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Interactive comment on “Age structure, carbonate production and shell loss rate in an Early Miocene reef of the giant oyster *Crassostrea gryphoides*” *by* M. Harzhauser et al.

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Dear Colleague Ando,

Thank you very much for your constructive review. I see that your main concerns are that we spend too few words on the excavation procedure and the overall taphonomy of the shell bed. This was partly because much of these details are given in Harzhauser et al. (2015, PPP). But of course it is an easy task to add some of the information to make the paper easier to understand for the reader. In the following, I try to reply to your comments in detail (these replies will be inserted in the final version).

Detailed observation of the fossil bed and the treatment of the exposed surface before

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

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

If associated fauna is detectable, what composition? As discussed by Harzhauser et al. (2015), the assemblage is not monospecific but contains about 46 molluscan species of which Crassostrea gryphoides predominates in individual numbers (79.4%). The species, such as the potamidid gastropod Ptychopotamides papaveraceus and the venerid bivalve Venerupis basteroti, lived partly within the oyster reef or were admixed from adjacent mudflats and shallow sublittoral habitats. A detailed description of the composition, distribution and paleoecology of the accompanying taxa is given in Harzhauser et al. (2015).

Taphonomical observations on the shell bed surface, vertical and oblique sections and their unified mode of occurrence by outcrop, photo and scanned image provide more detailed information Several pictures of the shell bed are already published by Harzhauser et al. (2015) and we don’t want to repeat too much of this. But I see your point and we add an additional figure showing a detail of the shell bed with the respective digital surface model and the manual interpretation. In addition we will add:

The distribution of the shells is not uniform, occasionally featuring areas of higher shell densities, which seem to reflect former colony-like concentrations.

Figure 1: 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.

digital surface model → Refer to some paper concerned with this model. Laser scanning has triggered a revolution in topographic terrain capturing, especially in the generation of digital terrain models. Methods for generating such models from laser scanning data are discussed by Kraus & Pfeifer (2001) and references therein.

Kraus, K. and Pfeifer, N.: Advanced DTM generation from LIDAR data, International Archives Photogrammetry Remote Sensing and Spatial Information Sciences, 34(3/W4), 23–30, 2001.

complete shells → How identified? How complete? Four categories of fragmentation were used: complete shells are fully preserved or display only minor damage, which might have occurred already during the life of the animal (n = 1121). The category low fragmentation comprises shells in which not more than $\frac{1}{4}$ of the assumed length is missing (n = 951). Moderate fragmentation is defined by representing at least $\frac{1}{2}$ of the original shell lengths (n = 1638). The category high fragmentation comprises 4458 specimens of strongly damaged shells representing less than $\frac{1}{4}$ of the complete shell. Note that the attribute fragmentation does not contain any information on abrasion

As the purpose(s) of this paper is (are) not described in the last part of introduction, it had better add a few purposes suggesting the significance and importance of this paper.

Crassostrea reefs flourished during the Miocene within the tropical reef belt (Mandic et al., 2004) but were also successful in more northern latitudes (Wiedl et al., 2013;

Harzhauser et al., 2010). Therefore, the main purpose of this paper is to quantify the growth performance of the Miocene giant oyster and to reveal its significance as part of the Miocene "carbonate factory". Moreover, we test if size frequency data deduced from fossil oyster shells allow a comparison with community structures of extant Crassostrea reefs. Wiedl, T., Harzhauser, M., Kroh, A., Ćorić, S., and Piller, W. E.: Ecospace variability along a carbonate platform at the northern boundary of the Miocene reef belt (Upper Langhian, Austria), Palaeogeogr. Palaeocl., 370, 232–246, doi: 10.1016/j.palaeo.2012.12.015, 2013.

Paragraphs in section "3.3 Length frequency data" seem to be ambiguous about the aim and not so well organized in context. At least it had better mention these data treatments and their significance clearly, referring to figures. In our opinion, the method of how to acquire the length data is discussed in chapter "3.2 Shell length and area". To make it more obvious, we will indicate the automatically measured shell lengths in the new figure and add a short sentence in the chapter 3.3: For extant Crassostrea reefs, the analysis of the cohorts is routinely performed using Bhattacharya's model or the EM-Algorithm of Dempster et al. (1977), which tries to detect normal distributions within the length–frequency data. For this purpose, the shell lengths data are presented in histograms, revealing the frequency of certain size classes within the dataset.

The manuscript will be acceptable after careful and moderate English corrections. We will send the final version for a review by a native speaker biologist.

The reviewer provided several additional comments on minor mistakes or ambiguous sentences. Most of these comments are self-explanatory and will not be discussed here in detail. We will accept the suggestions of the reviewer in the final version. Some points, however, need to be addressed here:

Crassostrea reef versus Crassostrea shell bed: We will refer to the excavated site as "shell bed" and will restrict the term "reef" to the biotic structures.

