

# RHAETIAN (LATE TRIASSIC) *MONOTIS* (BIVALVIA: PECTINOIDA) FROM THE EASTERN NORTHERN CALCAREOUS ALPS (AUSTRIA) AND THE END-NORIAN CRISIS IN PELAGIC FAUNAS

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**Abstract:** Species of marine bivalves of the pectinoid genus *Monotis* provide useful biochronologic indices for the Late Triassic (middle Norian–earliest Rhaetian). We report the succession of *Monotis* at Hernstein in Lower Austria where typical late Norian *Monotis salinaria* (Schlotheim) are overlain by strata with apparently the youngest *Monotis* known of demonstrable Rhaetian age: *Monotis hoernesii* Kittl and *Monotis rhaetica* sp. nov., a species closely related to *M. rudis* Gemmellaro. A Rhaetian (Sevatian 2) age is confirmed by the co-occurrence of *Monotis* with the platform conodont *Misikella posthernsteini* and close association with

the ammonoid *Paracochloceras*. A review of late Norian monotid species indicates that a profound extinction event occurred in the pelagic realm at or close to the Norian/Rhaetian boundary where *c.* 15 monotids (*Monotis s.l.* and *Maorimonotis*) became extinct. The surviving *Monotis* are dwarfed when compared to their Norian predecessors and may represent an ecological/phylogenetic response to the crisis.

**Key words:** *Monotis*, Bivalvia, extinction, Rhaetian, Upper Triassic, Austria.

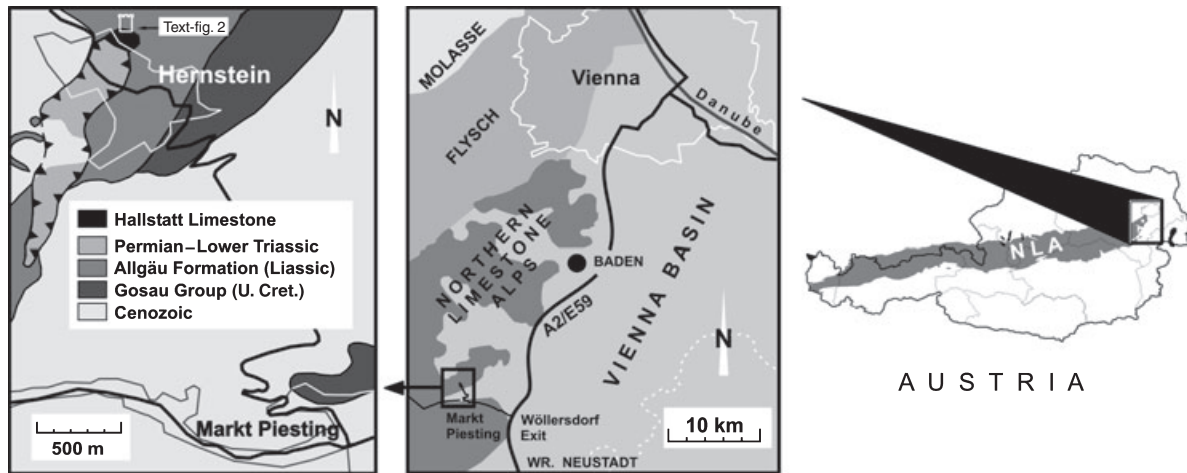
BIVALVE molluscs of the genus *Monotis* are perhaps the most abundant and biochronologically significant bivalves in many deep-water marine facies of the Late Triassic. They typically have widespread distributions and very limited temporal ranges making them among the best biochronologic macrofossils of the Late Triassic. Their biochronologic and palaeogeographic utility is probably a result of their living habits as inferred from their unique morphology and facies occurrence. In addition to being a major component in oxygen-reduced deep-marine facies of high palaeolatitude shelves and low latitude intraplatform basins, monotid bivalves are a conspicuous element in the various nodular and ‘filamentous’ red, white and grey pelagic limestones of the ancient Tethys Ocean, here collectively termed Hallstatt-type facies.

We report here on new occurrences of *Monotis* from the eastern part of the Northern Calcareous Alps, which are quite extraordinary in that they occur within Hallstatt facies of demonstrable Rhaetian (Sevatian 2) age and are, therefore, significantly younger than any known *Monotis* species. They occur, intercalibrated with conodonts and ammonoids, in sequence above typical late Norian *Monotis salinaria* (Schlotheim, 1820) and post-date an end-No-

rian extinction of most *Monotis* species. Additionally, these youngest *Monotis* species, like most others immediately preceding the end-Norian crisis, are dwarfed when compared to typical late Norian forms and may represent an ecologic and/or phylogenetic response to inimical conditions at or around the Norian/Rhaetian boundary.

## STRATIGRAPHIC AND GEOLOGIC SETTING

The fossils described herein occur within the upper part of the Hallstatt Limestone olistolith within the garden of Hernstein Castle in Lower Austria (47°53′53.6″ N, 16°06′05.8″ E) about 4 km north-east of Markt Piesting and 40 km south-west of Vienna (Text-fig. 1). This outcrop is on the eastern margin of the Northern Calcareous Alps, an approximately 500-km-long east–west-trending pile of nappes composed predominantly of Mesozoic sediments. Triassic limestones constitute a major part and occur in shore-parallel bands of intra-platform basins, platform carbonates, fringing reefs and deeper open-marine basins including the Hallstatt facies, forming originally



**TEXT-FIG. 1.** Maps showing geological detail of the Hernstein locality within the Hohe Wand Nappe (left) and simplified geology of the eastern part of the Northern Calcareous Alps (center) in eastern Austria (right).

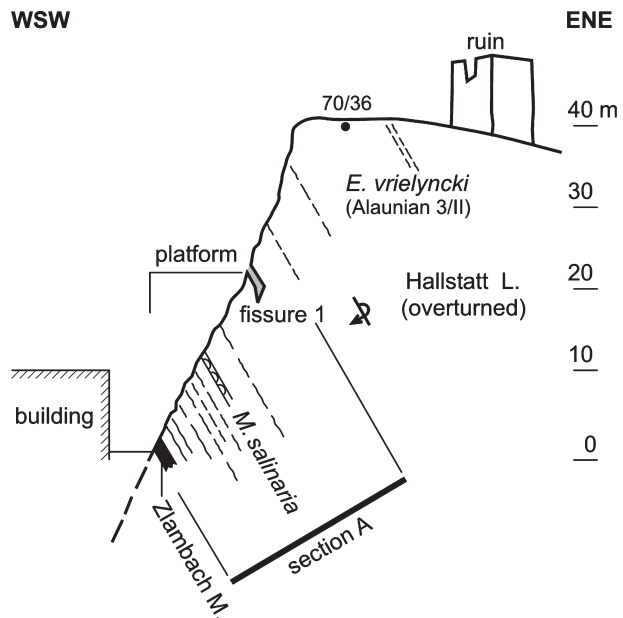
the north-western margin of the Tethys Ocean (Haas *et al.* 1995).

The section (Text-figs 2–3) is tectonically overturned and today occurs within an isolated remnant of the Hohe Wand Nappe (Plöchingner 1982), a regional sub-unit of the Juvavic nappe system representing the southernmost and originally ocean-nearest part of the Northern Calcareous Alps during Triassic time. The sequence consists of 32 m of Hallstatt Limestone that is stratigraphically overlain by dark grey soft marls of the Zlambach Formation exposed at the bottom of the outcrop. The contact between the Hallstatt Limestone and the Zlambach Formation is sharp and probably represents a fault parallel to bedding.

