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7

8 best regards

9 Mathias Harzhauser

10 |

1 **Age structure, carbonate production and shell loss rate in**
2 **an Early Miocene reef of the giant oyster *Crassostrea***
3 ***gryphoides***

4
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12

13 **Abstract**

14 We present the first analysis of population structure and cohort distribution in a fossil oyster
15 | **shell bedreef** based on more than 1121 shells of the giant oyster *Crassostrea gryphoides*
16 (Schlotheim, 1813). Data derive from Terrestrial Laser Scanning of a Lower Miocene shell
17 bed covering 459 m². Within two transects, individual shells were manually outlined on a
18 digital surface model and cross-checked based on high-resolution orthophotos, resulting in
19 accurate information on center line length and area of exposed shell surface. A growth model
20 was calculated, revealing this species as the fastest growing and largest *Crassostrea* known so
21 far. Non-normal distribution of size, area and age data hints at the presence of at least four
22 distinct recruitment cohorts. The rapid decline of frequency amplitudes with age is interpreted
23 to be a function of mortality and shell loss. The calculated shell half-lives range around few
24 years, indicating that oyster reefs were geologically short-lived structures, which could have
25 been fully degraded on a decadal scale.

26 *Crassostrea gryphoides* reefs were widespread and common along the Miocene circum-
27 Tethyan coasts. Given its enormous growth performance of ~150 g carbonate per year this
28 species has been an important carbonate producer in estuarine settings. Yet, the rapid shell
29 loss impeded the formation of stable structures comparable to coral reefs.

1

2 **1 Introduction**

3 The genus *Crassostrea* Sacco, 1897 comprises numerous commercially exploited species. The
4 modes of growth and population structures of extant *Crassostrea* species are of paramount
5 importance for oyster fishery (FAO, 2015). Consequently, a wealth of data exists on the
6 ontogeny, biology and ecological requirements. These data, in turn are a valuable base for the
7 interpretation of the autecology of fossil congeners. Extant *Crassostrea* are sessile bivalves
8 adapted to estuarine and intertidal environments where they have to cope with high
9 environmental stress. Whilst physicochemical stress is managed by genetic response (Zhang
10 et al., 2012), the formation of thick shells is a strategy against predation (Lombardi et al.,
11 2013; Robinson et al., 2014). The largest and fastest growing *Crassostrea* species flourished
12 during the Miocene and Early Pliocene and became replaced by comparatively smaller and
13 thinner species thereafter (Kirby and Jackson, 2004). Among these, *Crassostrea gryphoides*
14 (Schlotheim, 1813) is the largest, attaining shell lengths of up to 80 cm and individual ages of
15 more than 40 years (Harzhauser et al., 2010). The Pleistocene-Holocene extirpation of large
16 and thick-shelled *Crassostrea* species was explained by a shift from shallow-marine towards
17 estuarine-intertidal habitats to escape from predation (Kirby, 2000, 2001). At least for *C.*
18 *gryphoides* this model does not fit because the oyster lived as secondary soft-bottom dweller
19 in the intertidal zone of estuaries along the circum-Tethyan coasts (Laurain, 1980; Schultz,
20 2001; Mandic et al., 2004). This species evolved during the Late Oligocene in the European
21 Paratethys Sea and became ubiquitous in the Paratethys Sea, the proto-Mediterranean Sea and
22 the eastern Atlantic throughout the Early to Late Miocene. It might even have entered the
23 Indian Ocean during the Miocene (Newton and Smith, 1912) and reached the North Sea
24 during the Middle Miocene (Schultz, 2001). Pliocene records from the eastern Atlantic and
25 North Africa, however, may need verification (see Schultz, 2001 for a detailed list of
26 occurrences). This species became extinct around the Miocene/Pliocene boundary or with the
27 onset of the Pliocene cooling [3 Ma ago](#) at the latest.

28 Studies on growth in fossil *Crassostrea* species [\(and other oysters\)](#) and the resulting carbonate
29 production were published by Chinzei [\(1982, 1986, 1995\)](#), [Chinzei and Seilacher \(1993\)](#),
30 Kirby (2001) and Kirby and Jackson (2004). These studies are based on collection material
31 comparing species and specimens from different stratigraphic horizons. No study, however,
32 tried to capture the size and age structures of a fossil *Crassostrea* reef, presumably

1 representing a real population of coeval specimens. The lack of such studies is clearly linked
2 to the fact that fossil shell beds usually represent time-averaged assemblages (Kidwell, 1986,
3 1991), which only vaguely reflect original community structures. Although some in-situ
4 preserved fossil *Crassostrea* reefs are known (e.g. Hoşgör, 2008; Ragaini and Di Celma,
5 2009; Chinzei, 2013) no population data exist, which would allow a comparison with ~~surveys~~
6 ~~for~~ modern oyster reefs. Herein, we analyze an Early Miocene *Crassostrea* shell bedreef
7 covering an area of 459 m², which is permanently exposed at a geotainment park in Austria.
8 The shells are concentrated in a sheet-like, c. 20-cm-thick layer, which was formed by a major
9 storm or tsunami, amalgamating a single oyster reef in an event bed (Fig. 1A–C). Although,
10 the hydrodynamic process will have biased the original structure to some degree, ~~the patterns~~
11 ~~revealed in~~ our data suggest that no out-of-habitat transport occurred and the shell bed still
12 reflects the original composition and thus the population structure of an oyster reef from the
13 onset of the Miocene Climatic Optimum (Zachos et al., 2008; Goldner et al., 2014).
14 *Crassostrea* reefs flourished during the Miocene within the tropical reef belt (Mandic et al.,
15 2004) but were also successful in more northern latitudes (Wiedl et al., 2013; Harzhauser et
16 al., 2010). Therefore, the main purpose of this paper is to quantify the growth performance of
17 the Miocene giant oyster and to reveal its significance as part of the Miocene “carbonate
18 factory”. Moreover, we test if size frequency data deduced from fossil oyster shells allow a
19 comparison with community structures of extant *Crassostrea* reefs.

20

21 1.1 A taxonomic note

22 Although the type of *Crassostrea gryphoides* (Schlotheim, 1813) was described from the mid-
23 Miocene of Romania, the name is also used in biological literature for an extant backwater
24 species from India and Pakistan (Newton and Smith, 1912; Chatterji et al., 1985; Nagi et al.,
25 2011; Afsar et al., 2014; Trivedi et al., 2015). The taxonomic status of the extant species is
26 unclear; based on molecular data, Reece et al. (2008) considered *C. “gryphoides”* to be
27 closely related with *C. belcheri* (Sowerby, 1871), whilst molecular data of Trivedi et al.
28 (2015) suggest a close relation with *C. cuttakenses* (Newton and Smith, 1912), which was
29 originally described as subspecies of *C. gryphoides*. Whatever the taxonomic and systematic
30 status of the recent species may be, it is most probablyeertainly not conspecific with the
31 European fossil species. It differs in its more regular and elongate-ovoid outline (Durve and
32 Bal, 1960), the short and bean-shaped adductor muscle scar (Durve, 1974; Siddiqui and

1 Ahmed, 2002) and it is more unequivocal. Overall, the recent species is clearly smaller with
2 the largest specimen documented so far attaining 508 mm in length (Mahar and Awan, 2012)
3 but usually ranging around 50–120 mm (Chatterji et al., 1985; Nagi et al., 2011).
4 Nevertheless, the Miocene species is closely related to the extant Asian-Pacific Crassostreinae
5 species, which show a large genetic difference from Atlantic species (Littlewood, 1994; Ó
6 Foighil et al. 1995; Wang et al., 2004; Ren et al., 2010; Salvi et al., 2014). The Asian-Pacific
7 group (e.g.: *C. gigas*, *C. plicatula*, *C. ariakensis*) and Atlantic group (e.g.: *C. virginica*, *C.*
8 *rhizophorae*, *C. gasar*)Both groups differ considerably in mitochondrial genes, nuclear
9 genome and chromosome structures (Wang et al., 2004; Ren et al., 2010; Salvi et al., 2014).
10 The divergence between both groups seems to have happened already in Cretaceous times and
11 the diversification of the Asian Pacific group started during the Eocene (Ren et al., 2014).
12 Based on this genetic evidence and biogeographic separation, Salvi et al. (2014) introduced
13 the genus *Magallana* Salvi, Macali and Mariottini, 2014 for the Asian Pacific species group
14 with *Ostrea gigas* Thunberg, 1793 as type species. Salvi et al. (2014), however, did not
15 provide a formal “description or definition that states in words characters that are purported to
16 differentiate the taxon” (ICNZ Art. 13.1.1). The authors only refer to a description of the type
17 species. Therefore, *Magallana* is formally unavailable (see also Marshall, 2015) and we use
18 *Crassostrea* in its traditional sense.

19

20 **2 Geological setting and paleoenvironment**

21 The investigated oyster ~~shell bed~~reef was excavated at Stetten in Lower Austria (48° 22'
22 03.33 N, 16° 21' 33.22 E). It is part of the about 600-m-thick lower Miocene (upper
23 Burdigalian, = Karpatian regional stage) siliciclastic succession of the Korneuburg Basin,
24 which is a 20 km long and 7 km wide halfgraben within the Alpine-Carpathian thrust-belt
25 (Fig. 2) (Wessely, 1998). The basin fill ~~represents~~is dominated by an quick-alternation of
26 shoreface and tidal flat deposits, which were formed in an embayment of the Paratethys Sea
27 (Zuschin et al., 2014). More than 650 species-level taxa have been described from the area
28 (Sovis and Schmid, 1998, 2002) and the paleoenvironments are ~~fairly~~-well understood
29 (Harzhauser et al., 2002; Zuschin et al., 2014). The oyster reef flourished in an estuary fringed
30 by salt marshes, Taxodiaceae swamps and scattered *Avicennia* mangroves (Harzhauser et al.,
31 2002; Kern et al., 2010). The pollen record of the Stetten section documents a warm
32 subtropical climate with marked seasonality (Kern et al., 2010). A warm and wet summer

1 | season with c. 204–236 mm precipitation during the wettest month was ~~opposed~~alternating
2 | with by a rather dry winter season with precipitation of c. 9–24 mm during the driest month.
3 | The mean annual temperature ranged between 15.7–20.8 °C, with about 9.6–13.3 °C during
4 | the cold season and 24.7–27.9 °C during the warmest month. These data suggest similarities
5 | with the modern “Cwa” climate of Koeppen (1936). Today this climate covers parts of
6 | northern India extending into south-eastern Asia (south Nepal, Myanmar, northern Thailand)
7 | to East China and in central south Africa (east Angola, Zambia, north Zimbabwe, north
8 | Mozambique) (Peel et al., 2007; Kern et al., 2010). The distinct seasonality was also revealed
9 | in sclerochronologic analysis of one of the *Crassostrea* shells collected from the shell bed~~reef~~
10 | (Harzhauser et al., 2010). This shell exhibits a regular annual rhythm of at least 11 seasons
11 | with a temperature range of 9.8°C. Thus, the paleoclimatic and paleoenvironmental frame of
12 | the *C. gryphoides* shell bed~~reef~~ is comparable to the settings of modern *Crassostrea* reefs in
13 | the subtropical parts of the Asian Pacific.

14 | The fossil shell bed was excavated in a 3-months-campaign by the Natural History Museum
15 | Vienna in 2008. The oyster bed was covered by up to ten meters of silty sand and clay, which
16 | was successively removed. Due to the largely unconsolidated state of the surrounding silty
17 | sand, the excavation of the shell bed could be done manually with steel gravers and brushes;
18 | no water or any chemicals were added and all shells and fragments remained in their original
19 | position. The oyster shells themselves are well preserved and robust. Therefore, no artificial
20 | fragmentation occurred during the excavation.