"geotainment park" We agree that this term is not widely used and replace it by "geopark"

Miocene Climatic Optimum We will include appropriate references: Zachos et al. (2008) and Goldner et al. (2014).

Goldner, A., Herold, N., and Huber, M.: The challenge of simulating the warmth of the mid-Miocene climatic optimum in CESM1, Clim. Past, 10, 523–536, doi:10.5194/cp-10-523-2014, 2014. Zachos, J. C., Dickens, G. R., and Zeebe, R. E.: An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics, Nature, 451, 279–283, doi:10.1038/nature06588, 2008.

certainly not conspecific with the European fossil species – why? We already summarized the morphologic differences: The recent species differs in its more regular and elongate ovoid outline (Durve and Bal, 1960), the short and bean-shaped adductor muscle scar (Durve, 1974; Siddiqui and Ahmed, 2002) and in being more inequivalved. But we will replace "certainly" by "most probably".

Ad recent Crassostreinae: What are "both groups"? What is the Asian Pacific group? We agree that this part might be confusing. Therefore, we clarify this by adding species names for each group and replace "both" by Asian–Pacific versus Atlantic Crassostreinae species. Asian-Pacific group (e.g.: C. gigas, C. plicatula, C. ariakensis) and Atlantic group (e.g.: C. virginica, C. rhizophorae, C. gasar).

Though mentioned with no formal description in Salvi et al. (2014), how do you refer to "a description of the type species". We replace "description" by "designation" because Salvi et al. clearly designated the type species.

Predatory and hydrodynamic breakage looks different on the fracture property? How about artificial excavating works during making flat bedding surface? It is beyond the scope of this study to analyse the ratio between predatory and hydrodynamic breakage. In many cases it would be impossible to separate between both types. Therefore, we

included both terms.

manual outlines - What mean? & Area data - How do you get the areal data? shell margins, which comprise about 1000 points on average. What kind of points? Manual outlines are vector datasets in form of manually digitized polygons representing the boundaries of the identified specimens. They are created as thematic layer in an ArcGIS environment. The polygon is defined by features such as points (i.e. vertices connected with lines). Each polygon is a 2D visual representation of the manually digitized specimen from the adequate orthophoto and its corresponding digital surface model. Further, manually digitized data are organized into a table. This tabular structure has its elements, i.e. numerical and descriptive attributes. For instance, numerical attributes are ID, length, orientation, etc. Descriptive attributes are Taxon, side (left, right, unknown), state of preservation (complete, low, moderate, high fragmented), etc. The outline data are composed of about 1000 virtual points (nodes) on average per object and are also stored in the georeferenced ArcGIS database. These allow an automatic calculation of the surface area of each object by using The Calculate Geometry tool.

What the boundary? Why the edges are the . . . transform? What is this tree? The method of transforming the outline data into length data is described in detail by Harzhauser et al. (2015). The figure given below might help to understand the basics: shell length and area were evaluated by using the manually digitised outlines, which are based on the natural shell margins (see above). For each shell, this outline point number was reduced to 100 and then filtered to points with close to even spacing. In a next step, a Delaunay triangulation was calculated between the filtered outline points (Delaunay, 1934), constrained by the edges between the outline points. To find the center line for each oyster outline, the Voronoi diagram was formed (Voronoi, 1908) from the triangulation. The edges between neighboring Voronoi vertices within the boundary are the medial axis transform (MAT) for the oyster outline (Aichholzer et al., 1996). The longest path in this tree was found using Dijkstra's algorithm between MAT end points (Kirk, 2015).

Figure 2: constrained Delaunay triangulation (blue) and Voronoi diagram (red) of an oyster outline (green) with Voronoi vertices (cyan dots).

The Voronoi diagram (VD) is a dual of the Delaunay triangulation meaning that they present the same graph in different manner. Therefore, t the vertices of the DT (outline points) are nodes of the Voronoi diagram. Dualism between the DT and the VD means also that the circumcenters of the DT (center point of a circle passing through all DT vertices) are vertices of Voronoi regions. Here, the Voronoi vertices within the oyster boundary are shown with cyan colour. By taking the edges (blue lines) between the Voronoi vertices (cyan) within the boundary, the medial axis transform (MAT)* of the oyster is deduced. * The medial axis of an object is the set of all points having more than one closest point on the object's boundary. Originally referred to as the topological skeleton, it was introduced by Blum (1967) as a tool for biological shape recognition.

The MAT is also a connection map between the Voronoi vertices. To determine the longest path in the connected tree, the edge points (red) in it were selected. In the final step, the longest path and its length were determined by applying Dijkstra's algorithm* between all edge points in the connected tree. *Dijkstra's algorithm is an algorithm for finding the shortest paths between nodes in a graph or tree, which may represent, for example, road networks.