It is generally accepted that the Hallstatt facies was deposited in relatively deep and fully oxygenated marine settings adjacent to, and outboard of, the large Norian–Rhaetian carbonate platforms and reefs (Krystyn and Piller 2000). Lacking significant clastic input, the limestones are largely micritic with a texture that is mostly controlled by varying concentrations of pelagic micromolluscs (ammonoids and bivalves) and a microfauna of foraminifera, echinoderms (crinoids and holothurian sclerites) and conodont elements. An absence of current and/or wave indicators in these sediments supports a deeper-water setting well below mean storm wave-base. Nodular fabric, often accentuated by stylolites and shelly concentrations, of many Hallstatt-type limestones are most likely a result of stagnant sedimentation and subsolution (see Krystyn *et al.* 1971). Owing to the preserved, yet diagenetically altered, remains of aragonite-secreting skeletons of the macrofauna (e.g. ammonoids and halo-biid bivalves), it is obvious that water depths for these and other nodular pelagic limestones (e.g. the Jurassic Ammonitico Rosso) were above the lysocline and aragonite compensation depth. The Hallstatt Limestone of

Hernstein is somewhat different in exhibiting a massive to thick and indistinct bedding and no signs of hardgrounds or breaks in sedimentation. A higher accumulation rate and a comparably increased amount of benthic organisms (brachiopods) point to platform slope deposition in shallower conditions than the condensed ammonoid-shell-rich distal pelagic facies (Schlager 1974; Jenkyns 1974).

Notable features of Hallstatt limestones are synsedimentary fissures and their sediment fills (neptunian dikes and sills). The fissures can be a result of a variety of



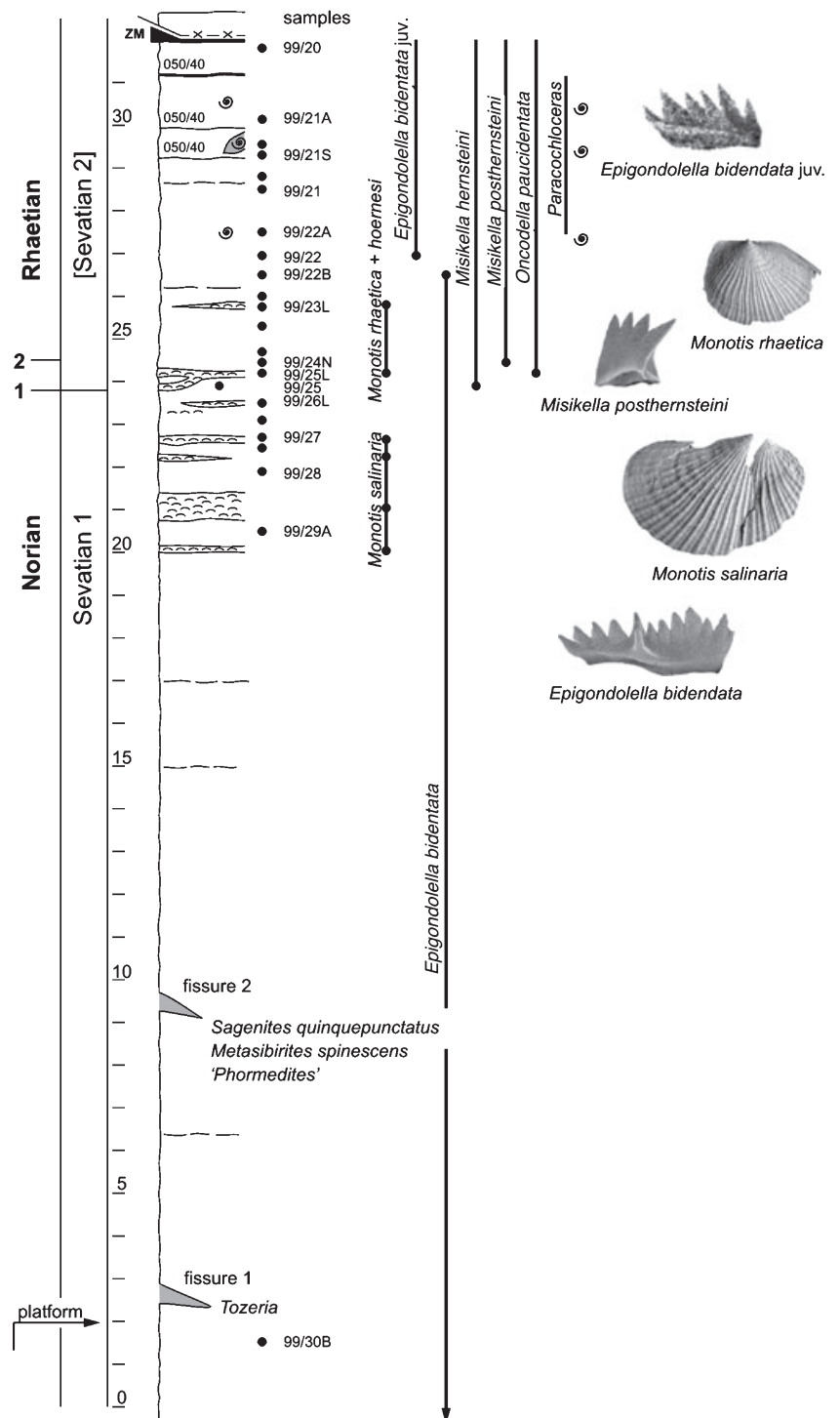
**TEXT-FIG. 2.** Sketch of outcrop, indicating overturned beds and major fissures and level with upper Norian (Sevatian 1) *Monotis salinaria* (Schlotheim 1820). The top of the exposure (point 70/36) contains middle Norian (Alaunian 3) conodonts including *Epigondolella vrielyncki*.

processes (e.g. differential compaction over basement structure, coeval faulting, gravitational instability; Schlager 1970) and were excellent fossil traps widespread in late Norian Hallstatt facies (Krystyn *et al.* 1971; Hornung 2005). The fissures are often easily recognized by their light grey spary calcitic walls, cross-cutting relationships, differences in carbonate textures, isotopic composition

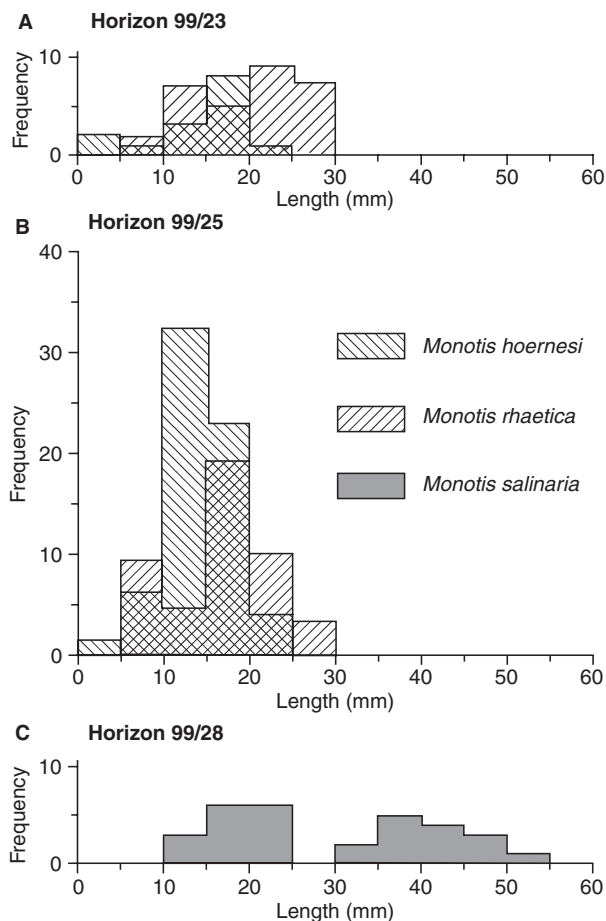
and the composition and age of the contained fauna of the fissure fills (Krystyn *et al.* 1971; Hornung 2005).

