 2013a, 2013b), except for a few that have poorly defined ranges and/or are known only from a single locality with dubious stratigraphy.

RANGE CHART METHODOLOGY

Ranges of genera are derived from a number of methods (see overview of current approaches to chronostratigraphy in SCOTT, 2014); those methods that are most important for the current compilation are discussed below. The range charts (Fig. 1–4) refer to the geologic time scale (GTS) of GRADSTEIN, OGG,

Steuber, Thomas, R. W. Scott, S. F. Mitchell, & P. W. Skelton. 2016. Part N, Revised, Volume 1, Chapter 26c: Stratigraphy and diversity dynamics of Jurassic–Cretaceous Hippuritida (rudist bivalves). Treatise Online 81:1–17, 7 fig., 1 table.

and Schmitz (2012). TimeScale Creator software (Ogg & Lugoswki, 2011) version 6.1.2 (2014) was used to create the chronostratigraphic templates for the charts presented here.

BIOSTRATIGRAPHY

Ranges of many genera of the Hippuritida are derived from conventional biostratigraphy, involving the calibration of their occurrences with ranges and zonations of benthic or planktic foraminifera and, ultimately, ammonites. This is the case for most Oxfordian–Cenomanian taxa and for Santonian–Campanian genera of the Caribbean. Biostratigraphic ranges for some Berriasian–lower Aptian genera have been largely confirmed by Sr-isotope stratigraphy (Masse & Steuber, 2007), and ranges of many Barremian–Turonian taxa are calibrated to numerical ages using graphic correlation (Scott, 2014).

Rudist ranges based on biostratigraphy adopted here are derived from the most recent regional correlations, such as for the Lower Cretaceous of southeastern Spain (Masse, Arias, & Vilas, 1998) and southern France (Masse, 1996, Masse & Fenerci-Masse, 2013a) and for the majority of American Caprinoidea d'Orbigny, 1847 (Mitchell, 2013a, 2013b).

GRAPHIC CORRELATION

Graphic correlation is a quantitative, nonstatistical method that integrates various types of stratigraphic data and enables their calibration to chronostratigraphy. This is accomplished by a graphic process of comparing species ranges in multiple reference sections and scaling thickness units of occurrences to numeric time units. The iterative graphing of successive sections produces a database of ranges so that rudist ranges can be integrated with ammonites and other zonal taxa. Graphic correlation is thus a transparent and testable deterministic technique to correlate the occurrence of fossils to geologic time as represented in rock units (Scott, 2014). The accuracy of these ranges depends on the number of sections, preservation, and correct identification of the species. The method is described in detail in Scott (2009), and examples of ranges and biozones of taxa of the Hippuritida that are the result of applying graphic correlation can be found in Scott and Kerans (2004), Scott and Filkorn (2007), and Scott (2010, 2014). As of 2010, the ranges of 98 rudist species have been calibrated to numerical ages (Scott 2010). Other quantitative methods, such as those described by Sadler (2004), have not yet been applied to rudist data.

STRONTIUM-ISOTOPE STRATIGRAPHY

Sr-isotope stratigraphy uses the changing Sr-isotopic composition of seawater for stratigraphic correlation (McArthur, 1994). This requires geochemical screening to gain confidence that the original Sr-isotope composition of seawater has not been altered during diagenesis and is still retained in the skeletal material used for analysis (McArthur & others, 1994; Steuber, 2003a). The thick, outer shell layer of many Hippuritida, originally composed of fibrous low-Mg calcite, is the preferred material for analysis and has been shown to have a large potential of retaining the original ultrastructure and geochemical composition (Steuber, 2003b). Sr-isotope stratigraphy provides rather precise numerical ages, approximately +/- 0.7 myr, for time periods with a distinct gradient in the Sr-isotope composition of seawater, such as the latest Jurassic–Hauterivian, late Barremian–mid-Aptian, and Coniacian–Maastrichtian (McArthur, 1994). One advantage of the method is that it allows for correlation across biogeographic provinces and is not dependent on the availability of useful stratigraphic marker species. The method is thus suitable for calibrating biostratigraphic ranges to numerical ages, ultimately enabling comparison of ranges of biota from different depositional environments and biogeographic realms. This is important for the evaluation of evolutionary patterns and their calibration to events or episodes of environmental change (Steuber, 2001; Steuber, Korbar, & others, 2005, 2009; Schlüter, Steuber, & Parente, 2008a). The method has been described in detail elsewhere (McArthur, 1994; McArthur & others, 1994; Crame & others, 1999; Steuber, 2003a, 2003b), and the data used in the present compilation of ranges of genera are discussed in Steuber and Schlüter (2012).

The Sr-isotopic composition of seawater has to be re-calibrated to numerical ages each time a new time scale becomes available. Consequently, the numerical ages for localities used here in the compilation of ranges of genera are different from those listed in Steuber and Schlüter (2012), which used GTS 2004 and the look-up table of McArthur, Howarth, and Bailey (2001; version 4b 08 04); they are here updated to GTS 2012 (Gradstein, Ogg, & Schmitz, 2012) using a re-calibration of the Sr-isotope evolution of seawater (McArthur, written communication, 2013).

RANGE CHARTS

Ranges of genera of the Hippuritida are grouped according to families, in some cases at the level of subfamilies, and presented in Figures 1–4, following the current systematics of the Hippuritida. A few genera of the Radiolitidae d'Orbigny, 1847, are not shown in the range charts. These genera are known only from single or few localities with imprecise stratigraphic data (*Bystrickya* Lupu, 1976, Santonian–early Maastrichtian; *Horehronia* Andrusov, 1976, Santonian–Campanian; *Kurtinia* Karacabey-Öztemür, 1980, Maastrichtian, but probably older according to associated taxa; *Orestella* Lupu, 1982, Campanian–Maastrichtian; *Paronella* Wiontzek, 1934, Upper Cretaceous; *Parabournonia* Douvillé, 1927, Santonian–Campanian). The taxonomic status of some genera is currently under discussion. These genera are shown without a qualifier in the range charts (Fig. 1–4), as they are not yet formally revised.

The stratigraphic distribution of Late Jurassic and Early Cretaceous rudists is predominantly derived from biostratigraphic correlation (Masse, 1996; Masse & Chartrousse, 1997; Masse, Arias, & Vilas, 1998; Skelton, 1999; Masse, 2003; Masse & others, 2007; Scott & others, 2010), for some genera supported by Sr-isotope stratigraphy (Masse & Steuber, 2007), and for others by integrating various data using graphic correlation (Scott & Kerans, 2004; Scott & Filkorn, 2007; Scott, 2010, 2014). Ranges for late Turonian–Maastrichtian Hippuritidae Gray, 1848, Radiolitidae, and Trechmannellidae Cox, 1933, are predominantly based on Sr-isotope stratigraphy of Upper Cretaceous localities from Jamaica to the Middle East (Steuber & Schlüter, 2012). Ranges of the Antillocaprinidae Mac Gillavry, 1937, are from Mitchell (2013a, 2013b), based mainly on the well-established biostratigraphy of Jamaican rudist-bearing formations (e.g., Mitchell, 2013c). Sr-isotope data exist for some critical upper Campanian–Maastrichtian localities of Jamaica (Steuber & others, 2002). Ranges of the Caprinuloideinae Damestoy, 1971; Caprinidae d'Orbigny, 1847; Rethinae Yanin, 1990; and Youngicaprininae Mitchell, 2013a, are based on graphic correlation and conventional biostratigraphy (Mitchell, 2013b; Scott, 2010, 2014).

A summary of ranges of rudist genera shows the total numbers of genera and the numbers of originations and extinctions for each substage (Fig. 5). The stratigraphic distribution of the total number of genera is further subdivided into aragonite-versus calcite-dominated taxa (Fig. 6), and extinction and originations are shown separately for taxa with different shell mineralogy (Fig. 7). Shells of the Hippuritidae and Radiolitidae are considered to be calcite-dominated, whereas the Antillocaprinidae; Caprinoidea; Caprinulidae Yanin, 1990; Caprotinidae Gray, 1848; Diceratidae Dall, 1895; Epidiceratidae