21 | Originally, the shell bed was nearly flat at the time of deposition but has now an undulate
22 | surface due postsedimentary tectonic activity. This tectonic phase occurred during the Middle
23 | Miocene at least 1–2 million years after deposition and caused a tilting of the units of ca. 25°
24 | in western direction. During that tilting, a NW–SE trending fault system developed that
25 | caused the current relief. Locally, the displacement by the faults is in the range of few cm.

26 | Harzhauser et al. (in press) describe the complex taphonomy of the shell bed, which was
27 | formed by a tsunami or an exceptional storm and represents an event deposit *sensu* Einsele et
28 | al. (1991) and Kidwell (1991). ~~Despite the bias of post-event processes, when the exhumed~~
29 | ~~shells were exposed for few years on the seafloor below fair weather base, the rapid~~
30 | ~~subsequent burial preserved most of the original distribution patterns.~~ As discussed by
31 | Harzhauser et al. (2015), the assemblage is not monospecific but contains about 46 molluscan
32 | species of which *Crassostrea gryphoides* predominates in individual numbers (79.4%). The

1 species, such as the potamidid gastropod *Ptychopotamides papaveraceus* and the venerid
2 bivalve *Venerupis basteroti*, lived partly within the oyster reef or were admixed from adjacent
3 mudflats and shallow sublittoral habitats. As shown by Harzhauser et al. (2015), the fossil bed
4 is parautochthonous. Although the oyster shell bed is clearly not in-situ but reworked, the
5 original community structure still seems to be reflected, which is the basic working
6 hypothesis of this paper. Lack of sorting is indicated by the accumulation of very small and
7 very large shells. Similarly, the equal contribution by left and right valves points to the
8 preservation of the primary composition and contradicts the hypothesis of hydrodynamic
9 sorting and selective transport. Despite the bias of post-event processes, when the exhumed
10 shells were exposed for few years on the seafloor, the rapid subsequent burial preserved most
11 of the original distribution patterns.

14 **3 Materials and Methods**

15 **3.1 Data acquisition by Terrestrial Laser Scanning and orthophotos**

16 Terrestrial Laser Scanning has triggered a revolution in topographic terrain capturing,
17 especially in the generation of digital terrain models. Methods for generating such models
18 from laser scanning data are discussed by Kraus & Pfeifer (2001) and references therein.

19 Terrestrial Laser Scanning was applied to document the site as georeferenced 3D point cloud
20 (Otepka et al., 2013). A Faro Focus Laser scanner with a nominal point measurement
21 accuracy of 1 mm (std. dev.) in each coordinate and a sampling distance of approximately 1
22 mm was used. The individual point clouds of each scan were transformed first into one
23 common coordinate system and then georeferenced by control points to Universal Transverse
24 Mercator (UTM) coordinates (resolution below 2 mm). A robust filter (pre-processing) was
25 applied to reduce measurement noise while preserving surface structures like sharp edges
26 (Nothegger and Dorninger, 2009). The surface triangulation is based on the Poisson surface
27 reconstruction method (Kazhdan et al., 2006). The points of this triangulation are used for
28 interpolating a regular grid of heights above the plane of the shell bed using the scientific
29 software OPALS (Pfeifer et al., 2014). In addition, a Canon 60D with a Canon EF 20 mm f2.8
30 was used to capture more than 300 photos from a moving platform. The camera was placed
31 approximately orthogonal to the fossil bed. From the photos with a nominal ground resolution

1 of approximately 0.6 mm per pixel an orthophoto mosaic was generated with a resolution of
2 0.5 mm per pixel. To detect patterns in the distribution and composition of shells two
3 transects (N–S, W–E) were defined, each represented by 42 m² with a central overlap (Fig. 1).
4 All objects within this area were manually outlined on the digital surface model and cross
5 checked based on the high-resolution orthophotos (Fig. 3).

6 Manual outlines are vector datasets in form of manually digitized polygons representing the
7 boundaries of the identified specimens. They are created as thematic layer in an ArcGIS
8 environment. The polygon is defined by features such as points (i.e. vertices connected with
9 lines). Each polygon is a 2D visual representation of the manually digitized specimen from
10 the adequate orthophoto and its corresponding digital surface model. Further, manually
11 digitized data are organized into a table. This tabular structure has its elements, i.e. numerical
12 and descriptive attributes. For instance, numerical attributes are ID, length, orientation, etc.
13 Descriptive attributes are Taxon, side (left, right, unknown), state of preservation (complete,
14 low, moderate, high fragmented), etc.

15 The outline data are composed of about 1000 virtual points (nodes) on average per object and
16 are also stored in the georeferenced ArcGIS database. These allow an automatic calculation of
17 the surface area of each object by using *The Calculate Geometry tool*.

18 In total, 10,284 objects were defined. Of these, 8169 objects were identified as *Crassostrea*
19 *gryphoides* of which 1121 are complete shells (see supplementary table); 86% of the
20 specimens display various degrees of fragmentation and are excluded from the size-frequency
21 analysis. Four categories of fragmentation were used: complete shells are fully preserved or
22 display only minor damage, which might have occurred already during the life of the animal
23 (n = 1121). The category low fragmentation comprises shells in which not more than ¼ of the
24 assumed length is missing (n = 951). Moderate fragmentation is defined by representing at
25 least ½ of the original shell lengths (n = 1638). The category high fragmentation comprises
26 4458 specimens of strongly damaged shells representing less than ¼ of the complete shell.
27 Note that the attribute fragmentation does not contain any information on abrasion. The
28 fragments usually show sharp fractures and therefore, the main cause for fragmentation seems
29 to be predatory and hydrodynamic breakage. The ratio between left and right valves is
30 balanced (0.98). The distribution of the shells is not uniform, occasionally featuring areas of
31 higher shell densities, which seem to reflect former colony-like concentrations.

1 3.2 Shell length and area

2 *Crassostrea gryphoides* shows a very broad range of morphologies, ranging from elongate
3 shells to strongly curved and sigmoidal shapes (Fig. 43). Therefore, measuring shell length as
4 straight line, as done in other extant and fossil *Crassostrea* species, is inadequate. To
5 overcome this problem, we evaluated shell length based on the 2D center line, ~~which is an~~
6 ~~imaginary curved line spanning the maximum growth length of the shell.~~ Centre line length is
7 the term used in photogrammetry and aims for capturing the real shell length as far as
8 possible. Here it is an imaginary curved line spanning the maximum length of the shell. The
9 advantage of this method is that the center line will approximate the “real” lengths of the
10 curved and irregularly shaped shells much better than any manual attempt in the field.

11 For the automatic determination of the center line we used the shell margins, which comprise
12 about 1000 points on average. For easier calculation the outline point number was reduced to
13 100 and then filtered to points with close to even spacing. In the next step, a Delaunay
14 triangulation was calculated between the filtered outline points (Delaunay, 1934), constrained
15 by the edges between the outline points. To find the center line for each oyster outline, the
16 Voronoi diagram was formed (Voronoi, 1908) from the triangulation. The edges between
17 neighboring Voronoi vertices within the boundary are the medial axis transform (MAT) for
18 the oyster outline (Aichholzer et al., 1996). The longest 2D path in this tree was found using
19 Dijkstra’s algorithm between MAT end points (Kirk, 2015).

20 The center line lengths of 1121 complete *Crassostrea* shells, rounded to the nearest mm,
21 range from 48 mm to 602 mm with a mean of 237 mm ($\sigma=89$ mm) (Fig. 54A). The data
22 distribution displays a positive skewness of 0.52 and the Shapiro-Wilk test excludes normal
23 distribution for raw data and log10-transformed measurements. Area data range from 1708
24 mm² to 56755 mm² with a mean of 16983 mm² ($\sigma=8414$ mm²) (Fig. 54B). These data show
25 also a positive skewness (0.83) and normal distribution is rejected by the Shapiro-Wilk test.

26 Based on the manual outlines, the exposed shell area can be deduced directly. Area data are
27 slightly underestimated because shells are not always exposed parallel to the bedding plane
28 but may be somewhat oblique. Despite the fact, that area data are somewhat biased by oblique
29 shells, the correlation between center line lengths and areas is highly significant (raw data: $r =$
30 0.92 , $p < 0.001$; log10-transformed: $r = 0.93$, $p < 0.001$) (Fig. 65).

1 **3.3 Length frequency data**

2 Non-normal distribution of length-frequencies is a common pattern in extant *Crassostrea*
3 reefs (e.g. Coakley, 2004; Baqueiro Cárdenas and Aldana Aranda, 2007; Harding et al., 2008;
4 Nurul Amin et al. 2008; Ross and Luckenbach, 2009; Goslier et al., 2014). It results from
5 seasonal and/or annual recruitment with distinct cohorts (sensu Powell et al., 2006, 2015;
6 Southworth et al., 2010). For instance, the (sub)tropical *C. madrasensis* and *C. rhizophorae*
7 display a distinct annual recruitment peak (Nurul Amin et al., 2008; Mancera and Mendo,
8 1996). In multiannual communities this results in a right-skewed distribution due to the loss
9 of old specimens by natural mortality and shell loss. For extant *Crassostrea* reefs, the analysis
10 of the cohorts is routinely performed using Bhattacharya's model or the EM-Algorithm of
11 Dempster et al. (1977), which tries to detect normal distributions within the length-frequency
12 data. Consequently, in order to test for cohort mixing, lengths of *C. gryphoides* were
13 subjected to mixture analysis, a maximum-likelihood method for estimating the parameters of
14 two or more univariate normal distributions, based on a pooled univariate sample (Hammer,
15 2015). Statistical analyses were performed in PAST versions 2.17c and 3.06 (Hammer et al.
16 2001). Akaike's Information Criterion (AIC) was used to test the goodness of fit of the
17 maximum likelihood estimates to the length-frequency data.

18 In log₁₀-transformed length frequency diagrams, the maximum likelihood based analysis
19 reveals lowest AIC values for four or five cohorts. Similarly, log-transformed area data have
20 lowest AIC values if four or five cohorts are detected. Assuming more groups does not lower
21 the AIC or the computed cohorts comprise unrealistic narrow cohort ranges, which are nested
22 within larger ones.

23 **3.4 Growth model**

24 Kirby et al. (1998), Kirby (2000, 2001) and Kirby and Jackson (2004) used ligamental
25 increments of fossil and recent *Crassostrea* species to estimate individual life spans, assuming
26 that increments are formed annually. The ligamental area of these *Crassostrea* species is
27 typically structured by alternating transversal, growth ridges and furrows, oriented
28 perpendicular to growth direction, corresponding to phases of rapid and low calcification. The
29 specimens from the Stetten site lack such well-defined ridges.~~The ligamental area of these~~
30 ~~*Crassostrea* species is typically structured by perpendicular convex ridges and concave~~
31 ~~furrows corresponding to phases of rapid and low calcification. The specimens from the~~

1 | ~~Stetten site lack such well defined convex tops~~. In all specimens of *C. gryphoides* analyzed by
2 | Harzhauser et al. (2010) for stable isotopes, the counting of increments would have resulted in
3 | a large overestimation of the life spans. Similarly, Alam and Das (1999) documented a clear
4 | misfit between growth increments and age for the extant *C. madrasensis*. Therefore, we
5 | restrict our age estimates solely on growth rates of *C. gryphoides* deduced from stable isotope
6 | profiles published by Harzhauser et al. (2010). According to these authors, a shell from
7 | Stetten attained 43 cm in length at an age of 11 years and ~~thea~~ second one from a slightly
8 | younger ~~site horizon~~ was 63 cm long at an age of 16 years. These values document an average
9 | growth rate of ~3.9 cm per year and might serve as a base for rough age estimates for the
10 | complete adult shells from the Stetten ~~biostromeshell bed~~.