Within Hallstatt-type facies, *Monotis* shell accumulations occur within synsedimentary fissures or as horizontal lenticular shell beds up to 30 cm thick (e.g. Krystyn *et al.* 1971). In the latter, the shell-supported fabric with fibrous calcite cement supports a conclusion of rapid

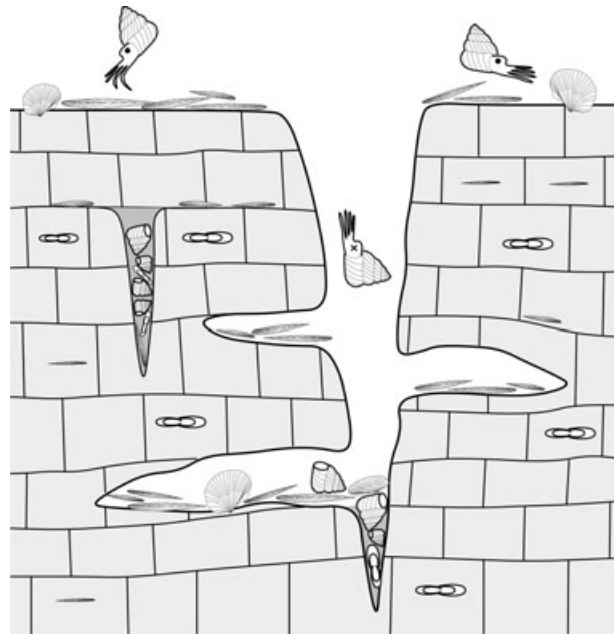
**TEXT-FIG. 3.** Stratigraphic log and biostratigraphic data. The section has been restored from its tectonically overturned outcrop expression (see Text-fig. 2). The favoured Norian/Rhaetian boundary (level 2) uses the FOD (First Occurrence Datum) of the conodont *Misikella posthernsteini* but can also be taken at the FOD *Misikella hernsteini* (level 1).



accumulation of skeletal material and syndimentary cementation in an otherwise sediment-starved setting. Zankl (1971) noted that monotid shells in Hallstatt facies are most commonly orientated concave-up and the fine-grained matrix lacks fragmented debris, indicating a lack of turbulence and little post-mortem transport. Schwarzscher (1948) suggested such flat clam accumulations were a result of either nearly *in situ* deposition of benthic dwellers or pseudoplanktonic life falling to the bottom as pelagic rain. We favour a benthic habit for *Monotis* and suggest they attached by a weak byssus to a semi-lithified (early cemented) sediment or shelly substrate. Although *Monotis* found within the neptunian sills may have been washed from adjacent sea-floor into the fissures soon after death, based on sedimentological data and size-frequency distributions of *Monotis* (Text-fig. 4), it is equally possible they represent *in situ* populations inhabiting the floors of cavernous fissures (Text-fig. 5). In the case of Hernstein, *M. salinaria* (Schlotheim, 1820) occurs in a normal-stratified succession through four 30-cm-thick,



**TEXT-FIG. 4.** Size-frequency distributions of *Monotis* species from Hernstein. The measurements were mostly taken on field-samples.



**TEXT-FIG. 5.** Representation of fissures in the Hallstatt Limestone showing living populations of *Monotis* on the sea-floor and in fissures, and the heteromorphic ammonoid *Paracochloceras*.

densely-packed layers, whereas *M. hoernesii* Kittl, 1912 and *M. rhaetica* sp. nov. are confined to relatively thin subparallel or discordant fissure fillings (sample numbers ending with L).

## BIOSTRATIGRAPHIC CONSTRAINTS

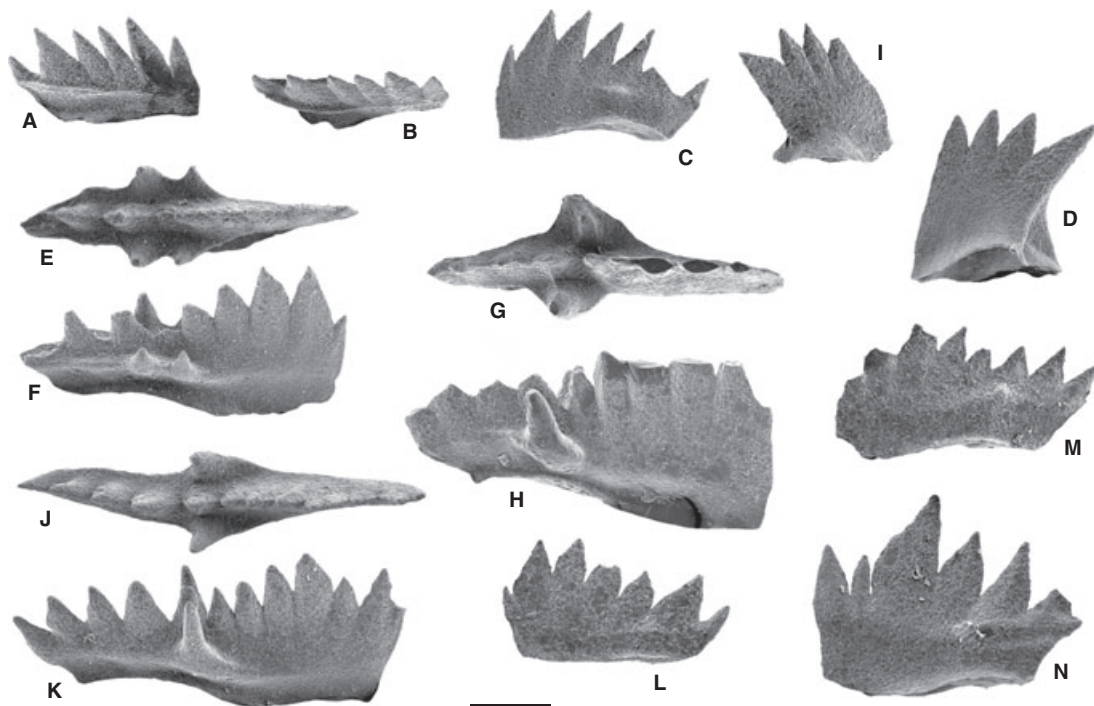
Because the boundary between the Norian and Rhaetian stages has not yet been selected by the Subcommittee on Triassic Stratigraphy, several operational definitions utilizing ammonoids and conodonts have been used in the past. In Europe, the Norian/Rhaetian boundary has been taken as base of the *Vandaites stuerzenbaumi* ammonoid Zone (e.g. Krystyn 1988), the base of the *Sagentites reticulatus* ammonoid Zone (e.g. Dagys and Dagys 1994) or the base of the '*Cochloceras*' *suessi* ammonoid Zone (e.g. Kozur 2003). A conodont-based boundary is most commonly taken to be the first appearance of *Misikella posthernsteini* (see Kozur 2003; Krystyn *et al.* 2007), which has been shown to correlate to the base of the *Paracochloceras suessi* Zone (Krystyn and Kuerschner 2005; Krystyn *et al.* 2007). In North America, a Norian/Rhaetian boundary is most often selected as the base of the *Paracochloceras amoenum* ammonoid Zone or its conodont correlative the *Epigondolella mosheri* Zone (e.g. Orchard and Tozer 1997). According to the best available correlations, the base of the *Epigondolella mosheri* Zone in North America may correspond to the first occurrence of *Misik-*

*ella posthernsteini* in the Tethyan sequence (Kozur 2003; Krystyn and Kuerschner 2005; Gallet *et al.* 2007; Krystyn *et al.* 2007). Only recently, the ammonoid genus *Cochloceras* (including the closely allied *Paracochloceras*), a biostratigraphic guide for the Sevatian 2, has officially been chosen as a proxy for a future internationally agreed Norian/Rhaetian boundary (see Ogg 2004). Hernstein has a certain importance as it demonstrates the considerable overlap of *Epigondolella bidentata* and *Misikella posthernsteini* and later that of juvenile epigondolellids with *Misikella posthernsteini*. Such juveniles are alternatively referred to the genus *Parvigondolella* and have been recently differentiated into several morphotypes according to their straight, up- or down-turned posterior (Orchard *et al.* 2007). All these morphotypes are represented within the 20 recovered specimens of *Epigondolella bidentata* juv. from the interval between 27 m and the section top.