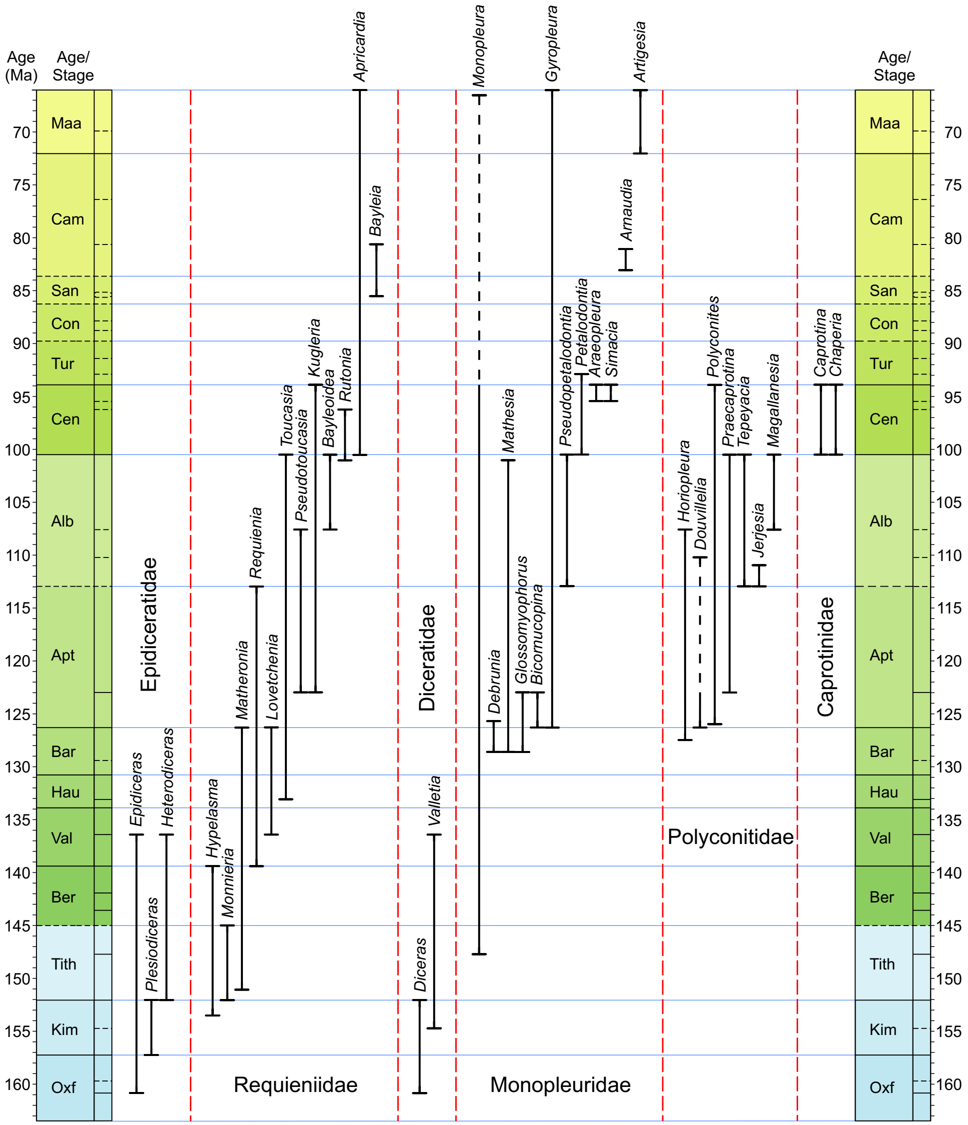

FIG. 1. Stratigraphic ranges of genera of the Epidiceratidae RENGARTEN, 1950; Requieniidae KUTASSY, 1934; Diceratidae DALL, 1895; Monopleuridae MUNIER-CHALMAS, 1873; Polyconitidae MAC GILLAVRY, 1937; and Caprotinidae GRAY, 1848.

RENGARTEN, 1950; and Plagioptychidae DOUVILLÉ, 1888, originally had aragonite-dominated shells. The Monopleuridae MUNIER-CHALMAS, 1873; Polyconitidae MAC GILLAVRY, 1937; Requieniidae KUTASSY, 1934; and Trechmannellidae are classified as having shells that originally contained both minerals, but none in a significantly dominant fraction. Note that there are a few genera that do not match these categories at the family level (e.g., *Parastroma* DOUVILLÉ, 1926, among the Hippuritidae), and that the proportion of these minerals may have changed with time in individual taxa (PASCUAL-CEBRIAN & others, 2016). The dominant shell mineralogy is also compared with the global evolution of carbonate platforms and the changing carbon-isotope evolution of Late Jurassic–Cretaceous seawater (Fig. 6).

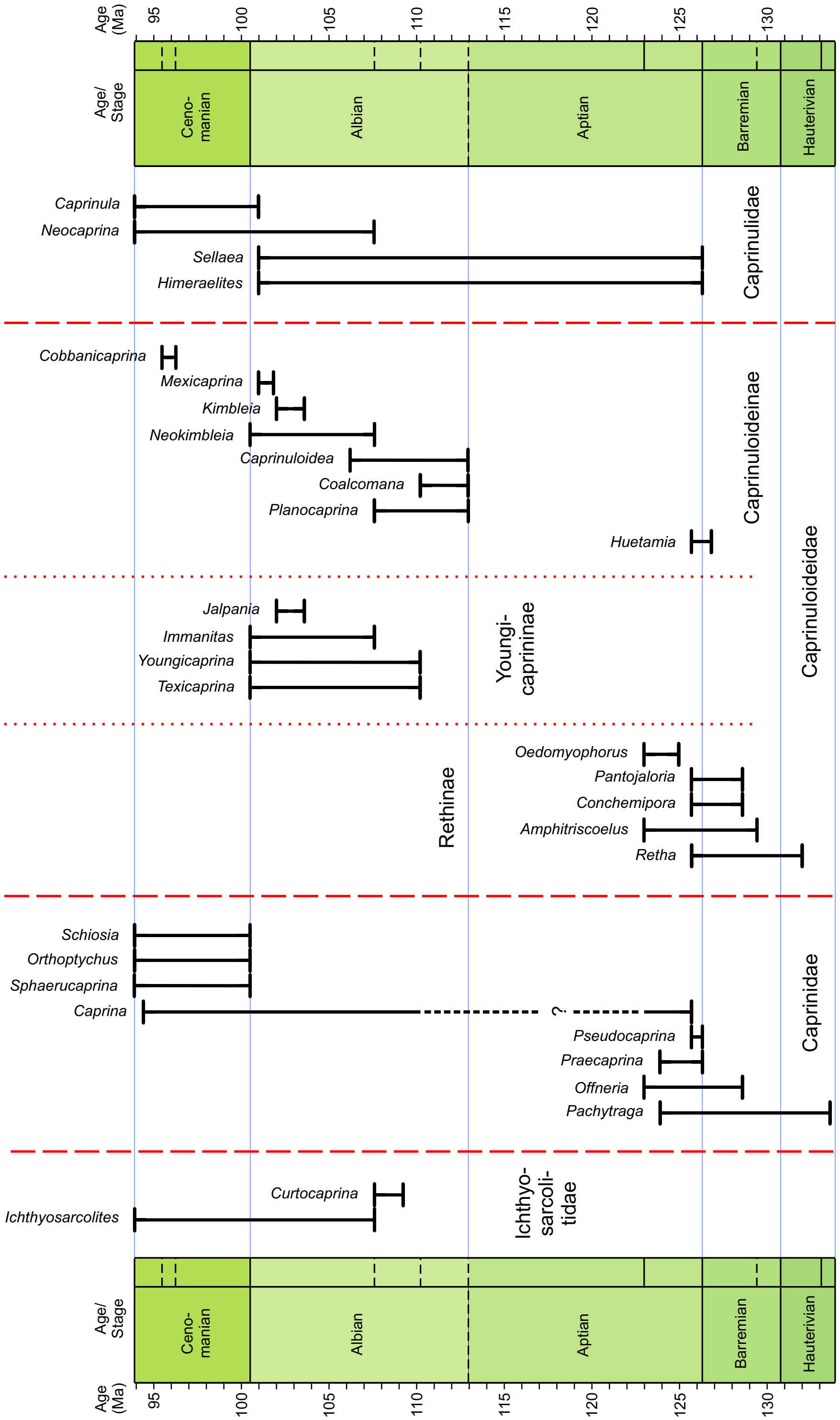

FIG. 2. Stratigraphic ranges of genera of the Ichthyosarcolitidae DOUVILLÉ, 1887; Caprinidae D'ORBIGNY, 1847; Caprinuloideidae DAMESTOY, 1971; and Caprinulidae YANIN, 1990.