11 | For juvenile shells, this estimate would be wrong due to the non-linear mode of growth
12 | known from extant *Crassostrea* species, which show very high initial growth rates (Kennedy
13 | et al., 1996). Similarly, growth rates of *Crassostrea gryphoides* seem to decline in very old
14 | and large specimens as shown for a 78-cm-long and 41-year-old shell from the ~~late-upper~~
15 | Langhian of Austria (Harzhauser et al., 2010). To cope with the non-linear growth, growth
16 | curves of extant *Crassostrea* species are routinely calculated with the von Bertalanffy
17 | equation (von Bertalanffy, 1934). This equation is $SL_t = SL_{max}(1 - e^{-k(t-t_0)})$, where SL_t is shell
18 | length at time t , SL_{max} is the asymptotic shell length, t_0 is the size at time 0, and k is a rate
19 | constant. Herein, we used the length of the center line of each shell as SL_t as this measure
20 | captures the real growth length of the partly strongly curved or sigmoid specimens. For SL_{max}
21 | we used the size-to-age data of the 78-cm-long shell, which is the largest individual known so
22 | far.

23 | **3.5 Ratio between chalky and foliate layers**

24 | The calcitic *Crassostrea* shells consist of two structures: thin but densely spaced foliate layers
25 | separated by thick layers of light-weight chalky material (Stenzel, 1971; Higuera-Ruiz and
26 | Elorza, 2009). This fast growing structure is interpreted to be a major adaptive advantage of
27 | *Crassostrea* to impede drilling predation and to prevent from sinking in the soft bottom
28 | (Seilacher, 1984; Chinzei, 1995; Kirby, 2001; Vermeij, 2014). In fossil shells the chalky layer
29 | is completely recrystallized and has the same density as the foliate layer. Nevertheless, it is
30 | optically easily recognized by its lighter color and the nearly opaque appearance. A polished
31 | longitudinal section of an articulated *C. gryphoides* shell (providing data for left and right
32 | shells) was scanned and the ratio between both shell structures was quantified by image

1 analysis (Fig. 76). This method is only an approximation to the true value, as the ratio may
2 vary locally (Durve and Bal, 1960; Chinzei, 1995), but it is clearly an improvement compared
3 to former studies that used only linear transects or sectors within the shell (Durve and Bal,
4 1960; Chinzei, 1995; Kirby, 2001).

5 ~~The image~~ analysis of the cross-section documents proportions of 64% chalky to 36% foliate
6 layers for the right shell and of 61% to 39% for the left shell. The density of the chalky layer
7 when wet ranges around 1.15–1.32 g cm⁻³ (Chinzei, 1995) and the density of the foliate layer
8 ranges around 2.2–2.5 g cm⁻³ (Chinzei, 1995; Yoon et al., 2003) and has a clear upper limit by
9 the density of calcite (2.7 g cm⁻³). Using 1.2 g cm⁻³ for the chalky layer and 2.2 g cm⁻³ for the
10 foliate layer as rough estimates, ~~result in a~~ mean density ~~results in of~~ 1.84 g cm⁻³ and 1.81 g
11 cm⁻³ for the right and left valves, respectively. Shell density in *Crassostrea* species is
12 independent from age and size (Lombardi et al., 2013) and therefore the density estimates can
13 be applied to the entire data set.

14 3.6 Shell volume

15 The volume of nine individual shells was determined using close range laser scanning
16 technology, which provides high resolution models with sub-mm resolution. The specimens
17 were selected from the collections of the Natural History Museum and vary in center length
18 from 141 mm to 406 mm; four of these shells represent left-right shell pairs of an individual
19 (Fig. 43). The data were captured with a measuring arm (METRIS MCA, 3600 M7). A hand-
20 help triangulation laser scanner (a laser plane and a camera) was mounted at the end of two
21 arms of fixed length with flexible joints. The laser scanner takes measurements with a
22 maximum scan rate of 80 stripes per second with a strip-width of about 200 mm; the camera
23 has a resolution of 1000 dots per strip.

24 In ~~thea~~ first step, more than half of each shell was scanned and in ~~thea~~ second step the other
25 half. The overlap between both parts was more than 70%, which was sufficient for successful
26 registration of the scanned parts. During this registration process, the geometric
27 transformation is determined, which puts the two 3D laser point clouds together based on the
28 points in the overlapping part. This procedure is done using the iterative closest point (ICP)
29 algorithm (Glira et al., 2015). The resulting point cloud is analyzed in order to reduce noise
30 and thus improve the surface description. Outliers (wrongly determined points not on the
31 surface) were manually eliminated. Additionally, the raw point cloud (over 1.5 million points

1 per shell) was uniformly sub-sampled to allow interactive handling. The final resolution is
2 better than 0.18 mm (i.e. around 25 points per mm²). For volume calculation the point cloud
3 has to be transformed into a closed mesh. Remaining holes, non-manifold surfaces and
4 additional not connected components were identified and removed. Finally, the surface area
5 of the mesh and its volume were computed using the algorithm of Mirtich (1996).

6 Based on the 9 measured shells a relation between center line length and volume can be
7 deduced. The largest shell measured is 406 mm long but no empirical volume data are
8 available for larger shells, because these cannot be removed from the ~~protected~~-site.
9 Therefore, the von Bertalanffy equation would not be applicable for shells larger than ~40 cm.
10 Consequently, we chose a logistic function to approximate the inverse von Bertalanffy

11 equation: $v = \frac{3.2439E06}{1+118.86e^{-0.0099889SL}}$, where v is the volume in mm³ and SL the center line length

12 in mm (Fig. 87). Applying this equation to all shells results in a total volume of 393273 cm³
13 with a mean shell volume of 350.8 cm³ (σ=313.7). These values do not change significantly if

14 a non-linear Gompertz growth model is assumed as frequently done for *Crassostrea* (Lopesz
15 et al., 2013; Ginger et al., 2013). The respective equation $v = 1.978E08 e^{-9.1401e^{0.0018762x}}$

16 results in a total volume of 398474 cm³. Applying the above discussed average shell gravity
17 of 1.82 g cm⁻³ results in a total carbonate mass of ~715 kg (logistic) to ~725 kg (Gompertz)
18 for all 1121 shells. Thus, based on the age models of the shells, the annual carbonate
19 production per shell can be calculated, which ranges from 74 g yr⁻¹ (σ=2.9) (Gompertz) to 83
20 g yr⁻¹ (σ=2.8) (logistic), accounting for ~150 g yr⁻¹ per living oyster individual (= two valves).

21

22 4 Discussion

23 4.1 From lengths to cohorts

24 Based on the assumption that the size-frequency ~~cohorts~~-groups represent age classes it is
25 apparent to establish length-at-age relationships. Applying the von Bertalanffy equation to the
26 length data reveals a strongly right-skewed distribution with 50% of the shells ranging
27 between 3 and 6 years (Fig. 98A). The frequency of specimens between 6 and 9 years
28 decreases rapidly and the contribution by shells older than 9 years is subordinate although
29 outliers with up to 16 years occur. Again the non-normal distribution of the von Bertalanffy

1 growth model data suggests cohort mixing and the mixture analysis assumes at least four
2 significant cohorts with low AIC value. Due to the rareness of large and aged shells, the
3 fourth cohort displays a rather low amplitude and we assume that at least two natural cohorts
4 may be amalgamated in this group. ~~This pattern~~ suggests more or less continuous
5 recruitment accentuated by very successful settlement peaks every 2 or 3 years. Similarly,
6 comparable patterns in extant *Crassostrea* reefs are linked to fluctuating mortality rates and
7 changing recruitment success (Southworth et al., 2010). The data show that old and large
8 shells are rare. The reason for this may be a generally high mortality during the early years of
9 growth, resulting in low survival rates and few old specimens. The high amount of fragments
10 of large shells, however, suggests that a distinctly higher proportion of large shells existed but
11 became successively destroyed.

12 **4.2 Shell loss and mortality**

13 The rapid decline of old shells is a combination of two processes. First, natural mortality will
14 result in a tail of large shells. Second, shells of died-off *Crassostrea* are known to have
15 surprisingly short half-lives ranging from few years to few decades (Powell et al., 2006. 2015;
16 Waldbusser et al., 2011). Natural degradation processes, such as fragmentation, dissolution
17 and hydrodynamic export may account for 30 % loss of shells per year (Southworth et al.,
18 2010). The high amount of fragments with sharp edges suggests that fragmentation is a major
19 factor in our case. The importance of hydrodynamic export cannot be evaluated due to the
20 limited outcrop area. Dissolution, however, is a minor factor as the well preserved shell-
21 surfaces lack any signs of chemical degradation. Based on the declining amplitudes of the
22 cohorts the total shell loss can be computed as exponential decay function (Fig. 98B)
23 revealing initial half-lives of less than 4 years. The high proportion of fragmented, abraded
24 and/or bioeroded oyster shells (fragments: n = 7047) would balance the “missing frequencies”
25 easily ~~and points to fragmentation as key factor~~. We have no evidence for age-specific shell
26 destruction and assume that all age classes were equally affected by ~~this~~
27 process fragmentation.

28 Overall, under the environmental conditions as present in the Early Miocene estuary, a died-
29 off *Crassostrea gryphoides* reef would have been fully degraded within one or two decades if
30 not buried below the taphonomically active zone (Olszewski, 2004). ~~In respect to~~ ~~T~~the high
31 sedimentation rates in the rapidly subsiding basin with rates ~~around 0.6m/kyr~~ (0.6m/kyr,

1 | Zuschin et al., 2014), warranted a rapid burial of the reef ~~is not unlikely~~, thus capturing the
2 | population structure.

3 | **4.3 Crassostrea as carbonate factory?**

4 | The image analysis based estimation of chalky and foliate layers shows that the values for
5 | chalky layers are slightly lower than reported for other fast-growing *Crassostrea* species. The
6 | amount-volume of chalky layers in left shells of the extant *Crassostrea* “*gryphoides*” (sensu
7 | Newton and Smith, 1912) is ~70% (Durve and Bal, 1960). The shells of the Miocene
8 | *Crassostrea titan* (Conrad, 1853) and *C. gravitesta* (Yokoyama, 1926) were reported to
9 | comprise even up to ~90% of chalky deposits (Chinzei, 1995; Kirby, 2001) but this may be a
10 | slight overestimation, neglecting the high amount of dense calcite in the hinge areas. A re-
11 | evaluation of the illustrated specimen of *C. gravitesta* in Chinzei (1995) using our method
12 | reveals a somewhat lower but still high value of 77% chalky layer. The gravity of the fast
13 | growing *C. titan*, *C. gravitesta* and *C. cahobasensis* (Pilsbry and Brown, 1917) was estimated
14 | to range around 1.35–1.40 g cm⁻³ (Chinzei, 1995; Kirby and Jackson, 2004). These values are
15 | very close to the empirical data on the fast growing *C. ariakensis* (Fujita, 1913) (1.44 ± 0.12 g
16 | cm⁻³) measured by Lombardi et al. (2013). Slightly higher values are given for *C. gigas* (1.63
17 | ± 0.35 g cm⁻³, mean = 1.58) by Chinzei (1995). Generally, species with low amounts of
18 | chalky layer have much higher densities; e.g., *C. virginica* shells range around 2.18–2.35 g
19 | cm⁻³ (Kirby and Jackson, 2004; Lombardi et al., 2013). Our gravity estimate of ~1.82 g cm⁻³
20 | for *C. gryphoides* is thus somewhat higher than expected for such a growth type. In fact, large
21 | parts of the shells are very light-weighted and fit well to the patterns discussed by Chinzei
22 | (1995) and Kirby (2001). The main difference is the large proportion of heavy shell material
23 | in the huge umbos and hinges.