Although the Hernstein locality was discussed by early workers (e.g. Bittner 1882), detailed geological and stratigraphical data were not reported until much later (Mostler *et al.* (1967). Subsequent publications described the Hernstein fauna rich in platform conodonts and holothurian sclerites (see Mostler 1967) and foraminifera (see

Fuchs 1970). Mostler *et al.* (1967) identified an overturned succession of older (lower Norian) '*Monotis salinaria salinaria*' passing downwards into younger (upper Norian or Sevatian) beds with '*Monotis salinaria haueri*'. Unfortunately, these *Monotis* taxa were only briefly described and never illustrated. Our observations on the *Monotis* and conodont succession depart somewhat from those of Mostler *et al.* (1967) and add further refinement to age assignment of various stratigraphic levels.

As shown in Text-fig. 3, most of the section, up to 26.5 m, contains conodont elements belonging to *Epigondolella bidentata*. The first occurrence of *Misikella hernsteini* occurs at 24 m and continues to the topmost sampled bed at 32 m. The first occurrence of *Misikella posthernsteini* is at 24.5 m stratigraphic height and continues to the youngest sampled bed. Ammonoids belonging to *Paracochloceras* occur in the uppermost part of the section between about 27 and 32 m. Assignment of the upper 8 m to the lower Rhaetian (= Sevatian 2) is confirmed by conodonts and in part by ammonoids as documented in Text-figure 6. As noted above, there are several identified fissures within the Hallstatt Limestone at the Hernstein locality, and while the age of any fissure-fill



**TEXT-FIG. 6.** Representative conodont elements providing the basis for age determinations. A–C, *Epigondolella bidentata* Mosher (juv.), horizon 99/21A, *E. bidentata*–*M. posthernsteini* IZ. A–B, lateral and upper views (PIUW 5000); C, lateral view (PIUW 5001). D, *Misikella posthernsteini* Kozur and Mock, horizon 99/21A, lateral view (PIUW 5002), *E. bidentata*–*M. posthernsteini* IZ. E–H, *E. bidentata* Mosher, lateral and upper views, horizon 99/23, *E. bidentata*–*M. posthernsteini* IZ (PIUW 5004, 5005). I, *Misikella hernsteini* (Mostler), horizon 99/21A, lateral view (PIUW 5003), *M. hernsteini* IZ. J–K, *E. bidentata* Mosher, horizon 99/29A, lateral and upper views (PIUW 5006), *E. bidentata* Z. L–N, *E. bidentata* Mosher (juv.), lateral views, horizon 99/29A (PIUW 5007, 5008, 5009), *E. bidentata* Z. Scale bar represents 150  $\mu\text{m}$ ; IZ, interval zone.

fauna may be considered suspect and, unless significant reworking has taken place, is younger than the fauna within enclosing sediments, as indicated in Text-fig. 3, most of the sampled horizons for conodonts, and to a lesser extent bivalves, are not from such fillings.

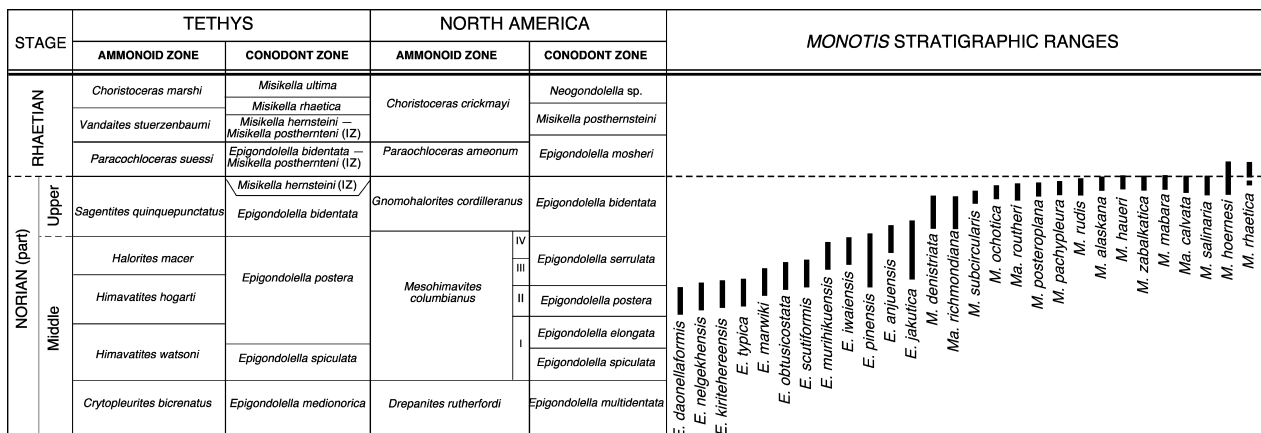
### THE END-NORIAN CRISIS AND SURVIVING MONOTIS

It has long been recognized that an extraordinary event took place at around the Norian/Rhaetian boundary that primarily affected the pelagic fauna dominated by monotid bivalves and ammonoids. Although shallow-water benthic bivalves show an increase in generic richness from the Norian into the Rhaetian (McRoberts 2001) and reef faunas flourished well into at least the early Rhaetian (e.g. Zankl 1969; Stanley 2003), the preliminary data on pelagic bivalves and ammonoids show very high extinction rates. Until this report, it has been assumed that extinction of *Monotis* species at the end of the Norian was complete with c. 15 species becoming extinct at or close to the end of the Norian (Text-fig. 7). Apart from an anomalous and, according to Tozer (1980), probably erroneous, report of *Monotis* from the Sinemurian of Siberia (Kiparisova *et al.* 1966; Efimova *et al.* 1968) resembling middle Norian *Eomonotis*, previously no *Monotis* species have been reported from rocks within or above the upper Sevatian. Moreover, ammonoids show a complete loss of all 14 genera of trachyostracean ammonoids belonging to the superfamilies Trachycerataceae, Clydonitaceae and Tropitaceae at the top of the *Reticulatus* ammonoid Zone (Krystyn 2003).

While the extinction of *Monotis* at the end of the Norian was limited to about 15 species (many more species are known from the middle Norian and early

late Norian), in terms of biomass, itself a function of individual abundance, the crisis was certainly quite profound. Late Norian *Monotis* occurrences, especially in high palaeolatitudes, achieved incredible densities in thick monospecific shell beds composed of packed and overlapping individuals, and represent a significant contributor to marine biomass. Particularly around the circum-Pacific margin, these shell accumulations reach exceptional thicknesses: up to 5 m in British Columbia, Alaska, Japan and New Zealand (Westermann 1962; Ando 1987; Silberling *et al.* 1997). *Monotis* shell beds in the Hallstatt facies are generally thinner (10–30 cm thick), but represent a significant component of total rock volume.