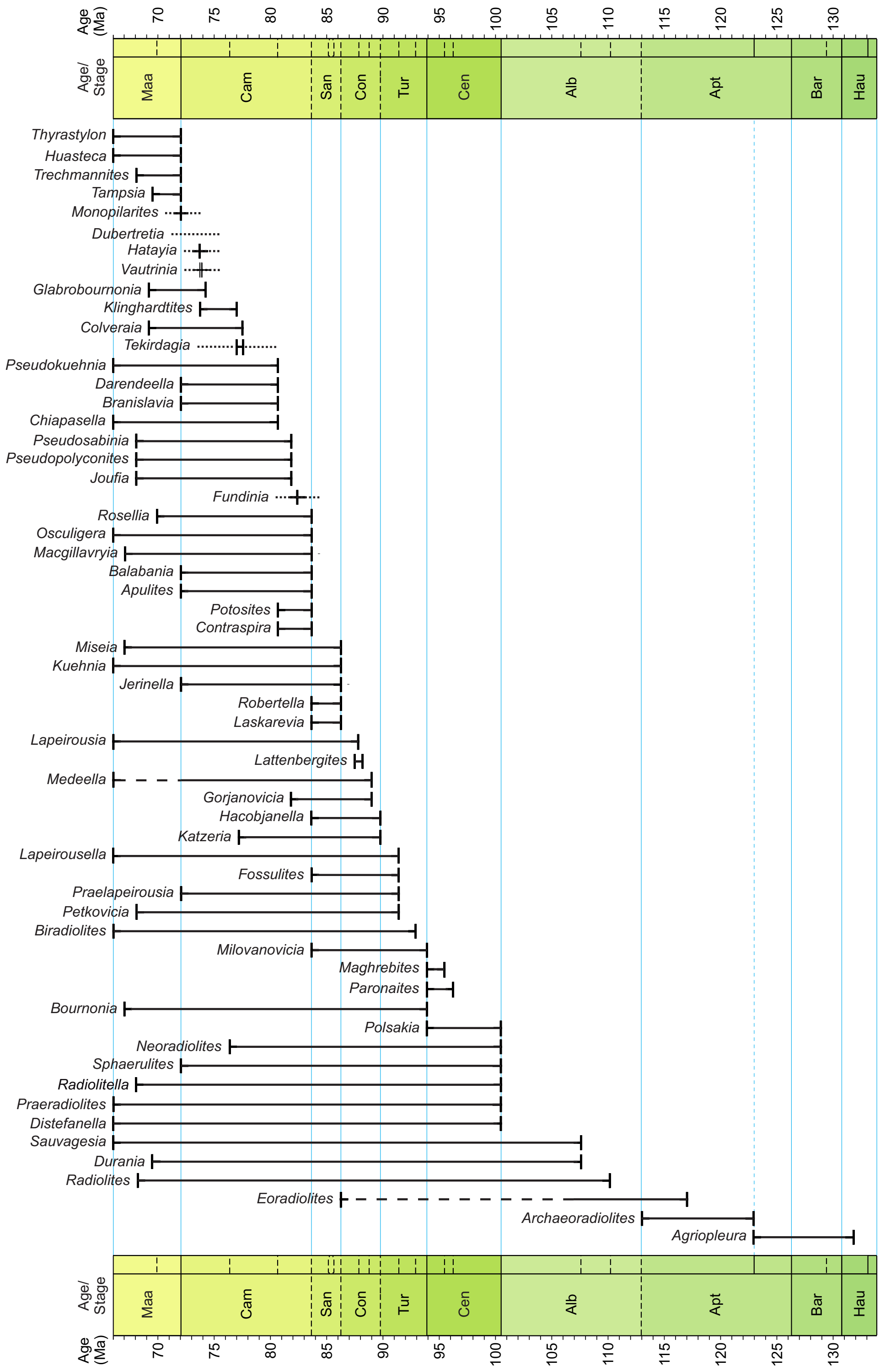

FIG. 3. Stratigraphic ranges of genera of the Radiolitidae D'ORBIGNY, 1847.

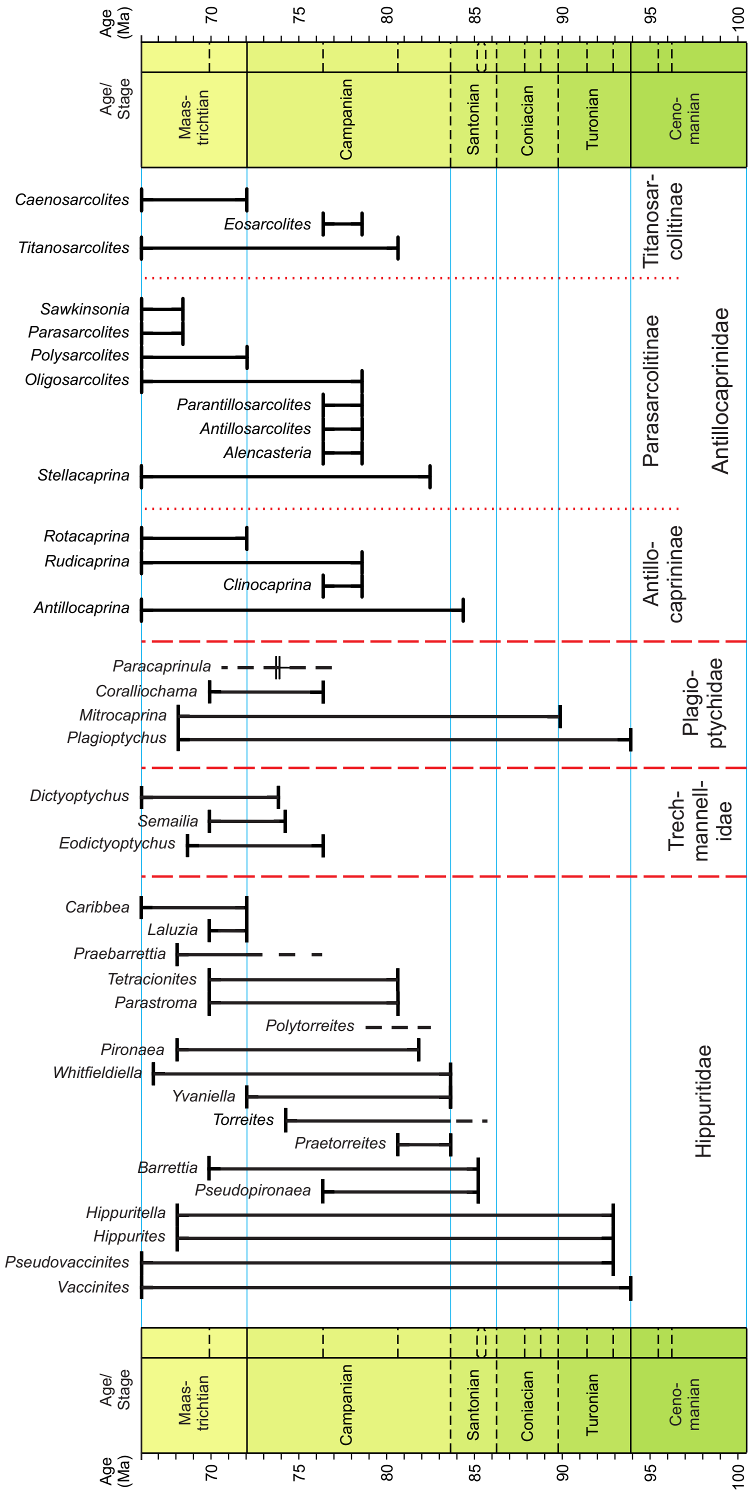

FIG. 4. Stratigraphic ranges of genera of the Hippuritidae GRAY, 1848; Trechmannellidae COX, 1933; Plagioptychidae DOUVILLÉ, 1888; and Antillocaprinidae MAC GILLAVRY, 1937.

ISSUES FOR DISCUSSION

PRECISION OF DATA

Ranges derived from the different methods outlined above vary in precision, although precision may not necessarily reflect accuracy. Ranges based on biostratigraphy can result in correlation with ammonite biozones. The position of such ammonite biozones as related to numerical ages is shown in the range charts following the data provided by OGG and LUGOSWKI (2011). Where biostratigraphic data do not allow for correlation with ammonite zones, the duration of the corresponding substage is shown as the range. In a few cases, this results in an apparent range of, e.g., base of lower Albian–top of lower Albian, although the genus in question may be known only from a few occurrences or even a single locality, the age of which is not known more precisely than "early Albian."

Ranges that result from Sr-isotope stratigraphy are based on numerical ages derived for localities with documented occurrence of the genus in question (STEUBER & SCHLÜTER, 2012). Precision of Sr-isotope stratigraphy is not typically better than +/- 0.7 myr, and older or younger occurrences of the taxon may be identified in future studies. However, as these ranges are based on occurrences at localities with a published numerical age, they are based on data that are testable and can be improved in future studies. In contrast, conventional biostratigraphy and specifically calibration to ammonite zones often requires assumptions that result in conclusions that are not always transparent and may be impossible to test.

The method of graphical correlation has the advantage that calibration to chronostratigraphy is based on fossil occurrences in well-documented outcrop sections or well cores. Fossil datums are integrated transparently with non-biostratigraphic datums in Global Boundary Stratotype Section and Points (GSSP) or their reference sections.

As with Sr-isotope stratigraphy, the age ranges of taxa derived from graphic correlation are preliminary, minimum ranges that may be extended as new data become available (SCOTT, 2014).

In order to compile a clear and testable database for future improvements of the current stratigraphic ranges of the genera of the Hippuritida, a database of localities of first and last occurrences of all genera is desirable. While such data in fact exist for a large number of genera, i.e., for ranges based on graphic correlation and Sr-isotope stratigraphy (SCOTT, 2014; STEUBER & SCHLÜTER, 2012), this goal has not yet been accomplished to the extent that justifies publication.