24 | A comparison of the growth curve of *C. gryphoides* with the von Bertalanffy growth models
25 | of fossil and extant *Crassostrea* species (Fig. 109) reveals this oyster as outstandingly fast
26 | growing species. Thus, *C. gryphoides* was an important carbonate producer in Neogene
27 | estuaries and lagoons where it lived as a secondary soft-bottom dweller in dense colonies in a
28 | mixed mode of shell-supported reclining and mud sticking (sensu Seilacher et al. 1985;
29 | Seilacher and Gishlick, 2014). Therefore, dense populations with more than 100 specimens
30 | individuals per m² can be expected. Even within the shell bed, which is clearly not in-situ, the
31 | average density is 129 shells (~64 individuals) per m² (including also moderately fragmented
32 | shells). This would point to a hypothetical annual carbonate production of up to 15 kg m⁻² with

1 the oyster reef. Although this calculation is just a very rough estimate, it indicates that the
2 carbonate production is in the range of fast growing coral reefs with productions of 6–10 kg
3 m⁻² yr⁻¹ (Montaggioni, 2005; Jones et al., 2015). A major difference, however, is the rapid
4 shell loss in *Crassostrea* reefs, which prevents the formation of rigid and stable structures
5 comparable to coral reefs.

6

7 **5 Conclusion**

8 *Crassostrea gryphoides* was the fastest growing and largest Crassostreinae species known so
9 far. Despite the fact, that this species could attain outstanding individual ages of four decades
10 (Harzhauser et al., 2010), the bulk of specimens analyzed herein lived less than 10 years,
11 typically growing up to about 300 mm in length.

12 The non-normal distribution in the size, area and age frequency data are best explained by the
13 presence of distinct recruitment cohorts, comparable to modern oyster reefs. About four
14 cohorts are detected by mixture analysis and the rapidly decreasing amplitudes of frequency
15 of these cohorts is interpreted to reflect the combined effect of mortality, ~~respectively~~ the
16 declining life expectancy with age, and the shell loss by biotic and physical factors. As no
17 accumulation of large and aged shells occurred, whilst the amount of fragments is high, we
18 assume that shell loss is an important factor to explain the strongly right-skewed distribution.
19 Shell half-lives ranged around 2–4 years and within less than two decades the seemingly rigid
20 and persisting structure of a *Crassostrea gryphoides* reef could have been completely
21 degraded. This may explain the rareness of in-situ *C. gryphoides* reefs in the fossil record
22 although the shells are frequent and ubiquitous.

23 The significant growth ~~performance-rate~~ is clearly boosted by the formation of up to 64 %
24 percentage of fast-growing and lightweight chalky material. The subtropical climate with
25 warm winter temperatures above c. 10°C and the nutrient-rich setting in an estuary will
26 additionally have supported the excessive growth.

27 Due to its fast growth and large shells, the carbonate production of *C. gryphoides* is
28 outstanding. Dense colonies might have produced around 15 kg m⁻² yr⁻¹ of carbonate, which is
29 within the range of fast growing coral reefs. Therefore, this oyster may have been a major
30 carbonate producer in the circum-Tethyan area throughout the Miocene. In contrast to coral
31 reefs, however, the high shell loss rates did not allow to form stable persistent structures.

1

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8

1 **References**

- 2 Afsar, N., Siddiqui, G., and Roberts, D.: Parasite inspection in five commercially important
3 oyster species (Mollusca: Bivalvia) of Pakistan. *J. Basic Appl. Sci.*, 10, 220–225, 2014.
- 4 Aichholzer, O., Aurenhammer, F., Alberts, D., and Gärtner, B.: A novel type of skeleton for
5 polygons. Springer, Berlin, Heidelberg, 752–761, 1996.
- 6 Alam, M. D. and Das, N. G.: Growth and age determination of an intertidal cupped oyster
7 *Crassostrea madrasensis* (Preston) (Bivalvia: Ostreidae) around Moheshkhali Channel, Bay
8 of Bengal. *Indian J. Mar. Sci.*, 28, 329–331, 1999.
- 9 Baqueiro Cárdenas, E. R. and Aldana Aranda, D.: Differences in the exploited oyster
10 (*Crassostrea virginica* (Gmelin, 1791)) populations from different coastal lagoons of the Gulf
11 of Mexico. *Transitional Waters Bull.*, 2, 21–35, 2007.
- 12 Berthome, J. P., Prou, J., and Bodoy, A.: Performances de croissance de l'huître creuse,
13 *Crassostrea gigas* (Thunberg) dans le bassin d'élevage de Marennes-Oléron entre 1979 &
14 1982. *Haliotis*, 15, 183–192, 1986.
- 15 Chatterji, A., Ansari, Z. A., Ingole, B. S., and Parulekar, A. H.: Length-weight relationship of
16 giant oyster *Crassostrea gryphoides* (Schlotheim). *Mahasagar-Bull. Nat. Inst. Oceanogr.*, 18,
17 521–524, 1985.
- 18 Chávez-Villalba, J., López-Tapia, M., Mazón-Suástegui, J., and Robles-Mungaray, M.:
19 Growth of the oyster *Crassostrea corteziensis* (Hertlein, 1951) in Sonora, Mexico. *Aquac.*
20 *Res.*, 36, 1337–1344, 2005.
- 21 [Chinzei, K.: Morphological and structural adaptations to soft substrates in the Early Jurassic](#)
22 [monomyarians *Lithotis* and *Cochlearites*. *Lethaia*, 15, 179–197, 1982.](#)
- 23 [Chinzei, K.: Shell structure, growth, and functional morphology of an elongate Cretaceous](#)
24 [oyster. *Palaeontology*, 29, 139–154, 1986.](#)
- 25 Chinzei, K.: Adaptive significance of the lightweight shell structure in soft bottom oysters.
26 *Neues Jahrb. Geol. P.-A.*, 195, 217–227, 1995.
- 27 Chinzei, K.: Adaptation of oysters to life on soft substrates. *Hist. Biol.*, 25, 223–231, 2013.
- 28 [Chinzei, K. and Seilacher, A.: Remote biomineralization I: fill skeletons in vesicular oyster](#)
29 [shells. *N. Jb. Geol. Paläont. Abh.*, 190, 349–361, 1993.](#)

- 1 Coakley, J. M.: Growth of the eastern oyster, *Crassostrea virginica*, in Chesapeake Bay.
2 Thesis, Faculty of the Graduate School of the University of Maryland, 1–263,
3 <http://drum.lib.umd.edu/bitstream/1903/1471/1/umi-umd-1590.pdf>, 2004.
- 4 Conrad, T. A.: Notes on shells with descriptions of new species. P. Acad. Nat. Sci. Phila., 6,
5 199–200, 1853.
- 6 Delaunay, B.: Sur la sphere vide. Otdelenie Matematicheskikh i Estestvennykh Nauk, 7, 793–
7 800, 1934.
- 8 Dellmour, R. and Harzhauser, M.: The Iván Canyon, a large Miocene canyon in the Alpine-
9 Carpathian Foredeep. Mar. Petrol. Geol., 38, 83–94, 2012.
- 10 Dempster, A. P., Laird, N. M., and Rubin, D. B.: Maximum likelihood from incomplete data
11 via the EM algorithm. J. Roy. Stat. Soc. B, 39, 1–38, 1977.
- 12 Durve, V. S.: Malacological differences between the oysters *Crassostrea gryphoides*
13 (Schlotheim) and *Crassostrea madrasensis* Preston. Indian J. Fish., 202, 624–625, 1974.
- 14 Durve, V. S. and Bal, D. V.: Some observations on shell-deposits of the oyster *Crassostrea*
15 *gryphoides* (Schlotheim). P. Indian AS-B, 54, 45–55, 1960.
- 16 Einsele, G., Ricken, W., and Seilacher, A.: Cycles and events in stratigraphy. 1–955,
17 Springer-Verlag, Berlin, 1991.
- 18 FAO: Food and Agriculture Organization of the United Nations. Fisheries and Aquaculture
19 Department. Aquaculture Fact Sheets. <http://www.fao.org/fishery/culturedspecies/search/en>
20 (last accessed May 14th 2015), 2015.
- 21 Fujita, T.: Nihon Suisan Dobutsugaku (Aquatic Zoology in Japan). Shokabo, Tokyo. Japanese
22 aquatic fisheries animals), vol 2., 1–292, Shokabu, Tokyo, 1913.
- 23 Ginger, K. W. K., Vera, C. B. S., Dineshram, R., Dennis, C. K. S., Adela, L. J., Yu, Z., and
24 Thiyagarajan, V.: Larval and post-larval stages of Pacific oyster (*Crassostrea gigas*) are
25 resistant to elevated CO₂. PLoS ONE, 8, e64147, 2013.
- 26 Glira, P., Pfeifer, N., Briese, C., and Ressler, C.: A correspondence framework for ALS strip
27 adjustments based on variants of the ICP Algorithm. J. Photogram., Remote Sensing, Geoinf.
28 Process. Accepted for publication, 2015.

- 1 Gmelin, J. F.: Caroli a Linnei systema natura per regna tria naturae, secundum classes,
2 ordines, genera, species, cum characteribus, disserentis, synonymis, locis etc. Editio decima
3 tertia, aucta, reformata, cura J. F. Gmelin, 1(6). Vermes testacea. G. E. Beer, Lipsiae, 3021–
4 4120, 1791.
- 5 [Goldner, A., Herold, N., and Huber, M.: The challenge of simulating the warmth of the mid-
6 Miocene climatic optimum in CESM1, *Clim. Past*, 10, 523–536.](#)
- 7 Groslier, T., Toft Christensen, H., Davids, J., Dolmer, P., Elmedal, I., Holm, M. W., and
8 Hansen, B. W.: Status of the Pacific Oyster *Crassostrea gigas* (Thunberg, 1793) in the
9 western Limfjord, Denmark - Five years of population development. *Aquatic Invasions*, 9,
10 175–182, 2014.
- 11 Hammer, Ø.: PAST, Paleontological Statistics Version 3.06. Reference manual. Natural
12 History Museum, University of Oslo, 225 p.,
13 <http://folk.uio.no/ohammer/past/past3manual.pdf>, 2015.
- 14 Hammer, Ø., Harper, D. A. T., and Ryan, P. D.: Past: Paleontological Statistics Software
15 Package for Education and Data Analysis. *Palaeontol. Electron.*, 4, 1–9, 2001.
- 16 Harding, J. M., Mann, R., and Southworth, M. J.: Shell length-at-age relationships in James
17 River, Virginia oysters (*Crassostrea virginica*) collected four centuries apart. *J. Shellfish*
18 *Res.*, 27, 1109–1115, 2008.
- 19 Harzhauser, M., Böhme, M., Mandic, O., and Hofmann, Ch.-Ch.: The Karpatian (Late
20 Burdigalian) of the Korneuburg Basin – a palaeoecological and biostratigraphical synthesis.
21 *Beitr. Paläont.*, 27, 441–456, 2002.
- 22 Harzhauser, M., Piller, W. E., Müllegger, S., Grunert, P., and Micheels, A.: Changing
23 seasonality patterns in Central Europe from Miocene Climate Optimum to Miocene Climate
24 Transition deduced from the *Crassostrea* isotope archive. *Global Planet. Change*, 76, 77–84,
25 2010.
- 26 Harzhauser, M., Djuricic, A., Mandic, O., Zuschin, M., Dorninger, P., Nothegger, C.,
27 Székely, B., Puttonen, E., Molnár, G., and Pfeifer, N.: Disentangling the history of complex
28 multi-phased shell beds based on the analysis of 3D point cloud data. *Palaeogeogr.*
29 *Palaeoclimatol. Palaeoecol.*, [437, 165–180, 2015.](#)