Blum, H.: A transformation for extracting new descriptors of shape, edited by Weiant, W.-D., Models for the perception of speech and visual form, Publisher MIT Press, Cambridge, 362–380, 1967. Aichholzer, O., Aurenhammer, F., Alberts, D., and Gärtner, B.: A novel type of skeleton for polygons, Springer, Berlin, Heidelberg, pp. 752–761, 1996. Voronoi, G.: Nouvelles applications des paramètres continus à la théorie des formes quadratiques. Deuxième mémoire. Recherches sur les parallélloèdres primitifs, J. reine angewandte Mathematik, 133, 97–178, 1908.

What is the difference between shell length (line 7) and centre line length? Centre line

length is the term used in photogrammetry and aims for capturing the real shell length as far as possible. Here it is an imaginary curved line spanning the maximum length of the shell. The advantage of this method is that the center line will approximate the "real" lengths of the curved and irregularly shaped shells much better than any manual attempt in the field.

What does "perpendicular convex ridges and concave furrows" mean? These terms are frequently used in describing the hinge of Crassostrea species (e.g. Kirby 2000, 2001). To avoid misunderstandings we will change this part into: The ligamental area of these Crassostrea species is typically structured by alternating transversal, growth ridges and furrows, oriented perpendicular to growth direction. The specimens from the Stetten site lack such well-defined ridges.

the taphonomically active zone we add a reference, which explains this term: Olszewski (2004) Olszewski, T.: Modeling the Influence of Taphonomic Destruction, Reworking, and Burial on Time-Averaging in Fossil Accumulations, Palaios, 19, 39âĂŤ50, 2004.

Thanks again for your careful review!

best regards Mathias Harzhauser

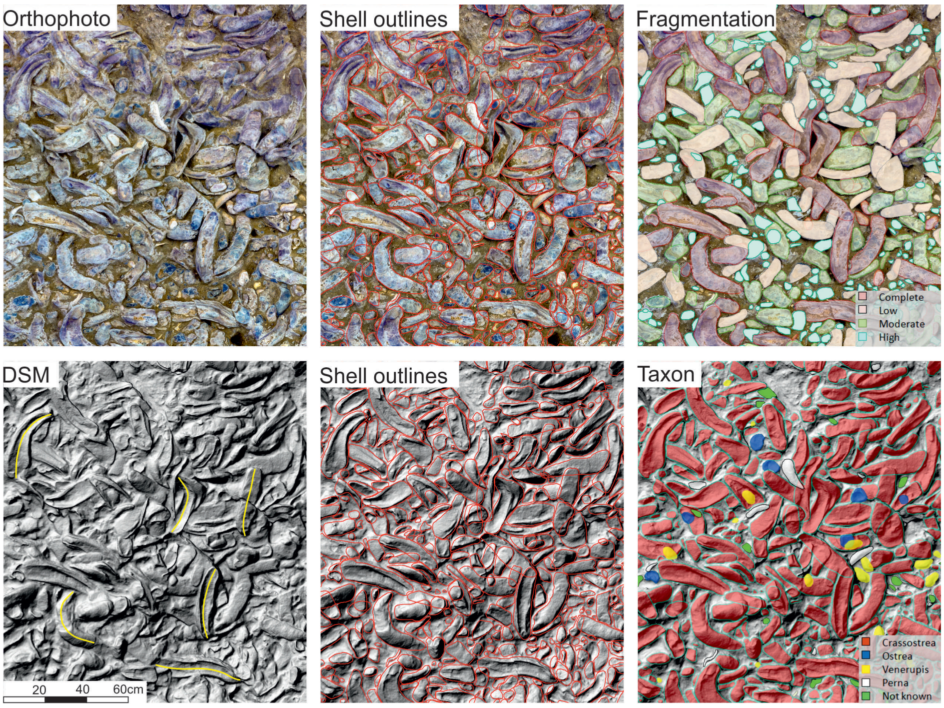

Fig. 1. Figure 1

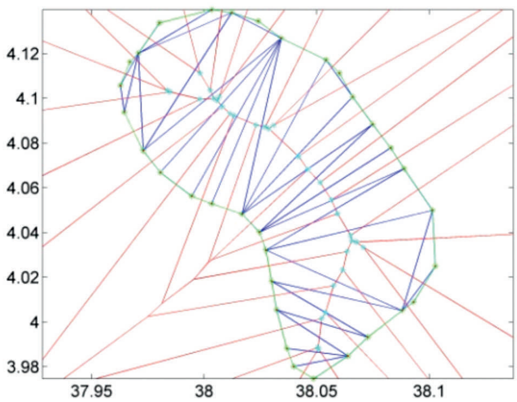

Fig. 2. Figure 2