STRATIGRAPHIC DISTRIBUTION OF THE HIPPURITIDA

Whereas a detailed analysis of rates and patterns of origination and extinction (e.g., FOOTE, 2000) of the Hippuritida is beyond the scope of this contribution, a few characteristic features of the diversity dynamics of the group can be noted. The general patterns of diversification and extinction have been outlined earlier (MASSE & PHILIP, 1986; ROSS & SKELTON, 1993; PHILIP, 1998a; STEUBER & LÖSER, 2000; STEUBER, 2002; SKELTON, 2003b), but are presented here with improved stratigraphic precision and include all currently accepted genera of the group (Fig. 5). Major differences in patterns presented here compared to previous compilations exist for many central and eastern Mediterranean Late Cretaceous taxa, many of which have been shown to be substantially older than previously believed (STEUBER & SCHLÜTER, 2012).

The number of genera increased in successive waves from the Oxfordian to the Campanian (Fig. 5), with peaks in the early Aptian (25 genera), late Albian (30 genera), late Cenomanian (31 genera), and late Campanian (62 genera). Two major reductions in the number of genera occurred during the mid-Aptian and during the Cenomanian/Turonian transition. The Hippuritida became extinct at the end of the Cretaceous, only about five million years after the final and highest peak of generic diversity that

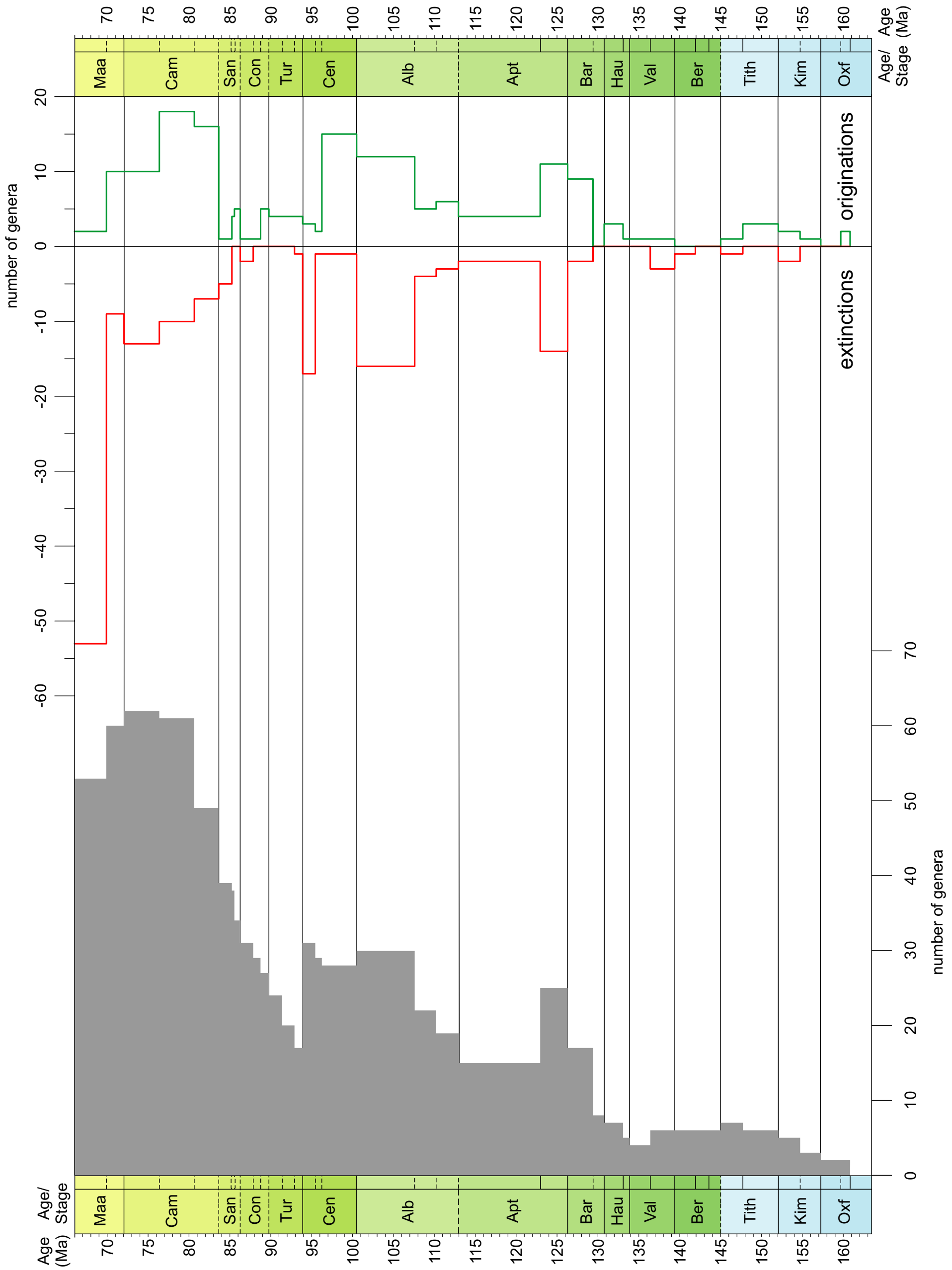

FIG. 5. Number of genera of the Hippuritida NEWELL, 1965, from the Oxfordian to the Maastrichtian, and number of originations (*green*) and extinctions (*red*) per substage.

had followed a long-term increase in the number of genera since the early Turonian.

Peaks of originations occurred during the late Barremian–early Aptian, late Albian–middle Cenomanian, and the Campanian (Fig. 5). Since the Coniacian, the number of extinctions gradually increased, but this was matched by a large number of originations in the Campanian, resulting in the highest number of genera during the evolution of the Hippuritida. This turnover, i.e., relatively large number of extinctions compensated by an even higher number of originations, resulted in an increasing degree of endemism of late Campanian–Maastrichtian rudists, with centers of high diversity developing in the Caribbean and Arabia. This increasing endemism may have been an important early milestone on the road to final extinction, as discussed below.

Comparing the numbers of originations and extinctions, only the late Cenomanian and the late Maastrichtian are characterized by a much larger number of extinctions than originations (Fig. 5). While a large number of extinctions also occurred at the end of the early Aptian and the late Albian, these are matched by a relatively large number of originations, resulting in the endemic late Aptian–Albian associations on both sides of the Atlantic Ocean.

The prominent mid-Aptian and Cenomanian/Turonian reductions in the number of genera affected predominantly aragonite-dominated genera (Fig. 6), including relatively derived taxa that flourished especially on the outer margins of platforms (Skelton & Gili, 2012). Other taxa, such as the calcite-dominated Radiolitidae (Fig. 6–7), continued to radiate across the Cenomanian–Turonian boundary. A similar pattern can be seen at the end of the Albian, when extinction did not affect calcite-dominated genera, and in the mid-Valanginian, when all (in this instance, relatively primitive) aragonite-dominated genera disappeared. The average duration of aragonite-dominated genera is significantly shorter than those of other genera of the Hippuritida (Table 1). A preservational bias of the fossil record of bivalves owing to the higher diagenetic reactivity of aragonite is not evident from the fossil record (Kidwell, 2005). Hence, the observations that aragonite-dominated genera have shorter durations and were more affected during crises in the evolution of the Hippuritida deserve further attention.

The Mg/Ca ratio of seawater has been considered to affect the mineralogical composition of marine calcifiers (Stanley & Hardie, 1998; Ries, 2010). During the evolution of the Hippuritida, the Mg/Ca molar ratio of seawater ratio was consistently low, below 2, favoring calcite rather than aragonite as the dominant marine carbonate (Stanley & Hardie, 1998; Steuber & Rauch, 2005; Gothmann & others, 2015). Due to the long residence time of Mg and Ca in seawater, rapid changes on time scales of a few million years are not possible, and the available data on seawater composition show no significant variation during the time period in question. The rise from the low Late Jurassic–Cretaceous Mg/Ca molar ratio of 2 to the modern value of 5 may have started in the Campanian, but data derived from geochemical modeling (Stanley & Hardie, 1998), rudist skeletal calcite (Steuber & Rauch, 2005), and coral aragonite (Gothmann & others, 2015) are inconclusive about the exact timing of this increase. Consequently, the Mg/Ca ratio of seawater cannot be considered as a main cause for extinction of aragonite-dominated genera, but the consistently low Mg/Ca ratio of the Late Jurassic–Cretaceous may have

Data	Number	Mean	Median	Minimum	Maximum	SD
all genera	167	12.3	8.5	0.5	80.8	11.8
calcite-dominated	76	13.5	10.8	0.5	41.8	10.7
aragonite-dominated	57	8.4	6.4	0.5	31.1	7.5
no dominance	34	16.2	8.9	1.4	80.8	17.0

Table 1. Duration (myrs) of genera of the Hippuritida Newell, 1965, with different shell mineralogy. Minimum possible duration was set at 0.5 myrs. *SD,* standard deviation.