- 1 Hertlein, L. G.: Descriptions of two new species of marine pelecypods from west Mexico.
2 Southern Calif. Acad. Sci. Bull., 50, 68–75, 1951.
- 3 Higuera-Ruiz, R. and Elorza, J.: Biometric, microstructural, and high-resolution trace element
4 studies in *Crassostrea gigas* of Cantabria (Bay of Biscay, Spain): anthropogenic and seasonal
5 influences. Estuar. Coast. Shelf S., 82, 201–213, 2009.
- 6 Hoşgör, I.: Presence of *Crassostrea gryphoides* (Schlotheim) from the lower-middle Miocene
7 sequence of Kahramanmaraş Basin (SE Turkey); its taxonomy, paleoecology and
8 paleogeography. Min. Res. Explor. Bull., 136, 17–28, 2008.
- 9 Jones, N. S., Ridgwell, A., and Hendy, E. J.: Evaluation of coral reef carbonate production
10 models at a global scale. Biogeosciences, 12, 1339–1356, 2015.
- 11 Kazhdan, M., Bolitho, M., and Hoppe, H.: Poisson surface reconstruction. P. fourth
12 Eurographics Sym. Geom. Proc., 7, 61–70, 2006.
- 13 Kennedy, V. S., Newell, R. I. E., and Eble, A. F.: The Eastern Oyster *Crassostrea virginica*.
14 College Park, Maryland, USA, Maryland Sea Grant College Publication UM-SG-TS-96-01,
15 1–750, 1996.
- 16 Kern, A., Harzhauser, M., Mandic, O., Roetzel, R., Ćorić, S., Bruch, A. A., and Zuschin, M.:
17 Millennial-scale vegetation dynamics in an estuary at the onset of the Miocene Climate
18 Optimum. Palaeogeogr. Palaeoclimatol. Palaeoecol., 304, 247–261, 2010.
- 19 Kidwell, S. M.: Models for fossil concentrations: Paleobiologic implications. Paleobiology
20 12, 6–24, 1986.
- 21 Kidwell, S. M.: The stratigraphy of shell concentrations, in: Taphonomy, Releasing the Data
22 Locked in the Fossil Record, edited by Allison, P. A. and Briggs, D. E. G., Plenum Press,
23 New York, 211–290, 1991.
- 24 Kirby, M. X.: Paleoecological differences between Tertiary and Quaternary *Crassostrea*
25 oysters, as revealed by stable isotope sclerochronology. Palaios, 15, 132–141, 2000.
- 26 Kirby, M. X.: Differences in growth rate and environment between Tertiary and Quaternary
27 *Crassostrea* oysters. Paleobiology, 27, 84–103, 2001.
- 28 Kirby, M. X. and Jackson, J. B. C.: Extinction of a fastgrowing oyster and changing ocean
29 circulation in Pliocene Tropical America. Geology, 32, 1025–1028, 2004.

1 Kirby, M. X., Soniat, T. M., and Spero, H. J.: Stable isotope sclerochronology of Pleistocene
2 and Recent oyster shells (*Crassostrea virginica*). *Palaios*, 13, 560–569, 1998.

3 Kirk, J.: Advanced Dijkstra's minimum path algorithm.
4 [http://www.mathworks.com/matlabcentral/fileexchange/20025-advanced-dijkstras-minimum-](http://www.mathworks.com/matlabcentral/fileexchange/20025-advanced-dijkstras-minimum-path-algorithm)
5 [path-algorithm](http://www.mathworks.com/matlabcentral/fileexchange/20025-advanced-dijkstras-minimum-path-algorithm), last accessed 2015-04-02, 2015.

6 Koeppen, W.: Das geographische System der Klimate, in: *Handbuch der Klimatologie*, edited
7 by Koeppen, W. and Geiger, R., Gebrüder Bornträger, Berlin, 1–44, 1936.

8 [Kraus, K. and Pfeifer, N.: Advanced DTM generation from LIDAR data, *Int. Arch. Photogr.*
9 *Remote Sensing Spatial Inf. Sci.*, 34\(3/W4\), 23–30, 2001.](#)

10 Laurain, M.: *Crassostrea gryphoides* et *C. gingensis* (Schlotheim, 1813) deux expressions
11 morphologiques d'une même espèce (Miocène, Bivalvia). *Geobios*, 13, 21–43, 1980.

12 Littlewood, D. T. J.: Molecular phylogenetics of cupped oysters based on partial 28S rDNA
13 gene sequences. *Mol. Phylogenet. Evol.*, 3, 221–229, 1994.

14 Lombardi, S. A., Chon, G. D., Jin-Wu Lee, J., Lane, H. A., and Paynter, K. T.: Shell hardness
15 and compressive strength of the Eastern oyster, *Crassostrea virginica*, and the Asian oyster,
16 *Crassostrea ariakensis*. *Biol. Bull.*, 225, 175–183, 2013.

17 Lopes, G. R., Araujo de Miranda Gomes, C. H., Tureck, C. R., and de Melo, C. M. R.:
18 Growth of *Crassostrea gasar* cultured in marine and estuary environments in Brazilian
19 waters. *Pesqui. Agropecu. Bras.*, 48, 975–982, 2013.

20 Mahar, M. A. and Awan, K. P.: Cultivation of oyster *Crassostrea gryphoides* (Schlotheim)
21 through rafts at Ambra creek coastal belt of Arabian sea, Sindh Pakistan. *Sindh Univ. Res. J.*
22 *(Sci. Ser.)*, 44, 119–124, 2012.

23 Mancera, E. and Mendo, J.: Population dynamics of the oyster *Crassostrea rhizophorae* from
24 the Ciénaga Grande de Santa Marta, Colombia. *Fish. Res.*, 26, 139–148, 1996.

25 Mandic, O., Harzhauser, M., Schlaf, J., Piller, W. E., Schuster, F., Wielandt-Schuster, U.,
26 Nebelsick, J. H., Kroh, A., Rögl, F., and Bassant, P.: Palaeoenvironmental Reconstruction of
27 an epicontinental Flooding - Burdigalian (Early Miocene) of the Mut Basin (Southern
28 Turkey). *Cour. Forsch.-Inst. Senckenberg*, 248, 57–92, 2004.

- 1 Marshall, B.: *Magallana Salvi*, Macali & Mariottini, 2014. Accessed through: World Register
2 of Marine Species at <http://marinespecies.org/aphia.php?p=taxdetails&id=836032> on 2015-
3 04-28, 2015.
- 4 Mirtich, B.: Fast and accurate computation of polyhedral mass properties. *J. Graphics Tools*,
5 1, 31–50, 1996.
- 6 Montaggioni, L. F.: History of Indo-Pacific coral reef systems since the last glaciation:
7 development patterns and controlling factors. *Earth-Sci. Rev.*, 71, 1–75, 2005.
- 8 Nagi, H. M., Shenai-Tirodkar, P. S., and Jagtap, T. G.: Dimensional relationship in
9 *Crassostrea madrasensis* (Preston) and *C. gryphoides* (Schlotheim) in mangrove ecosystem.
10 *Indian J. Geo-Mar. Sci.*, 40, 559–566, 2011.
- 11 Newton, R. B. and Smith. E. A.: On the survival of a Miocene oyster in Recent seas. *Rec.*
12 *Geol. Surv. India*, 42, 1–15, 1912.
- 13 Nothegger, C. and Dorninger, P.: 3D filtering of high-resolution Terrestrial Laser Scanner
14 point clouds for cultural heritage documentation. *Photogram., Fernerkundung, Geoinf.*, 1, 53–
15 63, 2009.
- 16 Nurul Amin, S. M., Zafar, M., and Halim, A.: Age, growth, mortality and population structure
17 of the oyster, *Crassostrea madrasensis*, in the Moheskhal Channel (southeastern coast of
18 Bangladesh). *J. Appl. Ichthyol.*, 24, 18–25, 2008.
- 19 Ó Foighil, D., Gaffney, P. M., and Hilbish, T. J.: Differences in mitochondrial 16S ribosomal
20 gene sequences allow discrimination among [*Crassostrea virginica* (Gmelin)] and Asian [*C.*
21 *gigas* (Thunberg), *C. ariakensis* Wakiya] oyster species. *J. Exp. Mar. Biol. Ecol.*, 192, 211–
22 220, 1995.
- 23 [Olszewski, T.: Modeling the influence of taphonomic destruction, reworking, and burial on](#)
24 [time-averaging in fossil accumulations, *Palaios*, 19, 39–50, 2004.](#)
- 25 Otepka, J., Ghuffar, S., Waldhauser, C., Hochreiter, R., and Pfeifer, N.: Georeferenced point
26 clouds: A survey of features and point cloud management. *ISPRS Int. J. Geo-Inf.*, 2, 1038–
27 1065, 2013
- 28 Peel, M. C., Finlayson, B. L., and McMahon, T. A.: Updated world map of the Köppen-
29 Geiger climate classification. *Hydrol. Earth Syst. Sc. Disc.*, 4, 439–473, 2007.

1 Pfeifer, N., Mandlbürger, G., Otepka, J., and Karel, W.: OPALS – A framework for airborne
2 laser scanning data analysis. *Comput. Environ. Urban*, 45, 125–136, 2014.

3 Pilsbry, H. A. and Brown, A.: Oligocene fossils from the neighborhood of Cartagena,
4 Colombia, with notes on some Haitian species. *P. Acad. Nat. Sci. Phila.*, 32–41, 1917.

5 Powell, E. N., Kraeuter, J. N., and Ashton-Alcox, K. A. How long does oyster shell last on an
6 oyster reef? *Estuar. Coast. Shelf S.*, 69, 531–542, 2006.

7 Powell, E. N., Klinck, J. M., Guo, X., Ford, S. E., and Bushek, D.: The potential for oysters,
8 *Crassostrea virginica*, to develop resistance to Dermo disease in the field: evaluation using a
9 gene-based population dynamics model. *J. Shellfish Res.*, 30, 685–712, 2011.

10 Powell, E. N., Mann, R., Ashton-Alcox, K. A., Kim, Y., and Bushek, D.: The allometry of
11 oysters: spatial and temporal variation in the length–biomass relationships for *Crassostrea*
12 *virginica*. *J. Mar. Biol. Assoc. U.K.*, online first, 18 pp., 2015.

13 Preston, H. B.: Report on a collection of Mollusca from the Cochin and Ennur Backwaters.
14 *Rec. Indian Mus.*, 12, 27–39, 1916.

15 Ragaini, L. and Di Celma, C.: Shell structure, taphonomy and mode of life of a Pleistocene
16 ostreid from Ecuador. *Boll. Soc. Paleont. Ital.*, 48, 79–87, 2009.

17 Reece, K. S., Cordes, J. F., Stubbs, J. B., Hudson, K. L., and Francis, E. A.: Molecular
18 phylogenies help resolve taxonomic confusion with Asian *Crassostrea* oyster species. *Mar.*
19 *Biol.*, 153, 709–721, 2008.

20 Ren, J., Liu, X., Jiang, F., Guo, X., and Liu, B.: Unusual conservation of mitochondrial gene
21 order in *Crassostrea* oysters: evidence for recent speciation in Asia. *BMC Evol. Biol.*, 10,
22 394, 2010.