An additional aspect of the end-Norian crisis is that among pelagic bivalves, and to some extent ammonoids and conodonts, surviving clades comprise species of significantly smaller maximum size than their Norian predecessors. As noted by Urlichs (1992) in his classic study of diminutive faunas from the Middle Triassic Muschelkalk of Germany, care must be taken to ensure that smaller looking faunas are not just composed of juveniles or a result of biostratigraphic sorting processes. Size-frequency histograms of dimensional data of Rhaetian *Monotis* largely show non-normal bimodal distributions (Text-fig. 4) with significant percentages of both juvenile and adult individuals and approximately equal proportions of left and right valves, and are not significantly reworked. Thus, Rhaetian *Monotis* can, in a limited way (*sensu* Gould and MacFadden 2004), be considered dwarfed as their maximum size is less than that normally achieved in late Norian *Monotis* species. For example, maximum lengths for *Monotis rhaetica* and *M. hoernesii* are c. 26 and c. 17 mm respectively, whereas late Norian *M. salinaria* can attain lengths of more than 50 mm, and many other late Norian species, such as *M. subcircularis*, can reach exceptionally



**TEXT-FIG. 7.** Global compilation of stratigraphic ranges of monotid species belonging to *Eomonotis*, *Monotis* (*s.l.*), and *Maoromonotis*. North American ammonoid and conodont zones adapted from Orchard and Tozer (1997) and Tethyan zonation from Gallet *et al.* (2007). IZ, interval zone.

large dimensions of up to 90 mm in length. As a phylogeny for late Triassic *Monotis* species has not yet been satisfactorily accomplished and precise temporally-constrained size data within lineages is lacking, it is premature to determine if the observed reduction represents interspecific sorting or a phyletic trend within one or more lineages. The trajectory towards smaller sizes in *Monotis* may have initiated just prior to the Norian/Rhaetian boundary, as has been recognized by Ward *et al.* (2004) who documented a trend towards smaller sizes in the uppermost Norian *Monotis* fauna from the Kennecott Point section of the Queen Charlotte Islands, British Columbia. Dwarfism is commonly associated with stressed environments and the recovery phases following mass extinction events. For example, the Early Triassic recovery faunas are well known for their diminutive size (Twitchett 2001; Fraiser and Bottjer 2004; Hautmann and Nützel 2005). Twitchett (2001) suggested that, at least during or shortly after a mass extinction, reduced primary productivity could lead to dwarfism. Available carbon isotope evidence (see below), however, suggests that reduced primary productivity was not a factor at the Norian/Rhaetian boundary.

The Norian/Rhaetian event may be associated with a perturbation in the global carbon cycle. Ward *et al.* (2001, 2004) identified a short-lived positive  $\delta^{13}\text{C}_{\text{org}}$  isotope excursion coinciding with the extinction of *Monotis* at Kennecott Point. A positive  $\delta^{13}\text{C}$  excursion was also recognized at approximately the same horizon at Williston Lake, British Columbia, where it corresponds to a sequence boundary and the highest occurrence of *Monotis subcircularis* Gabb, 1864 (Stephton *et al.* 2002). A complex negative  $\delta^{13}\text{C}_{\text{carb}}$  isotope anomaly from a reported Norian/Rhaetian boundary section in the Lagronegro Basin of southern Italy (Tanner *et al.* 2006) occurs well within the Rhaetian (i.e. above the FOD of *Misikella posternsteini*) and, based on covariance of C and O isotopes, may be a result of diagenesis and rock alteration. Conversely, recent analyses in Austria and Oman show relatively stable  $\delta^{13}\text{C}_{\text{org}}$  across the Norian/Rhaetian boundary (Richoz *et al.* 2007). While there are many potential sources for positive  $\delta^{13}\text{C}$  excursions (e.g. increased productivity or enhanced burial of organic matter), a short-lived increase in the burial flux of organic carbon ( $\text{C}_{\text{org}}$ ) relative to carbonate carbon ( $\text{C}_{\text{carb}}$ ) appears to be consistent with the disappearance of shelly *Monotis* faunas and the onset of organic-rich dysoxic shale in many pelagic settings. While we do not propose here a mechanism for the end-Norian biotic crisis, we believe that the extinction of most *Monotis* species and several clades of ammonoids, a post-extinction dwarfed *Monotis* fauna, and a potential positive carbon isotope excursion may be integrally linked.

## SYSTEMATIC PALAEOLOGY

Unless otherwise specified, all illustrated specimens are housed in the Naturhistorisches Museum, Vienna and bear the NHMW prefix. Other repositories mentioned in the text include those in the micropalaeontology collections of the Paläontologisches Institut, Universität Wien (PIUW prefix), Museum für Naturkunde der Humboldt Universität, Berlin (MB prefix) and Museo Geologico Gemellaro, Dipartimento di Geologia e Geodesia, Università di Palermo (GMGUP prefix). Morphologic terminology, linear dimensions and angular measurements generally follow those of Grant-Mackie (1978*b*) and Grant-Mackie and Silberling (1990), and are abbreviated and defined as follows: L, maximum length of valve measured parallel to hinge; H, maximum height perpendicular to L; W, maximum width or valve inflation; IFR, inflation ratio calculated as W/H; BP is the beak position calculated as the ratio of length posterior to the beak to that anterior of the beak; O, angular measure (in degrees) of obliquity as defined by the angle subtended the vertical axis, taken through the beak normal to the hinge line and the position on the posteroventral margin at the greatest distance from the beak;  $\alpha$ , truncation angle of the posterior auricle; PD<sub>30</sub>, plicae density as measured by the frequency of plicae through an arc of 30 degrees in the central part of disc at 10 mm from beak. Note, this measure of plicae density differs from that used by previous workers.

The suprageneric classification adopted here accepts *Monotis* species to be pectinoids following Cox (1969), Waller (1978; in Waller and Stanley 2005) and Carter (1990) and not pteroids as some authors have contended (e.g. Grant-Mackie 1978*a*, *c*; Grant-Mackie and Silberling 1990; Silberling *et al.* 1997). It has been common practice to subdivide *Monotis* into species groups and more formal subgenera (e.g. Ichikawa 1958; Grant-Mackie 1978*a*; Grant-Mackie and Silberling 1990). While such groupings may have value in discriminating different morphotypes within a species-rich genus, they are not constructed within a phylogenetic context and may, therefore, represent phenetically construed polyphyletic groupings.

Order PECTINOIDA Adams and Adams, 1858

Superfamily MONOTOIDEA Fischer, 1887

Family MONOTIDAE Fischer, 1887

Genus MONOTIS Bronn, 1830

*Type species. Pectinites salinarius* Schlotheim, 1820, by subsequent designation (Herrmannsen 1852). Type locality, Siriuskogel, Austria, from the upper Norian Hallstatt Limestone.

*Monotis salinaria* (Schlotheim, 1820)

## Plate 1, figures 1–9

- 1820 *Pectinites salinarius* Schlotheim, pp. 230–231 [not illustrated].  
 1830 *Monotis salinaria* (Schlotheim) Bronn, p. 279, pl. 4, fig. 12.  
 1912 *Monotis salinaria* Bronn; Kittl, p. 169, pl. 10, figs 1–6.  
 1958 *Monotis salinaria salinaria* (Schlotheim); Ichikawa, p. 176, pl. 23, figs 2–5, 11.  
 p. 1985 *Monotis salinaria* (Schlotheim); Silberling, p. 64, fig. 1a–b, [non fig. 1c–d (= *Monotis alaskana* Smith)].  
 1997 *Monotis (Monotis) salinaria* (Schlotheim); Silberling *et al.*, pl. 4, figs 11–13.

*Lectotype.* Schlotheim's original specimen, a left valve, selected and illustrated by Ichikawa (1958, pl. 23, fig. 3), upper Norian Hallstatt Limestone, Siriuskogel, near Ischl, Austria, MB Q. K. p. 1087 11 2).

*Material studied.* The collection from the Hernstein locality consists of more than 100 valves; the description below is largely based on 19 specimens including ten left and nine right valves.