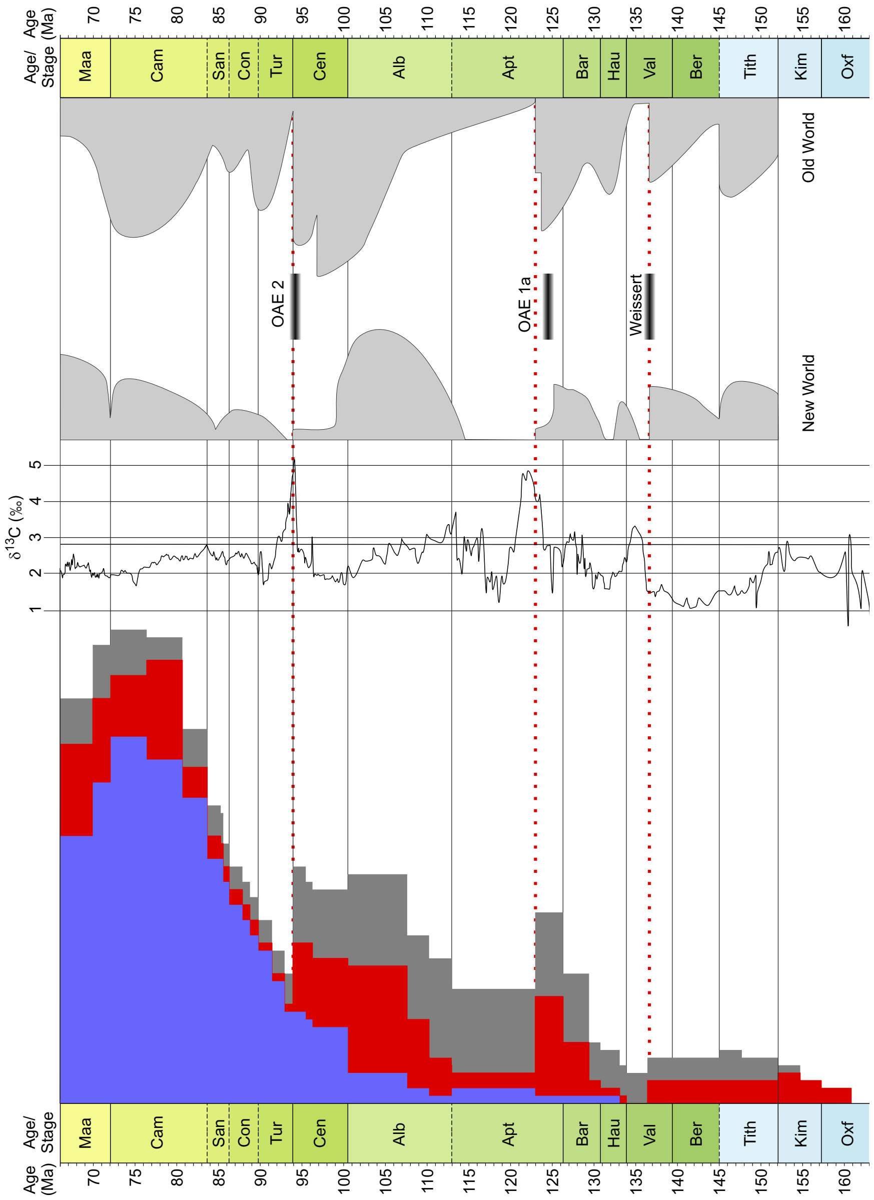

Fig. 6. Number of genera of the Hippuritida Newell, 1965, from the Oxfordian to the Maastrichtian, with calcite-dominated shells (*blue*), aragonite-dominated shells (*red*), and dominance of neither calcite nor aragonite (*gray*) compared with relative changes in the carbon-isotopic composition of marine carbonates (adapted from Shipboard Scientific Party, 2002; Jarvis & others, 2006; Emeis & Weissert, 2009; and Thiebault & others, 2012) and with the extent of carbonate platforms in the Americas (*New World*) and Europe, North Africa, and Arabia (*Old World*) (adapted from Skelton, 2003a). *Red dotted lines* indicate major extinctions among the Hippuritida. Oceanic anoxic events indicated by *gray bars:* mid-Valanginian (*Weissert*); early Aptian (*OAE 1a*); and Cenomanian/Turonian transition (*OAE 2*).

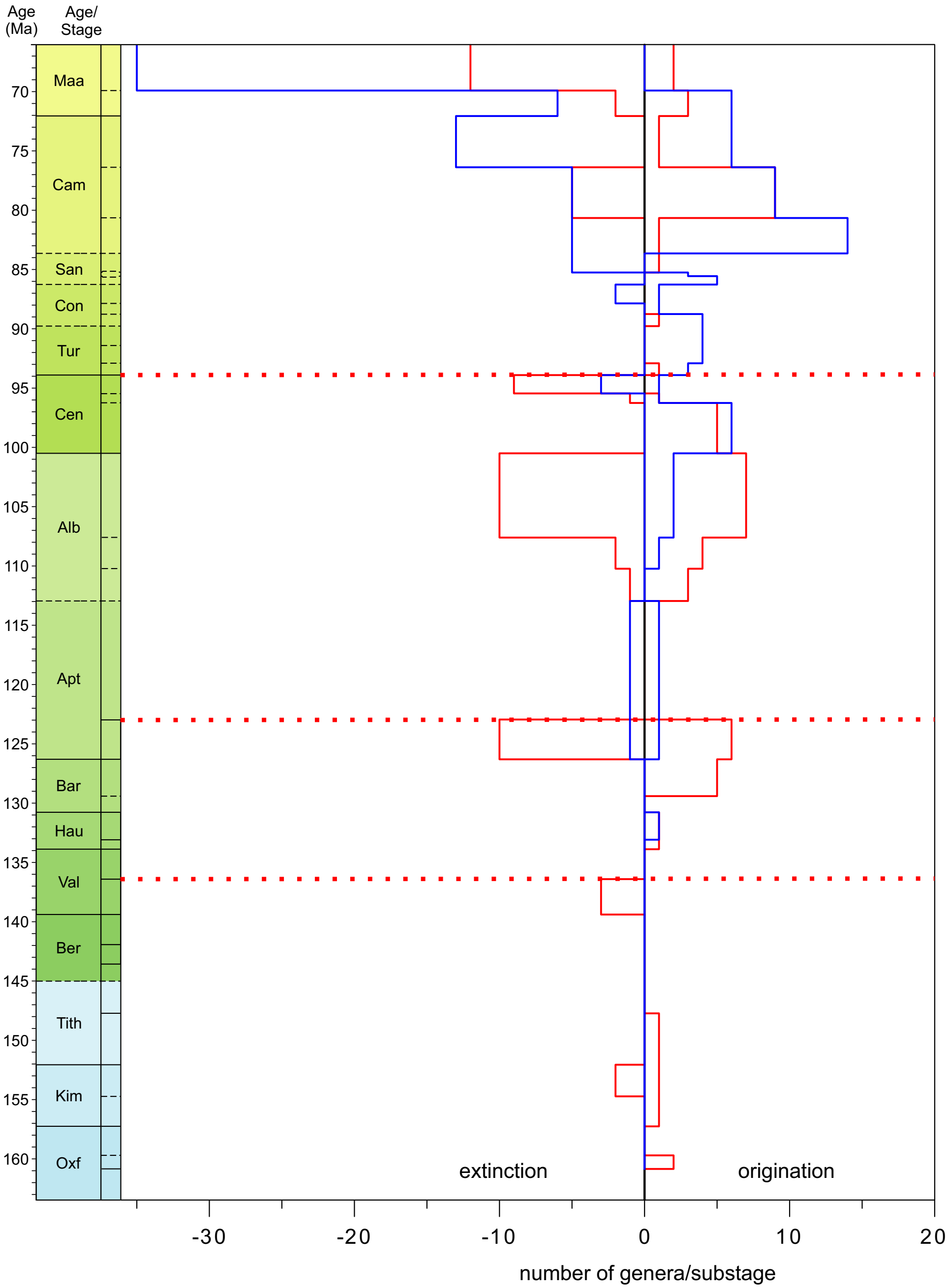

FIG. 7. Originations and extinctions of genera of the Hippuritida NEWELL, 1965, from the Oxfordian to the Maastrichtian, with calcite-dominated shells (*blue*) and aragonite-dominated shells (*red*). *Red dotted lines* indicate major extinctions among the Hippuritida.

favored the evolution of calcite-dominated Hippuritida and could have contributed to the higher risk of extinction of aragonite-dominated genera during episodes of environmental change.

The mid-Valanginian, mid-Aptian, and Cenomanian/Turonian extinction events broadly correspond to crises in carbonate platform evolution that have been associated with oceanic anoxic events (OAE), such as the Weissert event (mid-Valanginian), OAE 1a (early Aptian) and OAE 2 (Cenomanian/Turonian transition). These crises have been discussed in the context of major perturbations of the global carbon cycle and related changes in climate, nutrient cycling, chemical composition of seawater, and the $CaCO_3$ saturation of seawater (e.g., PHILIP & AIRAUD-CRUMIERE, 1991; PARENTE & others, 2008; FÖLLMI, 2012; SKELTON & GILI, 2012). Indeed, the episodes of sharp decreases in the number of genera, with aragonite-dominated genera being the main victims, show a remarkable correlation with positive carbon isotope excursions that reflect an increased burial of organic carbon (Fig. 6).