23 Robinson, E. M., Lunt, J., Marshall, C. D., and Smee, D. J.: Eastern oysters *Crassostrea*
24 *virginica* deter crab predators by altering their morphology in response to crab cues. *Aquat.*
25 *Biol.*, 20, 11–118, 2014.

26 Ross, P. G. and Luckenbach, M. W.: Population Assessment of Eastern Oysters (*Crassostrea*
27 *virginica*) in the Seaside Coastal Bays. Final Report. Virginia Coastal Zone Management
28 Program, College of William and Mary, Wachapreague, 101 pp.,
29 <http://www.deq.virginia.gov/Portals/0/DEQ/CoastalZoneManagement/task10-02-07.pdf>,
30 2009.

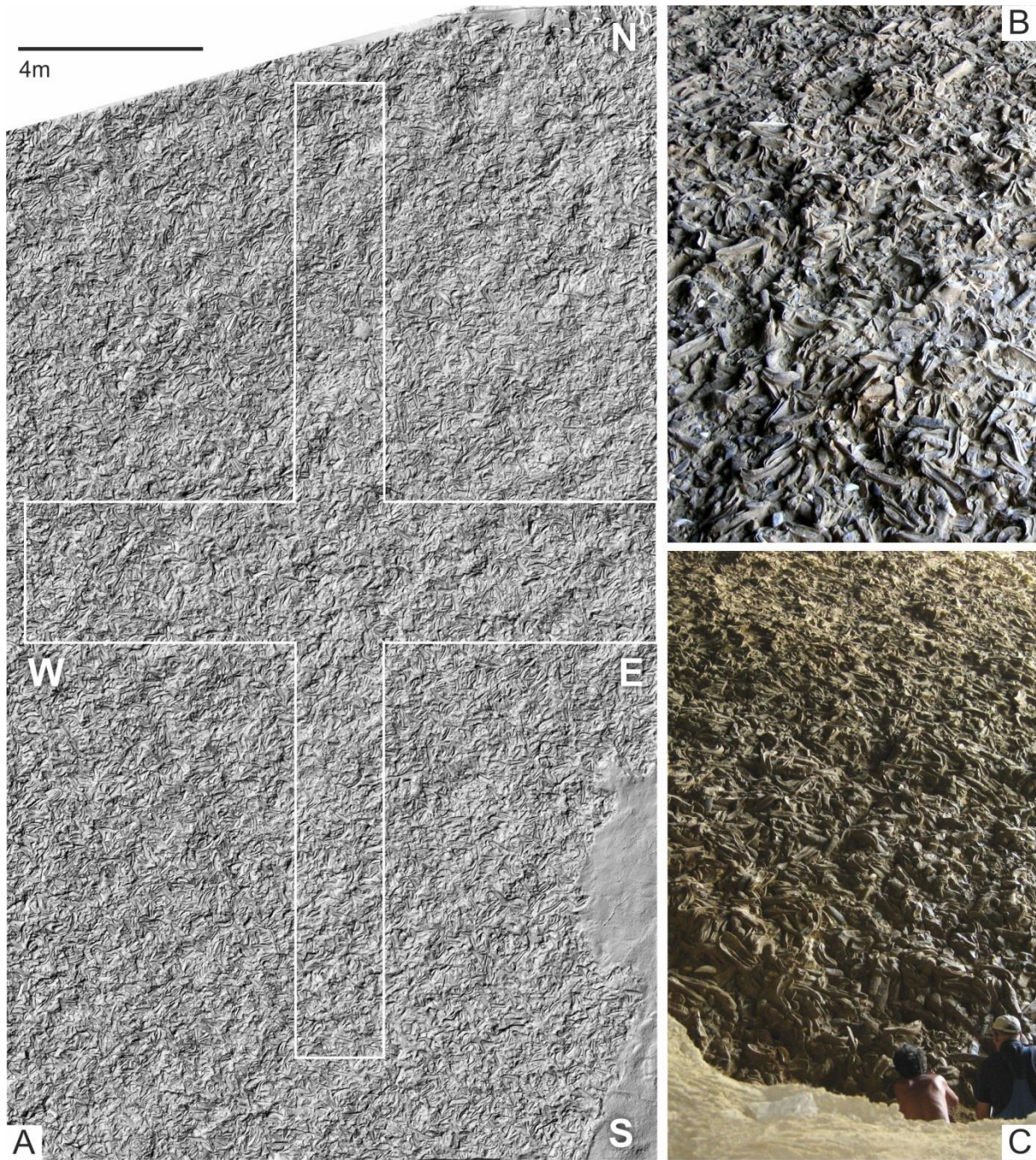
- 1 Sacco, F.: I molluschi dei terreni terziarii del Piemonte e della Liguria. Parte XXIII.
2 Pelecypoda (Ostreidae, Anomiidae e Dimyidae). Carlo Clausen, Torino, 1–46, 1897.
- 3 Salvi, D., Macali, A., and Mariottini, P.: Molecular phylogenetics and systematics of the
4 bivalve family Ostreidae based on rRNA sequence-structure models and multilocus species
5 tree. PLoS ONE 9(9): e108696. doi:10.1371/journal.pone.0108696, 2014.
- 6 Schlotheim, E. F. von: Beiträge zur Naturgeschichte der Versteinerungen in geognostischer
7 Hinsicht, in Leonhard's Taschenbuch für die gesammte Mineralogie mit Hinsicht auf die
8 neuesten Entdeckungen, edited by Leonhard, C. C., Series 1, 7, 1–134, 1813.
- 9 Schultz, O.: Bivalvia neogenica (Nuculacea – Unionacea), in: Catalogus Fossilium Austriae,
10 Wien, edited by Piller, W. E., Akademie der Wissenschaften, 1/1, 1–379, 2001.
- 11 Seilacher, A.: Constructional morphology of bivalves: evolutionary pathways in primary
12 versus secondary soft-bottom dwellers. Palaeontology, 27, 207–237, 1984.
- 13 Seilacher, A. and Gishlick, A. D.: Morphodynamics. CRS Press, 1–551, 2014.
- 14 Seilacher, A., Matyja, B. A., and Wierzbowski, A.: Oyster Beds: Morphologic response to
15 changing substrate conditions. Lect. Notes Earth Sci., 1, 421–435, 1985.
- 16 Siddiqui, G. and Ahmed, M.: Oyster species of the sub tropical coast of Pakistan (northern
17 Arabian Sea). Indian J. Mar. Sci., 31, 108–118, 2002.
- 18 Southworth, M., Harding, J. M., Wesson, J. A., and Mann, R.: Oyster (*Crassostrea virginica*,
19 Gmelin 1791) population dynamics on public reefs in the Great Wicomico River, Virginia,
20 USA. J. Shellfish Res., 29, 271–290, 2010.
- 21 Sovis, W. and Schmid, B.: Das Karpat des Korneuburger Beckens, Teil 1. Beitr. Paläont., 23,
22 1–413, 1998.
- 23 Sovis, W. and Schmid, B.: Das Karpat des Korneuburger Beckens, Teil 2. Beitr. Paläont., 27,
24 1–467, 2002.
- 25 Sowerby, G. B.: Monograph of the genus *Ostraea*. Conchologia Iconica, 18, 6–33, 1871.
- 26 Stenzel, H. B.: Oysters, in: Treatise on Invertebrate Paleontology, edited by Moore, R. C.,
27 Geological Society of America and the University of Kansas Press, Lawrence, N/3, 953–
28 1224, 1971.

- 1 Thunberg, C. P.: Tekning och Beskrifning på en stor Ostronsort ifrån Japan. Kongliga
2 Vetenskaps Academiens Nya Handlingar, 14, 140–142, 1793.
- 3 Trivedi, S., Aloufi, A. A., Ansari, A. A., and Ghosh, S. K.: Molecular phylogeny of oysters
4 belonging to the genus *Crassostrea* through DNA barcoding. *J. Entomol. Zool. Stud.*, 3, 21–
5 26, 2015.
- 6 Vermeij, G.: The oyster enigma variations: a hypothesis of microbial calcification.
7 *Paleobiology*, 40, 1–13, 2014.
- 8 von Bertalanffy, L.: Untersuchungen über die Gesetzmäßigkeiten des Wachstums. I.
9 Allgemeine Grundlagen der Theorie; mathematische und physiologische Gesetzmäßigkeiten des
10 Wachstums bei Wassertieren. *Arch. Entwickl. Mech. Org.*, 131, 613–652, 1934.
- 11 Voronoi, G.: Nouvelles applications des paramètres continus à la théorie des formes
12 quadratiques. Deuxième mémoire. Recherches sur les parallélogrammes primitifs. *J. reine
13 angew. Math.*, 133, 97–178, 1908.
- 14 Waldbusser, G. G., Steenson, R. A., and Gren, M. A.: Oyster shell dissolution rates in
15 estuarine waters: effects of pH and shell legacy. *J. Shellfish Res.*, 30, 659–669, 2011.
- 16 Wang, Y., Xus, Z., and Guo, X.: Differences in the rDNA-bearing chromosome divide the
17 Asian-Pacific and Atlantic species of *Crassostrea* (Bivalvia, Mollusca). *Biol. Bull.*, 206, 46–
18 54, 2004.
- 19 Wessely, G.: Geologie des Korneuburger Beckens. *Beitr. Paläont.*, 23, 9–23, 1998.
- 20 [Wiedl, T., Harzhauser, M., Kroh, A., Ćorić, S., and Piller, W. E.: Ecospace variability along a
21 carbonate platform at the northern boundary of the Miocene reef belt \(Upper Langhian,
22 Austria\), *Palaeogeogr. Palaeoclimatol.*, 370, 232–246, 2013.](#)
- 23 Yokoyama, M.: Fossil Mollusca from the oil-fields of Akita. *J. Fac. Sci., Imperial Univ.*
24 *Tokyo, Sect. 2*, 1/9, 377–389, 1926.
- 25 Yoon, G.-L., Kim, B.-T., Kim, B.-O., and Han, S.-H.: Chemical–mechanical characteristics of
26 crushed oyster-shell. *Waste Manag.*, 23, 825–834, 2003.
- 27 [Zachos, J. C., Dickens, G. R., and Zeebe, R. E.: An early Cenozoic perspective on greenhouse
28 warming and carbon-cycle dynamics, *Nature*, 451, 279–283, 2008.](#)

1 Zhang, G., Fang, X., Guo, X., Li, L., Luo, R., Xu, F., Yang, P., Zhang, L., Wang, X., Qi, H.,
2 Xiong, Z., Que, H., Xie, Y., Holland, P. W., Paps, J., Zhu, Y., Wu, F., Chen, Y., Wang, J.,
3 Peng, C., Meng, J., Yang, L., Liu, J., Wen, B., Zhang, N., Huang, Z., Zhu, Q., Feng, Y.,
4 Mount, A., Hedgecock, D., Xu, Z., Liu, Y., Domazet-Lošo, T., Du, Y., Sun, X., Zhang, S.,
5 Liu, B., Cheng, P., Jiang, X., Li, J., Fan, D., Wang, W., Fu, W., Wang, T., Wang, B., Zhang,
6 J., Peng, Z., Li, Y., Li, N., Wang, J., Chen, M., He, Y., Tan, F., Song, X., Zheng, Q., Huang,
7 R., Yang, H., Du, X., Chen, L., Yang, M., Gaffney, P. M., Wang, S., Luo, L., She, Z., Ming,
8 Y., Huang, W., Zhang, S., Huang, B., Zhang, Y., Qu, T., Ni, P., Miao, G., Wang, J., Wang,
9 Q., Steinberg, C. E., Wang, H., Li, N., Qian, L., Zhang, G., Li, Y., Yang, H., Liu, X., Wang,
10 J., Yin, Y., and Wang, J.: The oyster genome reveals stress adaptation and complexity of shell
11 formation. *Nature*, 490, 49–54, 2012.