*Description.* Valves of moderate size (max. L, 49 mm; max. H, 32 mm) and moderate convexity (max. W, 6.5 mm in a right valve), nearly equivalved but with left valve having slightly greater inflation values (mean IFR of LV, 0.25; mean IFR of RV, 0.20), suboval in outline, and moderately oblique (mean O, 46°). Beaks small, slightly raised above hinge, prosogyrous, and positioned far anterior (BP, 2.3). Dorsal hinge margin straight, about half length of the valve. Posterior auricles smooth, relatively small, well separated from main disc by furrow, and with posterior margin intersecting hinge margin at an obtuse angle ( $\alpha$ , 114–126°). Anterior byssal aurical not observed. Radial plicae pronounced and rounded in cross-section, with a clear definition between rib and interplacae space, and bundled into two or three orders. Primary plicae between 22 and 30 in number (mean, 26) and of moderate density (PD<sub>30</sub>, 5.4). Secondary plicae inserted between primaries at a distance of 15–23 mm from beak. Tertiary plicae, if present, relatively few in number and first appear

near posteroventral margin only in large specimens. Strength of plicae nearly uniform except towards posterodorsal third of disc where they become somewhat subdued. Plicae generally curve away from medial line (normal to hinge) of valve and become increasingly wavy towards posterior margin of the valve as radial plicae intersect commarginal concentric folds. Curvature of plicae is somewhat more pronounced towards anterior valve margin. Interplacae spaces are usually equal to or 1.5 times width of primary plicae across most of disc, but become narrower in anterior third. Concentric folds prominent in posterior third of valve, weak in early growth stages on remaining part of disc and absent in later growth stages across anterior and ventral sectors. In well-preserved specimens, surface of disc covered with very fine, narrowly-spaced commarginal growth striae. See Table 1 for measurements.

**TABLE 1.** Summary measurements including sample size (*n*), maximum and minimum values, mean ( $\bar{x}$ ), and standard deviation ( $\sigma$ ) for each parameter.

	RD <sub>30</sub>	L (mm)	H (mm)	W (mm)	BP	$\alpha$ (°)	O (°)	pP
<i>M. rhaetica</i>								
<i>n</i>	36	17	17	17	16	11	14	16
min	3	7.4	5.2	1.2	1.2	140.0	42	12
max	7	26.1	16.6	3.4	2.5	153.3	56	27
$\bar{x}$	5.4	15.6	11.6	2.4	1.7	146.5	49.0	21.2
$\sigma$	1.07	5.36	3.74	0.48	0.41	4.50	3.40	4.58
<i>M. hoernesii</i>								
<i>n</i>	28	20	20	20	19	15	18	20
min	10	9.2	7	1.3	1.3	132	27	36
max	16	16.7	13.8	2	2.5	150	44	58
$\bar{x}$	12.8	12.6	9.9	1.8	1.7	139.8	35.4	49.1
$\sigma$	1.60	2.16	1.94	0.22	0.32	5.43	4.09	5.58
<i>M. salinaria</i>								
<i>n</i>	16	11	11	11	11	3	7	10
min	4	10.7	6.5	1.7	1.6	110	39	22
max	8	48.8	32.4	6.5	3.4	126	57	37
$\bar{x}$	5.4	28.6	19.5	3.9	2.4	118.0	46.1	28.9
$\sigma$	1.09	13.83	9.35	1.37	0.64	8.00	6.57	6.30

## EXPLANATION OF PLATE 1

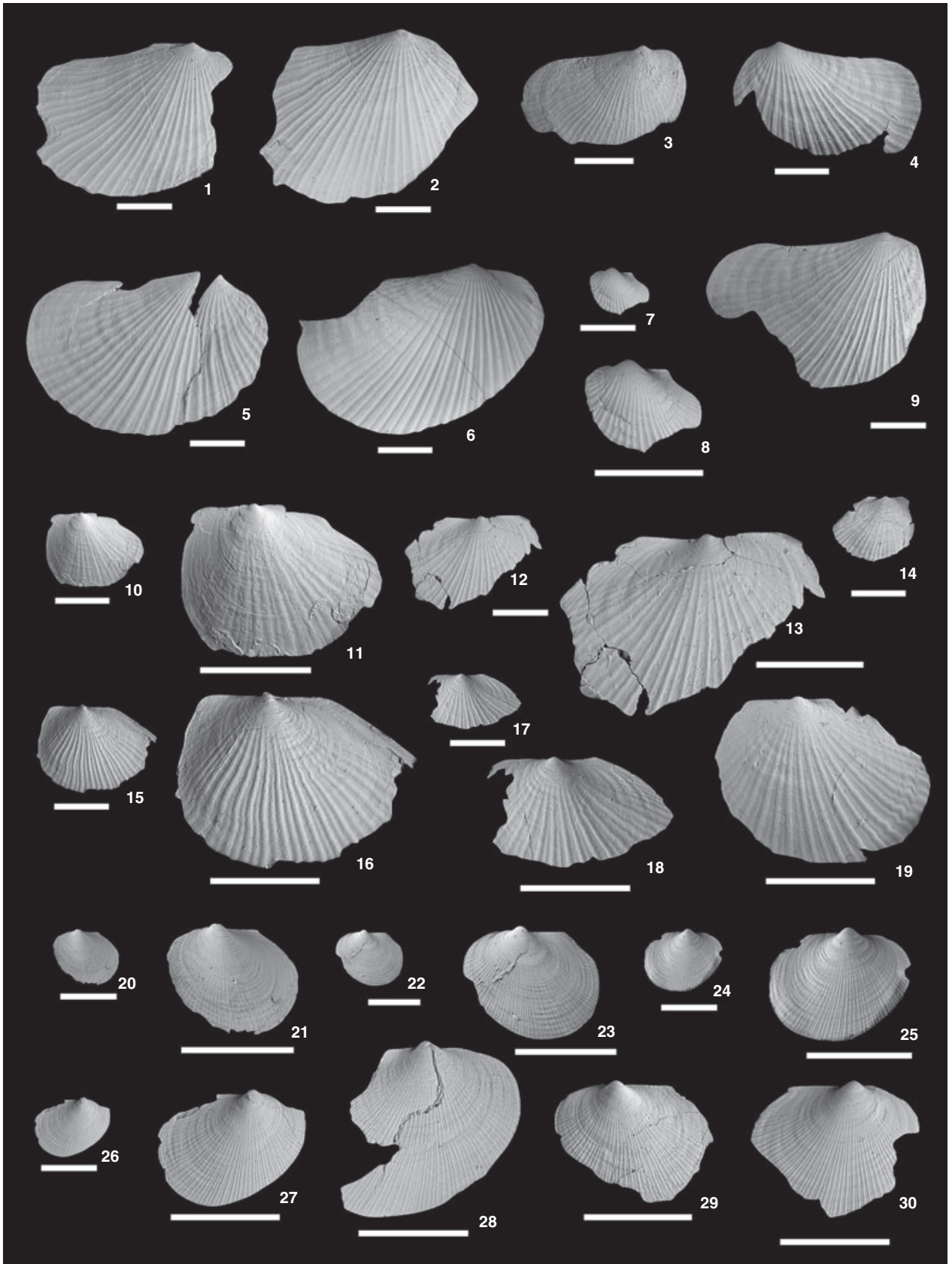
Figs 1–9. *Monotis salinaria* (Schlotheim, 1820), upper Norian *Epigondolella bidentata* conodont Zone. 1, 0001, right valve. 2, 0002, right valve. 3, 0003, right valve. 4, 0004, left valve. 5, 0005, right valve. 6, /0006, right valve. 7–8, 0007, left valve. 9, 0008, right valve.