However, a closer evaluation reveals some significant differences between these three major phases of carbonate platform crises and reduction in the number of rudist genera. Whereas the Cenomanian/Turonian extinction event occurred during an episode of peak Cretaceous global paleotemperature, the Valanginian and Aptian extinction events coincided with climatic cooling (STEUBER RAUCH, & others, 2005; FÖLLMI, 2012; SKELTON & GILI, 2012).

At least for the early Aptian OAE 1a, there is a substantial stratigraphic mismatch between evidence for climate change, sea-level change, calcification crises of calcareous plankton, and rudist extinction (MASSE & FENERCI-MASSE, 2013b), which suggests that any possible linkage between these phenomena would have had to play out through a complex history of changes (SKELTON & GILI, 2012). While many carbonate platforms along the northern Tethyan margin drowned during the time of the mid-Early Aptian OAE 1a and their biota regionally disappeared, others survived (BOVER-ARNAL & others, 2015). On the Arabian shelf, aragonite-dominated Caprinidae were abundant carbonate producers well after OAE 1a, and finally disappeared from the sedimentary record during a third-order sea-level highstand, around the early-late Aptian boundary (STROHMENGER & others, 2010). Platform demise during the mid-Valanginian Weissert event and at the Cenomanian/Turonian transitions appears to be more globally synchronous (PHILIP & AIRAUD-CRUMIERE, 1991; FÖLLMI, 2012), although these events have been less intensely studied when compared with the early Aptian crisis.

Extinctions related to the Weissert event and the OAE 1a preceded the positive carbon-isotope excursions, while the Cenomanian/Turonian event appears to have coincided with the extinction. A similar pattern exists with the areal extent of carbonate platforms, despite somewhat different patterns on both sides of the Atlantic (Fig. 6). The causal and temporal relationships between environmental change, perturbations in the carbon cycle and the related carbon-isotope excursions, as well as changes in seawater composition and carbonate saturation are topics of ongoing debate and research (SKELTON & GILI, 2012; FÖLLMI, 2012).

No major extinction events are recorded from the Turonian to the Maastrichtian. This time interval appears to have been a period of comparatively minor environmental change and evolutionary pressure, as also reflected in less significant variations in the carbon-isotope record when compared to the Valanginian–Cenomanian interval.

The final extinction of the Hippuritida at the end of the Cretaceous, referred to as the Cretaceous–Paleogene boundary (K/Pg), was discussed recently (STEUBER & SCHLÜTER, 2012) and is considered to have been abrupt (STEUBER & others, 2002; SCHLÜTER & others, 2008b), rather than stepwise (JOHNSON & KAUFFMAN, 1996). Latest Maastrichtian rudist occurrences are typically of similar species-richness when compared with older Late Cretaceous associations, but are highly endemic. The increasing isolation of endemic populations together with a globally reduced area of carbonate platforms during the late Maastrichtian may have contributed to the extinction (Steuber & Schlüter, 2012), as endemic clades are more likely to become extinct during episodes of environmental change (Jablonski & Raup, 1995). The K/Pg impact and related environmental perturbations were possibly the ultimate cause that wiped out the already highly isolated and endemic associations of the late Maastrichtian Hippuritida (Steuber & Schlüter, 2012).

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REFERENCES

Andrusov, Dmitrij. 1976. Neue Rudistenfaunen aus den Westkarpaten und vom Ochridsee. Geologica Carpathica 27:11–34.

Bilotte, Michel. 1985. Le Crétacé supérieur des plates-formes est-pyrénéenes. Strata (2)5:1–438.

Bover-Arnal, Telm, Enric Pascual-Cebrian, P. W. Skelton, Eulàlia Gili, & Ramon Salas. 2015. Patterns in the distribution of Aptian rudists and corals within a sequence-stratigraphic framework (Maestrat Basin, E Spain). Sedimentary Geology 321:86–104.

Cestari, Riccardo, & Dario Sartorio. 1995. Rudists and Facies of the Periadriatic Domain. Agip. Milan. 207 p.

Coogan, Alan H. 1977. Early and middle Cretaceous Hippuritacea (rudists) of the Gulf Coast. *In* D. G. Bebout & R. G. Loucks, eds., Cretaceous carbonates of Texas and Mexico. Bureau of Economic Geology, The University of Texas at Austin, Report of Investigation 89:32–70, 18 pl.

Cox, Leslie R. 1933. The evolutionary history of the rudists with a report of the demonstration at the British Museum (Natural History), on Saturday, February 17th, 1933. Proceedings of the Geologist's Association, London 44:379-388.

Cox, Leslie R., N. D. Newell, D. W. Boyd, C. C. Branson, Raymond Casey, A. L. Chavan, A. H. Coogan, Colette Dechaseaux, C. A. Fleming, Fritz Haas, L. G. Hertlein, E. G. Kauffman, A. Myra Keen, Aurèle LaRocque, A. L. McAlester, R. C. Moore, C. P. Nuttall, B. F. Perkins, H. S. Puri, L. A. Smith, T. Soot-Ryen, H. B. Stenzel, E. R. Trueman, R. D. Turner, & John Weir. 1969. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part N, Mollusca 6, Bivalvia, vol. 2. The Geological Society of America & The University of Kansas Press. Boulder & Lawrence. p. 491–952.

Crame, J. Alistair, J. M. McArthur, Duncan Pirrie, & J. B. Riding. 1999. Strontium isotope correlation of the basal Maastrichtian stage in Antarctica to the European and US biostratigraphic schemes. Journal of the Geological Society, London 156:957–964.

Dall, William H. 1895. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosahatchie River. Part III. A new classification of the Pelecypoda. Wagner Free Institute of Science of Philadelphia, Transactions 3(3):483–570.

Damestoy, Guy. 1971. Essai de classification phylogénique des caprinidés (lamellibranches). Muséum National d'Histoire Naturelle, Bulletin (sér. 2) 42(5):1003–1008.

Douvillé, (Joseph) Henri F. 1887. Sur quelques formes peu connues de la famille des Chamidés. Société Géologique de France, Bulletin (séries 3) 15:756–802, pl. 28–31.

Douvillé, (Joseph) Henri F. 1888. Étude sur les caprines. Société Géologique de France, Bulletin (séries 3) 16:699–730, pl. 22–23.

Douvillé, (Joseph) Henri F. 1926. Quelques fossiles du Crétacé supérieur de Cuba. Compte Rendu Sommaire et Bulletin de la Société Géologique de France (séries 4) 26:127–138, 2 pl.

Douvillé, (Joseph) Henri F. 1927. Nouveaux rudistes du Crétacé de Cuba. Compte Rendu Sommaire et Bulletin de la Société Géologique de France (séries 4) 27:49–56.

Emeis, Kay-Christian & Helmut Weissert. 2009. Tethyan–Mediterranean organic carbon-rich sediments from Mesozoic black shales to sapropels. Sedimentology 56:247–266.

Föllmi, Karl B. 2012. Early Cretaceous life, climate, and anoxia. Cretaceous Research 35:230–257.

Foote, Michael. 2000. Origination and extinction components of taxonomic diversity: general problems. Paleobiology 26:74–102.

Gili, Eulàlia, J.-P. Masse, & P. W. Skelton. 1995. Rudists as gregarious sediment-dwellers, not reef-builders, on Cretaceous carbonate platforms. Palaeogeography, Palaeoclimatology, Palaeoecology 118:245–267.

Gothmann, Anne M., Jarosław Stolarski, J. F. Adkins, Blair Schoene, K. J. Dennis, D. P. Schrag, Maciej Mazur, & M. L. Bender. 2015. Fossil corals as an archive of secular variations in seawater chemistry since the Mesozoic. Geochimica et Cosmochimica Acta 160:188–208.

Gradstein, Felix M., J. G. Ogg, & M. D. Schmitz, eds. 2012. The Geologic Time Scale 2012. Elsevier. Amsterdam. 1176 p.

Gray, John E. 1848. On the arrangement of the Brachiopoda. The Annals and Magazine of Natural History (series 2) 2(12):435–440.

Jablonski, David, & D. M. Raup. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. Science 268:389–391.

Jarvis, Ian, A. S. Gale, H. C. Jenkyns, & M. A. Pearce. 2006. Secular variation in Late Cretaceous carbon isotopes: a new δ^{13}C carbonate reference curve for the Cenomanian–Campanian (99.6–70.6 Ma). Geological Magazine 143:561–608.

Johnson, Claudia C., & E. G. Kauffman. 1996. Maastrichtian extinction patterns of Caribbean province rudistids. *In* Norman MacLeod, & Gerta Keller, eds., Cretaceous-Tertiary Mass Extinctions: Biotic and Environmental Changes. Norton & Co. New York. p. 231–273.

Karacabey-Öztemür, Necdet. 1980. Two new genera of Radiolitidae (*Balabania* n. gen, *Kurtinia* n. gen.) from Turkey. Türkiye Jeoloji Kurumu Bülteni 23:79–86. 4 pl.

Kidwell, Susan M. 2005. Shell composition has no net impact on large-scale evolutionary patterns in mollusks. Science 307:914–917.