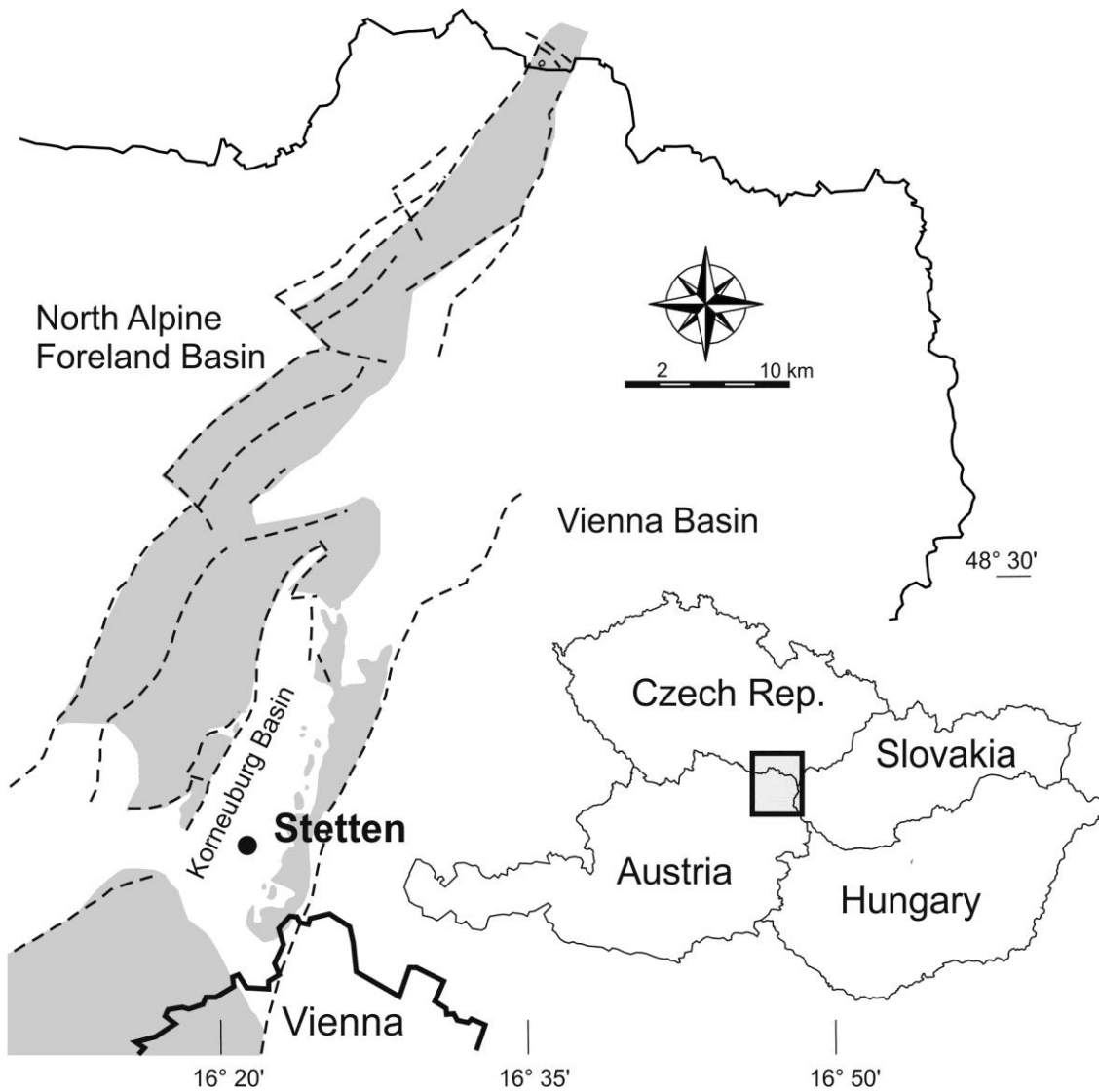
12 Zuschin, M., Harzhauser, M., Hengst, B., Mandic, O., and Roetzel, R.: Long-term ecosystem
13 stability in an Early Miocene estuary. *Geology*, 42, 1–4, 2014.

14



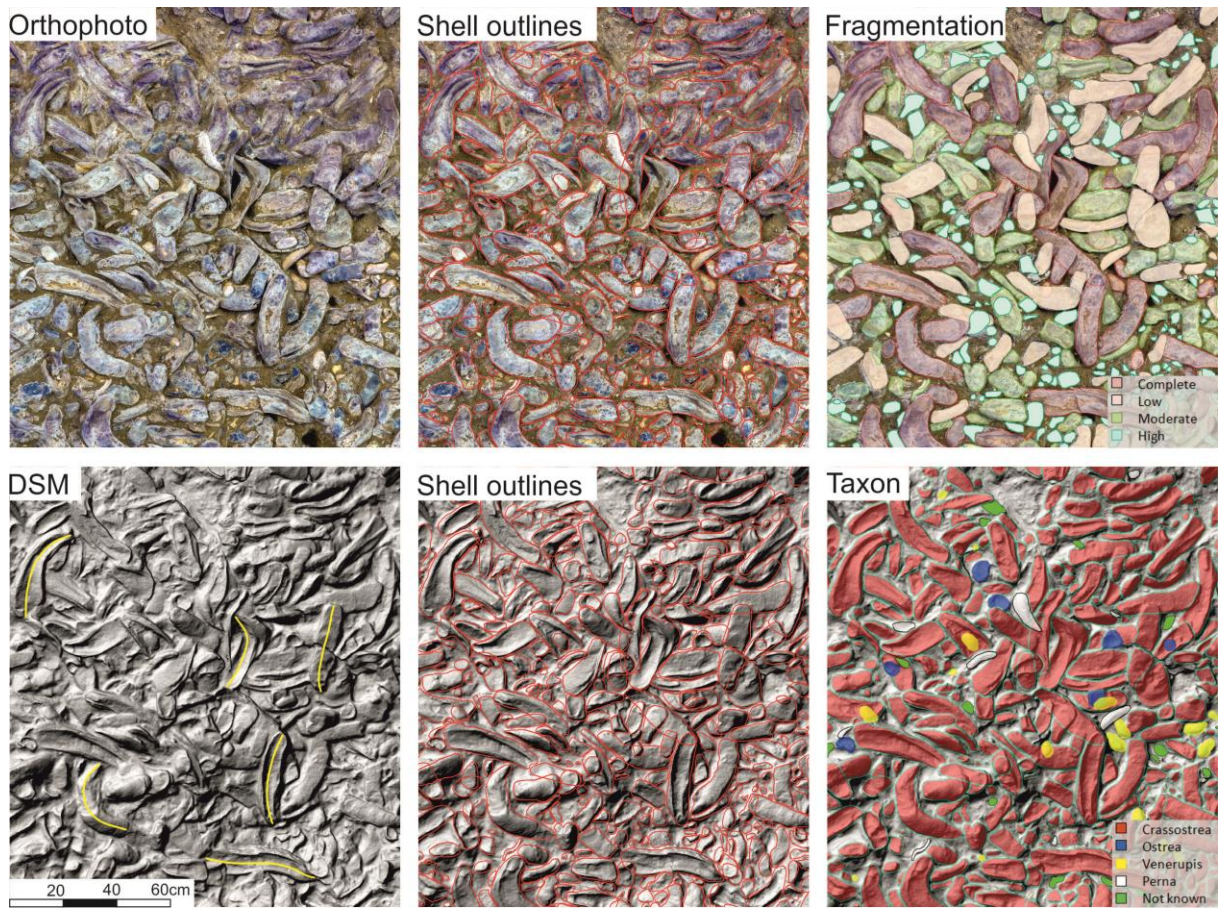
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Figure 1. Part of the digital surface model of the shell bed; the white cross indicates the area, within which all objects were digitally outlined and evaluated. It contains 1121 complete shells of *C. gryphoides* and 7047 fragments of that species (A). outcrop pictures of the shell bed illustrating the density and extent of the shell bed (B–C), B: width c. 2 m; C: see workers as scale).



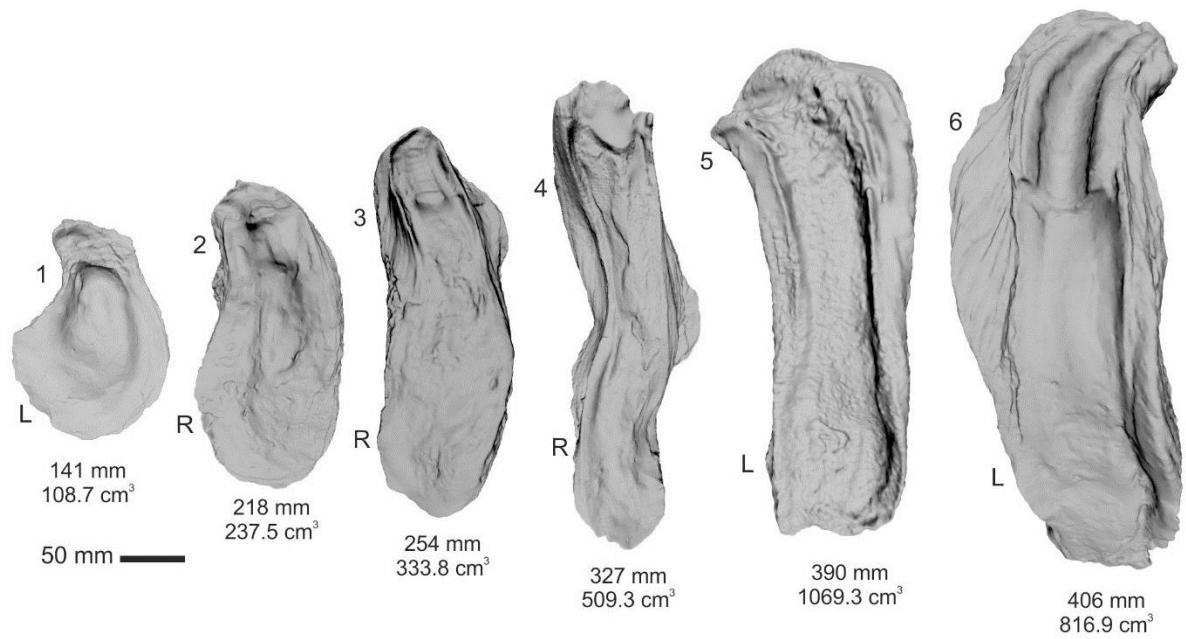
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Figure 2. Geographic position of the Stetten site within the Korneuburg Basin north of Vienna in Austria; shaded areas represent pre-Miocene basement; dashed lines are major faults (modified from Dellmour and Harzhauser, 2012).