Figs 10–19. *Monotis rhaetica* sp. nov., lower Rhaetian *Epigondolella bidentata*–*Misikella posthernsteini* conodont Interval Zone. 10–11, holotype, 0009, left valve. 12–13, paratype, 0010, right valve. 14, paratype, 0011. 15–16, paratype, 0012, left valve. 17–18, paratype, 0013, left valve. 19, paratype, 0014.

Figs 20–30. *Monotis hoernesii* Kittl, 1912, lower Rhaetian *Epigondolella bidentata*–*Misikella posthernsteini* conodont Interval Zone. 20–21, 0015, left valve. 22–23, 0016, left valve. 24–25, 0017, right valve. 26–27, 0018, right valve. 28, 0019, right valve. 29, 0020, left valve. 30, 0021, right valve.

All specimen numbers prefixed by NHMW 2007z0111/. Scale bars represent 10 mm.





**Occurrence.** Reported here from the upper Norian *Epigondolella bidentata* conodont Zone (Hernstein samples 99/29A, 99/28, 99/27). Quite common in upper Norian Hallstatt Limestone of the Northern Calcareous Alps (see Ichikawa 1958 for a complete listing).

**Remarks.** Based on size, oblique outline, plicae density, and pattern of concentric folds and posterior truncation angle, the specimens reported here fit comfortably within Schlotheim's (1820) original description of *Pectinites salinaria*, later emended by Kittl (1912) and subsequently illustrated by Ichikawa (1958). Previous descriptions are in full agreement with those made on the basis of a cast of the lectotype made available to us. Additional topotype material from Siriuskogel, Austria, illustrated by Kittl (1912, pl. 10, figs 1–6), are also similar in all essential characteristics to both the holotype and material described here. It should be noted, however, that the fragile and rarely preserved anterior auricle which is known from this species (e.g. Ichikawa 1958) was not observed in our Hernstein specimens. The *Monotis* described by Mostler *et al.* (1967) from their Hernstein level 'M1' probably comes from the same horizon as our *Monotis salinaria* and agrees in dimensions (L, 60 mm; W, 9 mm) yet has a slightly lower primary rib count (18) than those described herein.

As many have remarked (e.g. Ichikawa 1958; Westermann 1966; Grant-Mackie and Silberling 1990) *Monotis salinaria* is similar to *M. haueri* Kittl, 1912. In addition to a narrower posterior truncation angle, *M. salinaria* has a slightly greater number, and consequently more densely packed, primary plicae. As has been noted by some workers (e.g. Grant-Mackie and Silberling 1990; Silberling *et al.* 1997) *M. salinaria* is quite similar to the North American *M. alaskana* Smith, 1927. However, the Alaskan species exhibit a greater number of primary ribs (c. 30) compared to *M. salinaria* (c. 22).

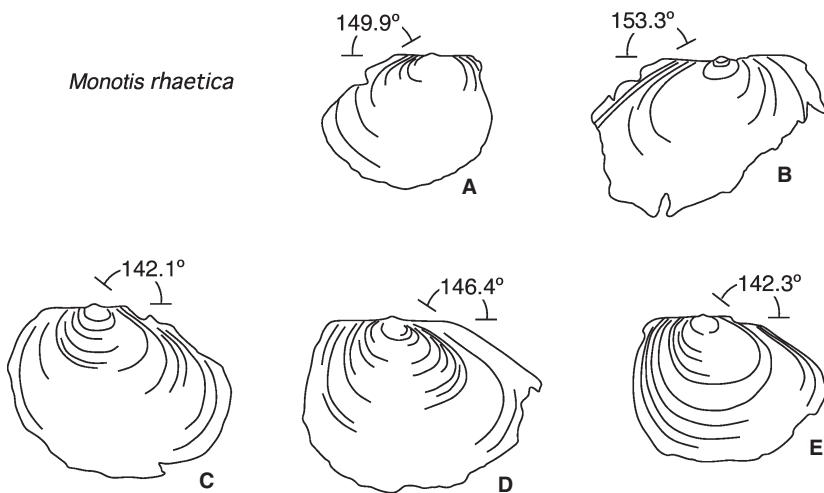
*Monotis rhaetica* sp. nov.

Plate 1, figures 10–19; Text-figure 8A–E

**Derivation of name.** After the Rhaetian Stage of the Upper Triassic named by Gümbel for the Rätikon.

**Types.** Holotype NHMW 2007z0111/0009 (Pl. 1, figs 10–11), a left valve; paratypes NHMW 2007z0111/0010–2007z0111/0014 (Pl. 1, figs 12–19).

**Type locality and horizon.** Hernstein section (Austria), lower Rhaetian (Sevatian 2), *Epigondolella bidentata*–*Misikella*



**TEXT-FIG. 8.** Graphical representation of valve outlines, commarginal ornament, and posterior truncation angles for *Monotis rhaetica* sp. nov. (A–E) and closely related *M. rudis* Gemmellaro, 1882 (F–G) and *M. digona* Kittl, 1912 (H–I). A, NHMW 2007z0111/0011; B, NHMW 2007z0111/0010; C, NHMW 2007z0111/0014; D, NHMW 2007z0111/0012; E, NHMW 2007z0111/0009; F, MGUP 002.316; G, MGUP 002.316; H, NHMW 1897 I 41; I, NHMW 1897 I 42.

*posthernsteini* conodont Interval Zone, Hallstatt Limestone, holotype horizon 99/25L, paratype horizons 99/25L and 99/23L.

*Material studied.* Including the types, the collection from the Hernstein locality consists of more than 100 individual valves of which 22 left and 14 right valves contributed greatly to the description.

*Diagnosis.* *Monotis* of moderate size; obliquely ovate; beaks small and prosogyrate to opisthogyrate, well anterior, situated at about one-third valve length; posterior auricle poorly differentiated from disc, with broadly obtuse posterior truncation angle ( $\alpha$ ) greater than 140 degrees, lacking sinus; anterior auricle not observed; radial ornament with *c.* 21 primary plicae that become wavy in posterior sector.

*Description.* Valves small to moderate size (max. L, 26 mm; max. H, 17 mm), weakly inflated, and nearly equivalved (max. W, 3.5 mm; mean IFR of LV, 0.19; mean IFR of RV, 0.26). Valves obliquely oval (mean O, 48°), but some display a nearly polygonal outline with an exaggerated postumbonal length. Beaks small and broad, weakly prosogyrate to essentially opisthogyrate and situated well anterior (mean BP, 1.7). Hinge straight and equal to slightly more than one-half of total valve length. Posterior auricles poorly developed and not differentiated from main disc by furrow, generally smooth, intersect hinge margin at a broadly obtuse angle (mean  $\alpha$ , 145°) and without visible sinus. Radial plicae rounded in cross-section, of moderate relief, occurring in two, or more rarely, three orders. Primary plicae first appear 2–4 mm from beak, 21–27 in number (mean, 21.2) and of moderate density (mean PD<sub>30</sub>, 5.4). Secondary plicae have lower relief than primaries and are variably inserted 9–14 mm from beak. Tertiary plicae, where present, typically insert only next to longest of secondaries. Plicae in anterior third of disk are slightly curved away from medial line, those in the remainder are relatively straight, except towards posterior margin where they may become wavy and occasionally exhibit deflections as they intersect concentric wrinkles. Interplicae spaces are on average equal to *c.* 1.5 times width of primary plicae. Most valves with a concentric ornament consisting of commarginal wrinkles of moderate amplitude and regular spacing; commarginal growth striae visible only in a few well-preserved specimens are faint and typically irregularly spaced. See Table 1 for measurements.

*Occurrence.* Reported here from the lower Rhaetian (Sevastian 2) *Epigondolella bidentata*–*Misikella posthernsteini* conodont Interval Zone (Hernstein samples 99/23L, 99/25L).