Kutassy, Endre (Andreas). 1934. Pachyodonta Mesozoica (Rudistis exclusis). *In* Werner Quenstedt, ed., Fossilium Catalogus, I: Animalia, Pars 68. W. Junk. 's-Gravenhage. 202 p.

Lupu, Denisa. 1976. Un nouveau radiolitidé: *Bystrickya andrusovi* n. gen. nov. sp. du Sénonien supérieur de la haute vallée du Hron (Hrehronie, Carpates slovaques). Geologica Carpathica 27(1):35–43.

Lupu, Denisa. 1982. A new denomination of the taxon 'Orestia' Lupu, 1972. Dari de Seama ale Sedintelor Institutul de Geologie si Geofizica (Bucharest) 67(3):83.

Mac Gillavry, Henry James. 1937. Geology of the province of Camaguey, Cuba, with revisional studies of rudist paleontology. Utrecht Rijks-Universiteit, Geographische en Geologische Mededeelingen, Physiographisch-Geologische Reeks 14:1–168, 10 pl.

Masse, Jean-Pierre. 1996. Lower Cretaceous rudist biostratigraphy of southern France: A reference for Mesogean correlations. *In* Gloria Alencáster, & B. E. Buitrón-Sánchez, eds., Number devoted to the Third International Conference on Rudists. Revista Mexicana de Ciencias Geológicas 12(2):236–256, 6 pl.

Masse, Jean-Pierre. 1998. Rudists: Lower Cretaceous. *In* P.-C. de Graciansky, Jan Hardenbol, Thierry Jacquin, & P. R. Vail, eds., Mesozoic and Cenozoic sequence stratigraphy of European basins. SEPM (Society for Sedimentary Geology) Special Publication 60:775.

Masse, Jean-Pierre. 2003. Integrated stratigraphy of the Lower Aptian and applications to carbonate platforms: a state of the art. *In* Eulàlia Gili, M. H. Negra, & P. W. Skelton, eds., North African carbonate platform systems. NATO Science Series, IV. Earth and Environmental Sciences 28:203–214.

Masse, Jean-Pierre, Consuelo Arias, & Lorenzo Vilas. 1998. Lower Cretaceous rudist faunas of southeast Spain: an overview. *In* J.-P. Masse, & P. W. Skelton, eds., Quatrième Congrès International sur les Rudistes. Geobios, Mémoire spécial 22:193–210.

Masse, Jean-Pierre, & Alexandre Chartrousse. 1997. Les *Caprina* (rudistes) de l'Aptien inférieur d'Europe occidentale: systématique, biostratigraphie et paléobiogéographie. Geobios 30:797–809.

Masse, Jean-Pierre, & Mukerrem Fenerci-Masse. 2013a. Stratigraphic updating and correlation of Late Barremian–Early Aptian Urgonian successions and their marly cover, in their type region (Orgon-Apt, SE France). Cretaceous Research 39:17–28.

Masse, Jean-Pierre, & Mukerrem Fenerci-Masse. 2013b. Drowning events, development and demise of carbonate platforms and controlling factors: The Late Barremian–Early Aptian record of Southeast France. Sedimentary Geology 298:28–52.

Masse, Jean-Pierre, Mukerrem Fenerci-Masse, Lorenzo Vilas. & Consuelo Arias. 2007. Late Aptian-Albian primitive Radiolitidae (bivalves, Hippuritoidea) from Spain and SW France. Cretaceous Research 28:697–718. 2 tables.

Masse, Jean-Pierre, & Jean Philip. 1986. L'évolution des rudistes au regard des principaux événements géologiques du Crétacé. Centres de Recherches Exploration-Production Elf-Aquitaine, Bulletin 10:437–456.

Masse, Jean-Pierre, & Thomas Steuber. 2007. Strontium isotope stratigraphy of early Cretaceous rudist bivalves. *In* R. W. Scott, ed., Cretaceous Rudists and Carbonate Platforms: Environmental Feedback. SEPM (Society for Sedimentary Geology) Special Publication 87:159–165.

McArthur, John M. 1994. Recent trends in strontium isotope stratigraphy. Terra Nova 6:331–358.

McArthur, John M., R. J. Howarth, & T. R. Bailey. 2001. Strontium isotope stratigraphy: LOWESS Version 3. Best-fit line to the marine Sr-isotope curve for 0 to 509 Ma and accompanying look-up table for deriving numerical age. Journal of Geology 109:155–169 (look-up table version 4b 08 04).

McArthur, John M., W. J. Kennedy, Meng Chen, M. F. Thirlwall, & A. S. Gale. 1994. Strontium isotope stratigraphy for Late Cretaceous time: Direct numerical calibration of the Sr isotope curve based on the US Western Interior. Palaeogeography, Palaeoclimatology, Palaeoecology 108:95–119.

Mitchell, Simon F. 2013a. A revision of selected Lower Cretaceous American caprinoid rudists: implications for phylogeny and biostratigraphy. Caribbean Journal of Earth Science 45:45–75.

Mitchell, Simon F. 2013b. Revision of the Antillocaprinidae Mac Gillavry (Hippuritida, Bivalvia) and their position within the Caprinoidea d'Orbigny. Geobios 46:423–446.

Mitchell, Simon F. 2013c. Lithostratigraphy of the Central Inlier, Jamaica. Caribbean Journal of Earth Science 46:31–42.

Mitchell, Simon F. 2014. Erratum to "Revision of the Antillocaprinidae Mac Gillavry (Hippuritida, Bivalvia) and their position within the Caprinoidea d'Orbigny" [Geobios 46 (2013), 423–446] Geobios 47: p. 75.

Munier-Chalmas, Ernest C. P. A. 1873. Prodrome d'une classification des rudistes. Journal de Conchyliologie, Paris (série 3) 21(1):73.

Newell, Norman D. 1965. Classification of the Bivalvia. American Museum Novitates 2206:1–25.

Ogg, James (database coordinator), & Adam Lugowski (software developer). 2011. TSCreator visualization of enhanced Geologic Time Scale 2004 database (Version 6.1.2; 2014); http://www.tscreator.org.

Orbigny, Alcide D. d'. 1847. Sur les Brachiopodes ou Palliobranches (deuxième mémoire). Comptes

Rendus Hebdomadaires des Séances de l'Académie des Sciences 25:266–269.

Parente, Mariano, Gianluca Frijia, Matteo Di Lucia, H. C. Jenkyns, R. G. Woodfine, & Francesco Baroncini. 2008. Stepwise extinction of larger foraminifers at the CenomanianTuronian boundary: A shallow-water perspective on nutrient fluctuations during Oceanic Anoxic Event 2 (Bonarelli Event). Geology 36:715–718.

Pascual-Cebrian, Enric, Stefan Götz, Telm Bover-Arnal, P. W. Skelton, Eulàlia Gili, Ramon Salas, & Wolfgang Stinnesbeck. 2016. Calcite/aragonite ratio fluctuations in Aptian rudist bivalves: Correlation with changing temperatures. Geology 44:135–138.

Philip, Jean. 1998a. Biostratigraphie et paléobiogéographie des rudistes: évolution des concepts et progrès récents. Bulletin de la Société Géologique de France 169:689–708.

Philip, Jean. 1998b. Rudists: Upper Cretaceous. *In* P.-C. de Graciansky, Jan Hardenbol, Thierry Jacquin, & P. R. Vail, eds., Mesozoic and Cenozoic sequence stratigraphy of European basins. SEPM (Society for Sedimentary Geology) Special Publication 60:774–775.

Philip, Jean, & Christine Airaud-Crumiere 1991. The demise of the rudist bearing carbonate platforms at the Cenomanian/Turonian boundary: a global control. Coral Reefs 10:115–125.

Polšak, Ante, Vera Bauer, & Teofil Slišković. 1982. Stratigraphie du Crétacé supérieur de la plate-forme carbonatée dans les Dinarides externes. Cretaceous Research 3:124–133.

Rengarten, Vladimir P. 1950. Rudistovye fatsii melovykh otlozhenii Zakavkazia [Rudist facies of the Cretaceous of Transcaucasus]. Nauk, Akademiia Nauk SSSR 130 [eer. Geologicheskaia, 51]:1–92, 16 pl.

Ries, Justin B. 2010. Review: geological and experimental evidence for secular variation in seawater Mg/Ca (calcite-aragonite seas) and its effects on marine biological calcification. Biogeosciences 7:2795–2849.

Ross, Donald J., & P. W. Skelton. 1993. Rudist formations of the Cretaceous: a palaeoecological, sedimentological and stratigraphic review. *In* V. Paul Wright, ed., Sedimentology review. Blackwell, London. 1:73–91.

Sadler, Peter M. 2004. Quantitative biostratigraphy—achieving finer resolution in global correlation. Annual Reviews Earth and Planetary Sciences 32:187–213.

Schlüter, Malte, Thomas Steuber, & Mariano Parente. 2008a. Chronostratigraphy of Campanian–Maastrichtian platform carbonates and rudist associations of Salento (Apulia, Italy). Cretaceous Research 29:100–114.