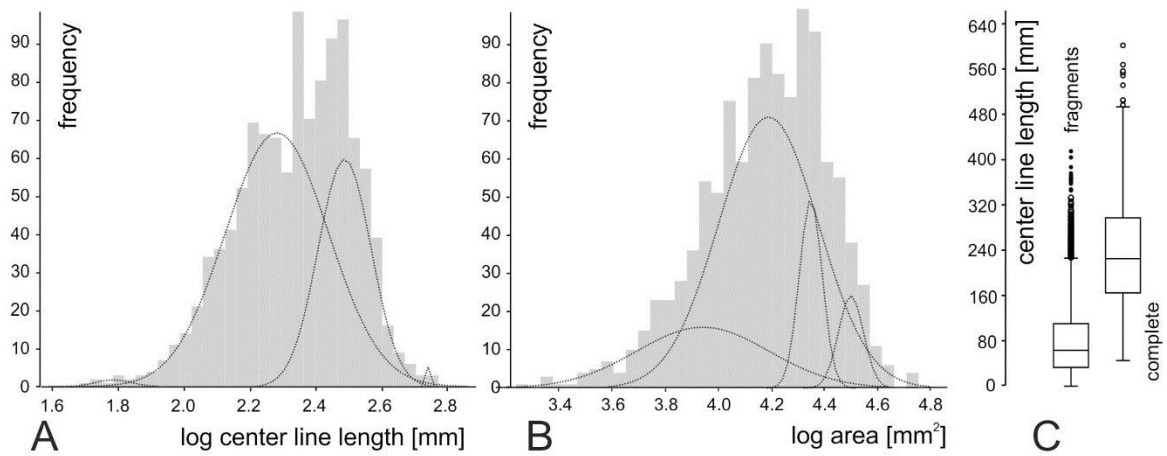
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Figure 3. Examples of the data acquisition: orthophoto and digital surface model (DSM) are used to define shell outlines manually. Together with various attributes, such as degree of fragmentation and taxon ID, these data are georeferenced in an ArcGIS database. Yellow lines in the DSM are examples of center lines.



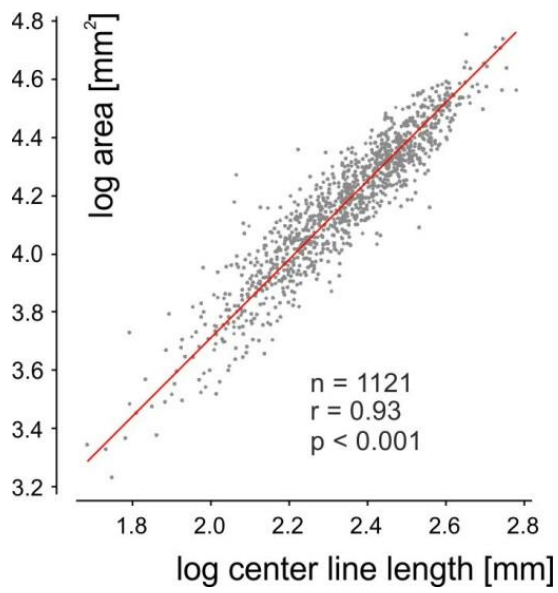
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Figure 43. Models of 6 shells based on high resolution laser scanning data of shells from the collections of the Natural History Museum. These specimens document the broad range of morphologies and were used for volume calculations; L = left shell, R = right shell.



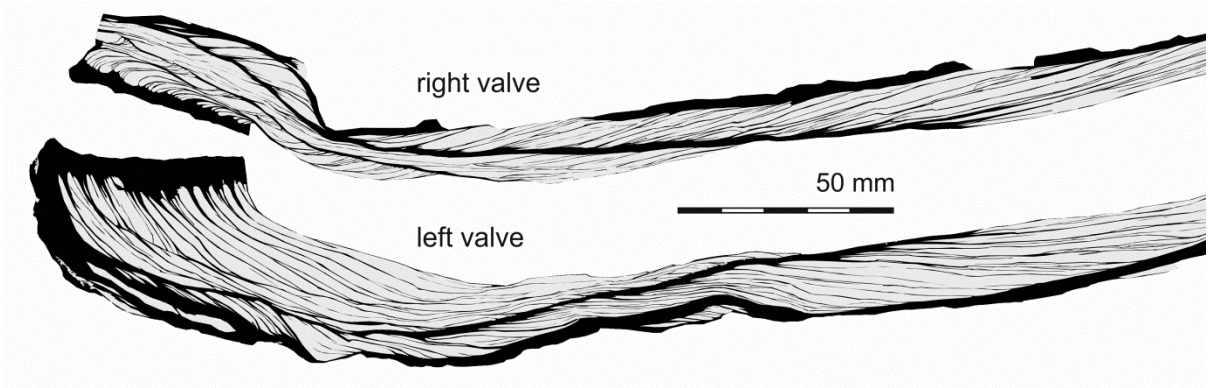
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Figure 54. Size frequency diagrams for center line length and area data (log transformed) with cohorts (dashed lines) as detected by mixture analysis (A–B). Box-plot illustrating the strongly right-skewed distribution for fragments (n=7047) and a clear separation from the size distribution pattern of complete shells (n=1121) (C).



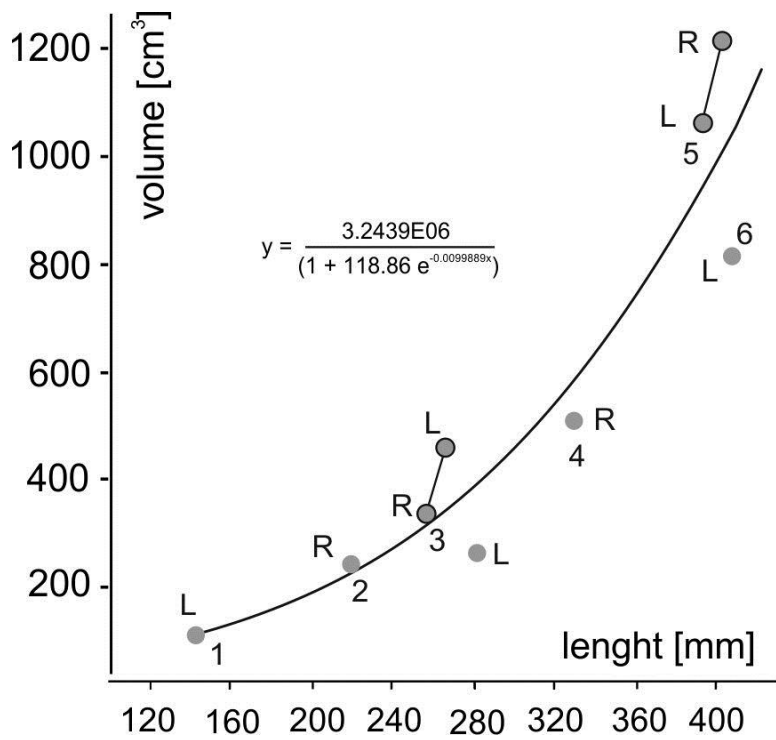
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Figure 65. Regression analysis revealing a significant correlation between length and area of complete shells.



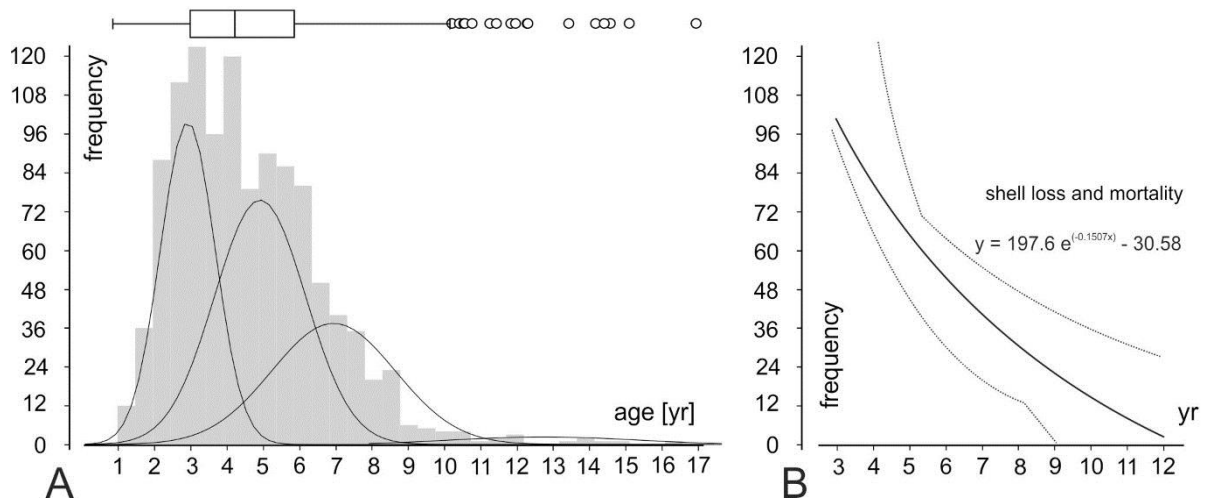
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Figure 76. Longitudinal section through *C. gryphoides* from the oyster reef site showing the high amount of chalky layers (grey) and the low amount of foliate layers (black).



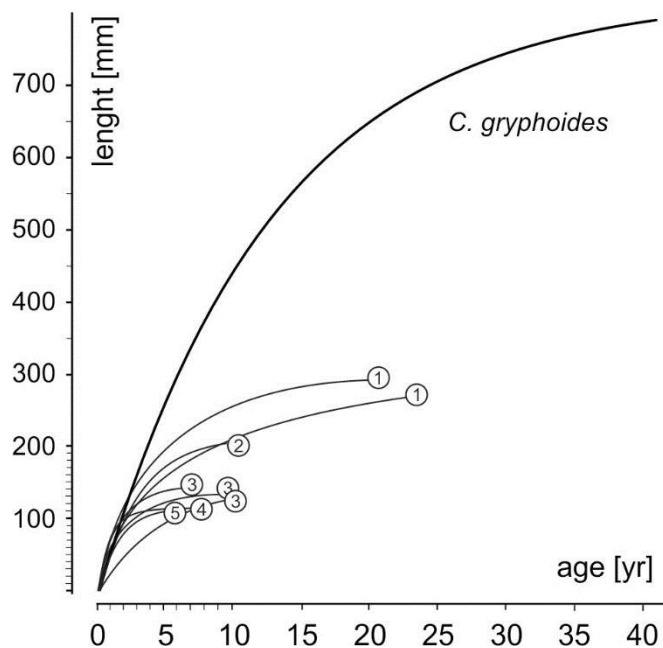
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Figure 87. Logistic function showing the relation between center line length and shell volume based on empirical measurements of 9 shells (dots); L = left shell, R = right shell; shell pairs are linked; numbers correspond to specimens illustrated in Fig. 43.



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Figure 98. Age frequency data and box-plot of the shells based on center length data transformed with the von Bertalanffy growth equation. Four cohorts are detected by mixture analysis (A). Combined effect of natural mortality and shell loss based on an exponential decay equation derived from the amplitudes of detected cohorts (dashed lines represent 95% confidence intervals) (B).



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3 | Figure 109. Comparison of von Bertalanffy growth model of *Crassostrea gryphoides* with
 4 | selected fossil and extant *Crassostrea* species. 1: *C. titan* (Conrad, 1853), Miocene,
 5 | California, USA (Kirby, 2001), 2: *C. madrasensis* (Preston, 1916), recent, Bangladesh (Nurul
 6 | Amin et al., 2008); 3: *C. virginica* (Gmelin, 1791), recent and Pleistocene Virginia, USA
 7 | (Kirby, 2001; Powell et al., 2011); 4: *C. corteziensis* (Hertlein 1951), recent, Mexico
 8 | (Chávez-Villalba et al., 2005); 5: *C. gigas* (Thunberg, 1793), recent, Marennes-Oleron,
 9 | France (Berthome et al., 1986).

10

- 1 Supplementary table: Center line length and area data for 1121 complete shells of *Crassostrea*
- 2 *gryphoides*. Age, volume, and carbonate mass data are derived from the equations discussed
- 3 in the text.
- 4 Table available online at: <http://www-biogeosciences-discuss.net/XXXX>