*Remarks.* Mostler *et al.* (1967) referred smaller, more densely-ribbed specimens from their younger horizon 'M2' at the Hernstein locality to *Monotis salinaria haueri*. Based primarily upon stratigraphic position and lacking morphologic details on these specimens, we tentatively place them within *Monotis rhaetica*.

*Monotis rhaetica* differs from the related species *M. salinaria* (Schlotheim, 1820) and *M. haueri* Kittl, 1912 in several important characteristics. As with other coarsely ribbed Norian species, such as *M. rudis* Gemmellaro, 1882 and *M. digona* Kittl, 1912 (see below), *M. rhaetica* has a narrow and poorly differentiated posterior auricle with a very broad posterior truncation angle greater than 140 degrees as compared to average values of 120 degrees for *M. salinaria* and 130–140 degrees for *M. haueri*. In addition, *M. rhaetica* exhibits more subdued plicae on the anterior and especially posterior sectors of the disc.

Our new species also resembles, and is probably closely related to *Monotis rudis* Gemellaro, 1882 and its likely synonym *M. digona* Kittl, 1912. Gemmellaro (1882, p. 470) named *M. rudis* for two specimens (one left and one right valve) co-occurring with finer-ribbed *M. stoppani* Gemmellaro, 1882 and *M. limaeformis* Gemmellaro, 1882, from pelagic chert-bearing limestones within the Sicano Basin at two localities: Monte Gallo and Monte Irione near Prizzi, Sicily. Although Gemmellaro regarded the age of these specimens as Carnian, presumably following the inverted zonal scheme of Mojsisovics (1869), we believe them to be Norian as they occur with and above typical Norian ammonoids and halobiid bivalves. Extensive and well-dated Norian/Rhaetian cherty pelagic-type facies are exposed nearby (e.g. Cafiero and De Capoa Bonardi 1982; Gullo, 1996). Morphologically, the rib densities of *Monotis rudis* are comparable to *M. rhaetica* from Hernstein, although the rib-strength across the disc is markedly different, with *M. rudis* exhibiting very weak, or even no radial plicae on the posterior and anterior sectors. Additionally, *M. rudis* shows undulations and waviness in plicae across most of the disc whereas *M. rhaetica* exhibits wavy plicae only on the posterior portion. Perhaps most significant are the differences in the posterior auricle truncation angle that are less than 140 degrees (the average of the two specimens). Kittl (1912, pl. 10, figs 12–15) compared similar specimens from the Norian of Austria (Falmbergalm near Gosau and Kriemooskogel near Goisern) and Montenegro (Zabijo) to *M. rudis* (although he incorrectly attributed the species to Stoppani). He (Kittl 1912, p. 173, pl. 10, figs 16–18) based *M. digona* on three poorly preserved right valves from grey Hallstatt Limestone at Siriuskogel, near Ischl, Austria. These specimens appear to be conspecific with, and therefore a junior synonym of, *M. rudis* discussed above. The two species have equivalent obliquity and posterior truncation angles but in *M. digona* the radial plicae appear to be slightly more uniform in strength across the entire disc. Comparisons in the outlines and commarginal growth ornament in these closely related species are shown in Text-figure 8.

*Monotis hoernesii* Kittl, 1912

Plate 1, figures 20–30

- 1855 *Avicula (Monotis) lineata* Hörnes, p. 51, pl. 2, fig. 15.  
 1912 *Monotis hoernesii* Kittl, p. 173, pl. 10, figs 19–21 [holotype, fig. 21].  
 1912 *Monotis dalmatina* Kittl, p. 173, pl. 10, fig. 22.  
 non 1962 *Monotis* cf. *M. hoernesii* Kittl.; Westermann, pp. 764–767, pl. 113, fig. 6a–b.

*Holotype.* Original specimen of Hörnes (1855, pl. 2, fig. 15) re-illustrated by Kittl (1912, pl. 10, fig. 21), presumably upper Norian, Hallstatt Limestone, Siriuskogel, near Ischl, Austria, NHMW 162/1956.

*Material studied.* The collection from the Hernstein locality consists of more than 80 valves of which 28 (five left and 23 right valves) contributed to the description.

*Description.* Valves small (max. L, 17 mm; max. H, 14 mm), nearly equivalved and weakly inflated (for both RV and LV, max. W, 2.0 mm; mean IFR, 1.8). Shell outline obliquely oval (mean O, 35.7°) with beaks positioned approximately in anterior third of valves (mean BP, 1.7). Beaks small, broad, protrude slightly above straight hinge line, poorly separated from byssal (anterior) and posterior hinge areas. Posterior auricles poorly developed, pass gradually into main part of disc, with posterior margin intersecting hinge at a shallow obtuse angle (mean  $\alpha$ , 140°), and with slight concavity with posterior margin of valve to form a very shallow sinus. Radial plicae low, vary between subangular to rounded in cross-section and bundled into two or, more rarely, three orders. Primary plicae numerous, between 43 and 55 (mean, 49), densely packed (mean RD<sub>30</sub>, 12.6), first appear c. 2–3 mm from beak. Secondary plicae considerably weaker and less numerous than primaries and inserted between some of them c. 7–10 mm from beak. There is some minimal dorsalward curvature to plicae in posterior region of valves, as well as some waving of plicae in this region; otherwise plicae are generally straight. Interplicae spaces are slightly larger than width of primary plicae. Ordinarily the valves display weak, regularly spaced concentric wrinkles. See Table 1 for measurements.

*Occurrence.* Reported here from the lower Rhaetian *Epigondolella bidentata*–*Misikella posthernsteini* conodont Interval Zone (Hernstein samples 99/23L, 99/25L). Elsewhere, Kittl (1912) reported this species from upper Norian Hallstatt localities in Austria including Falmbergalm (near Gosau) and Siriuskogel (near Ischl) among others, many of them becoming Rhaetian in the new stratigraphic terminology. Assuming a correct synonymy with *Monotis dalmatina* Kittl, 1912, this species also occurs in the Norian? of Crna Gora, Montenegro.

*Remarks.* Kittl (1912, p. 173) erected this species to accommodate small ovate, finely ribbed forms that were

originally given the name *Avicula (Monotis) lineata* Hörnes, 1855, but whose specific name was already in use for a completely different form: *Monotis lineata* Münster, 1833, which itself had been determined by Mojsisovics (1874) to belong to *Halobia*. As originally pointed out by Kittl (1912), and later reiterated by Westermann (1962), this species is similar to the pteriomorphian *Halobia*; however, this genus has a much straighter and longer hinge, and large, clearly differentiated auricles extending to the anterior dorsal margin. *Monotis hoernesii* resembles in outline, smooth posterior ear, and nature of the ribs, *M. dalmatina* Kittl, 1912, which was described from Crna Gora, Montenegro. Westermann (1962) and later Grant-Mackie (1978a) commented on the similarity, but noted that direct comparison is difficult because *M. hoernesii* was based on only left valves and *M. dalmatina* on a single right valve. In his original description of *M. dalmatina* Kittl (1912) also remarked on their similarity, but suggested that the beak of *M. hoernesii* has a slightly more compressed anterior and anteriorly positioned beak. Topotype material examined by Westermann (1962) and the collections described herein suggest that both left and right valves are of essentially equal inflation, permitting a more confident basis for the synonymy. Westermann (1962) compared a single internal mould of a left valve from the Norian Pine Pass section in north-east British Columbia to *M. hoernesii*. This single Canadian specimen, however, is much less oblique than Kittl's original specimens and those described herein. Moreover, ribbing morphology in monotids is quite differently expressed on the valve interiors when compared to valve exteriors and should not, in itself, provide a sufficient basis for species identification. Based on the co-occurrence of *M. hoernesii* with the conodont *Misikella posthernsteini*, we extend the range of this species into the Rhaetian, making it the only known *Monotis* species to survive the end-Norian biotic crisis.

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