Schlüter, Malte, Thomas Steuber, Mariano Parente, & Jörg Mutterlose. 2008b. Evolution of a Maastrichtian-Paleocene tropical shallow-water carbonate platform (Qalhat, NE Oman). Facies 54:513–527.

Scott, Robert W. 1995. Global environmental controls on Cretaceous reefal ecosystems. Palaeogeography, Palaeoclimatology, Palaeoecology 119:187–199.

Scott, Robert W. 2009. Chronostratigraphic database for Upper Cretaceous Oceanic Red Beds (CORBs). *In* Hu Xiumian, Wang Chengshan., R. W. Scott, Michael Wagreich, & Luba Jansa, eds., Cretaceous Oceanic Redbeds: Stratigraphy, Composition, Origins, Paleogeographic, and Paleoclimatic Significance. SEPM (Society for Sedimentary Geology) Special Publication 91:31–53.

Scott, Robert W. 2010. Numerical ages of selected rudist Bivalvia: Preliminary results. *In* Sacit Özer, Bilal Sarı, & P. W. Skelton, eds., Jurassic-Cretaceous Rudists and Carbonate Platforms. Turkish Journal of Earth Sciences 19:769–790.

Scott, Robert W. 2014. A Cretaceous chronostratigraphic database: construction and applications. Carnets de Géologie (Notebooks on Geology) 14 (2):15–37, 7 appendices.

Scott, Robert W., & H. F. Filkorn. 2007. Barremian-Albian rudist zones, U.S. Gulf Coast. *In* R.W. Scott, ed., Cretaceous Rudists and Carbonate Platforms: Environmental Feedback. SEPM (Society for Sedimentary Geology) Special Publication 87:167–180.

Scott, Robert W., & Charles Kerans. 2004. Late Albian carbonate platform chronostratigraphy, Devils River Formation cycles, west Texas. Courier Forschungs-Institut Senckenberg 247:129–148.

Scott, Robert W., Wan Xiaoqiao, Sha Jingeng, & Wen Shi-xuan. 2010. Rudists of Tibet and the Tarim Basin, China: significance to Requieniidae phylogeny. Journal of Paleontology 84:444–465.

Shipboard Scientific Party. 2002. Leg 198 summary. *In* T. J. Bralower, Isabella Premoli Silva, M. J. Malone, & others, eds., Proceedings ODP, Initial Reports, 198, College Station TX (Ocean Drilling Program), p. 1–84. doi:10.2973/odp.proc.ir.198.101.2002.

Skelton, Peter W. 1999. Synoptic guide to Kimmeridgian rudists for the Kelheim field visit. *In* Richard Höfling, & Thomas Steuber, eds., Fifth International Congress on Rudists: Abstracts and Field Trip Guides. Erlanger Geologische Abhandlungen Sb 3:83–89, 3 pl.

Skelton, Peter W. 2000. Rudists and carbonate platforms—growing together, dying together. Accademia Nazionale di Scienze, Lettere ed Arti di Modena, Collana di Studi 21:231–235.

Skelton, Peter W. 2003a. Changing climate and biota. *In* P. W. Skelton, ed., The Cretaceous World. University of Cambridge Press. Cambridge. p. 163–184.

Skelton, Peter W. 2003b. Rudist evolution and extinction: A North African perspective. *In* Eulàlia Gili, M. E. H. Negra, & P. W. Skelton, eds., North African Cretaceous Carbonate Platform Systems. NATO Science Series, IV. Earth and Environmental Sciences 28:215–227.

Skelton, Peter W. 2013a. Rudist classification for the revised Bivalvia volumes of the Treatise on Invertebrate Paleontology. Caribbean Journal of Earth Science 45:9–33.

Skelton, Peter W. 2013b. Rudist classification: nomenclatural correction of 'Suborder Radiolitidina Skelton, 2013' to 'Suborder Hippuritidina Newell, 1965'. Caribbean Journal of Earth Science 45:34.

Skelton, Peter W., & Eulàlia Gili. 2012. Rudists and carbonate platforms in the Aptian: a case study on biotic interactions with ocean chemistry and climate. Sedimentology 59:81–117.

Stanley, Steven M., & L. A. Hardie. 1998. Secular oscillations in the carbonate mineralogy of reef-building and sediment-producing organisms driven by tectonically forced shifts in seawater chemistry. Palaeogeography, Palaeoclimatology, Palaeoecology 144:3–19.

Steuber, Thomas. 2000. Skeletal growth rates of Upper Cretaceous rudist bivalves: Implications for carbonate production and organism–environment feedbacks. *In* Insalaco, Enzo, P. W. Skelton, & T. J. Palmer, eds., Carbonate Platform Systems: Components and Interactions. Geological Society, London, Special Publication 178:21–32.

Steuber, Thomas. 2001. Strontium isotope stratigraphy of Turonian–Campanian Gosau-type rudist formations in the Northern Calcareous and Central Alps (Austria and Germany). Cretaceous Research 22:429–441.

Steuber, Thomas. 2002. Plate tectonic control on the evolution of Cretaceous platform carbonate production. Geology 30:259–262.

Steuber, Thomas. 2003a. Strontium isotope stratigraphy of Cretaceous hippuritid rudist bivalves: Rates of morphological change and heterochronic evolution. Palaeogeography Palaeoclimatology Palaeoecology 200:221–243.

Steuber, Thomas. 2003b. Strontium isotope chemostratigraphy of rudist bivalves and Cretaceous carbonate platforms. *In* Eulàlia Gili, M. E . H. Negra, & P. W. Skelton, eds., North African Cretaceous Carbonate Platform Systems. NATO Science Series, IV. Earth and Environmental Sciences 28:229–238.

Steuber, Thomas, Tvrtko Korbar, Vladimir Jelaska, & Ivan Gušić. 2005. Strontium-isotope stratigraphy of Upper Cretaceous platform carbonates of the island of Brac (Adriatic Sea, Croatia): implications for global correlation of platform evolution and biostratigraphy. Cretaceous Research 26:741–756.

Steuber, Thomas, & Hannes Löser. 2000. Species richness and abundance patterns of Tethyan Cretaceous rudist bivalves (Mollusca: Hippuritacea) in the central-eastern Mediterranean and Middle East. Palaeogeography, Palaeoclimatology, Palaeoecology 162:75–104.

Steuber, Thomas, S. F. Mitchell, Gavin Gunter, Dieter Buhl, & H. U. Kasper. 2002. Catastrophic extinction of Caribbean rudist bivalves at the Cretaceous-Tertiary boundary. Geology 30:999–1002.

Steuber, Thomas, Sacit Özer, Malte Schlüter, & Bilal Sarı. 2009. Description of *Paracaprinula syriaca* Piveteau (Hippuritoidea, Plagioptychidae) and a revised age of ophiolite obduction on the African-Arabian Plate in southeastern Turkey. Cretaceous Research 30:41–48.

Steuber, Thomas, & Markus Rauch. 2005. Evolution of the Mg/Ca ratio of Cretaceous seawater: Implications from the composition of biological low-Mg calcite. Marine Geology 217:199–213.

Steuber, Thomas, Markus Rauch, J.-P. Masse, Joris Graaf, & Matthias Malkoc. 2005. Low-latitude seasonality of Cretaceous temperatures in warm and cold episodes. Nature 437:1341–1344.

Steuber, Thomas, & Malte Schlüter. 2012. Strontium-isotope stratigraphy of Upper Cretaceous rudist bivalves: Biozones, evolutionary patterns and sea-level change calibrated to numerical ages. Earth-Science Reviews 114:42–60.

Strohmenger, Christian J., Thomas Steuber, Ahmed Ghani, D. G. Barwick, S. H. A. Al-Mazrooei, & N. O. Al-Zaabi. 2010. Sedimentology and chemostratigraphy of Shu'aiba depositional sequences (Abu Dhabi, United Arab Emirates). *In* F. S. P. Van Buchem, M. I. Al-Husseini, Florian Maurer, & H. J. Droste, eds., Aptian Stratigraphy and Petroleum Habitat of the Eastern Arabian Plate. GeoArabia, Special Publication 4(2):341–365.

Thiebault, Nicolas, Dorothée Husson, Rikke Harlou, Silvia Gardin, Bruno Galbrun, Emilia Huret, & Fabrice Minoletti. 2012. Astronomical calibration of upper Campanian–Maastrichtian carbon isotope events and calcareous plankton biostratigraphy in the Indian Ocean (ODP Hole 762C): Implication for the age of the Campanian–Maastrichtian boundary. Palaeogeography, Palaeoclimatology, Palaeoecology 337–338:52–71.

Wiontzek, Herbert. 1934. Rudisten aus der Oberen Kreide des mittleren Isonzogebietes. Palaeontographica, Abt. A (80):1–40, 1 pl.

Yanin, Boris T. 1990. Kriterii sistematiki rudistov. *In* V.V. Menner, ed., Sistematika i Filogeniia Bespozvonochikh. Kriterii Vydeleniia Vyschikh Taksonov. Nauka. Moscow. p. 57–69.