REVIEWER 3

This paper presents an exceptionally well documented case study of a phenomenon rarely seen in modern environments but common in the deep time fossil record: pyrite formation within shells. The authors present a wealth data on the relative frequency and association of pyrite with other taphonomic indicators of residence time and also provide data on the actual ages of the shells based on amino-acid racemization. The results provide a powerful case for the development and preservation of pyrite in closed spaces of dead organisms and shows that pyrite linings are most frequent in areas of higher sedimentation rates and slow mixing or bioirrigation. The authors even present data that indicate an upward increase in pyrite formation within shells of the later 20^{th} century that parallels evidence for increased eutrophication owing to anthropogenic activity. In fact, the presence of pyrite may be a more sensitive indicator of sluggish rates of bioirrigation than ichnofabrics. The paper is extremely well written, well organized and thoroughly referenced. And supported by a large data set and thorough statistical analysis. I noted only a few minor errors in the text and references, which are marked on the pdf. I also have the following queries, mainly out of interest in the subject; I refer to relevant line numbers. The authors may wish to comment on them.

Line 75. Here and elsewhere, throughout, the term “microniches” is not quite right; perhaps “microenvironments” is preferable.

Response: We thank the reviewer for all critical comments. We have replaced microniches with microenvironments (although “microniche” is frequently used in titles of several references about this topic).

183, see also 613.: this paragraph well explains the tight closure of Varicorbula valves. But is there a reason that Varicorbula shells remain closed after death instead of splaying open at the hinge ligaments as do most bivalves? Does the ligament groove serve as a sort of locking devise? This may explain why they are most frequently pyrite lined. Perhaps a brief discussion of comparative taphonomy of these clams would be useful here.

Response: We assume that these shells were located in the uppermost sediment zones in the upper 3 cm after their death, i.e., their disarticulation would be partly acting against sediment at their living locations. Although we did not perform experiments to check how much does the groove and the periostracum overlap increases the strength of articulation, it seems that these traits, including the option that the groove locks valves to some degree after the death, can provide some buffer against disarticulation. In addition, *V. gibba* possesses a relatively small internal ligament that, as in other members of the superfamily Myoidea, generates a small opening moment that is not sufficient to open valves against the sediment pressure (Trueman, 1954, Yonge, 1982).

We have added this information in the Discussion as follows: “*Therefore, tightly-articulated shells of V. gibba with low opening moments of a small internal ligament that can be insufficient to open valves against the sediment pressure (as in other members of the superfamily Myoidea, Trueman, 1954; Yonge, 1982) and with internal conchiolin layers and can be intrinsically susceptible to the formation of reducing conditions.”*

180s and 480s: Alternatively, do these clams frequently perish within their burrows as opposed to many that seem to rise to the surface during mortality. Under such conditions, burial within sediment may not require obrution, but I do not think this applies to most other articulated and closed bivalves let alone completely articulated multi-element skeletons.

Response: It would be great to know an answer to this question – laboratory experiments showed that during an anoxic/hypoxic event, *V. gibba* emerges to the surface, as most other invertebrates. However, when the source of mortality is not related to oxygen depletion, and is rather related to predation (qualitative observations indicate that this is one source of mortality as many articulated shells are also drilled), then we assume that the scenario with the initial location occurring in the sediment is possible. As we mentioned above, several intrinsic traits and/or this within-sediment effect could ultimately reduce probability of disarticulation and thus lead to relatively high frequencies of articulated shells, although it is difficult to disentangle these effects at this stage (as many of these shells are in the uppermost cm, we think that articulation cannot be explauned by rapid burial to deeper sediment levels by some episodic event).

319-320: how is it that pyrite formation does not set in until after 10 years in the sediments? If, as assumed the development of sulfides is associated or at least initiated with decay of organic matter contained within the enclosed spaces of shell cavities. But one would guess that such OM should be largely gone after just a year or so. Is the issue that the initial sulfides are monosulfide gels that only later recrystallize to recognizable pyrite?
Response: This part refers to median ages, not to minimum ages, and the mode is younger than 10 years - primarily indicating yearly scales of pyrite formation – in other words, the pyrite formation can most likely occur almost immediately after the death of V. gibba. In Discussion, we have added: "*Age distributions of valves with and without pyrite linings show right-skewed shapes in the mixed layer at prodelta sites, with median age equal to 7-10 (without pyrite) and 7-18 years (with pyrite linings) at Po (in the upper 20 cm) and to 11 (without pyrite) and 15 years (with pyrite linings) at Panzano (in the upper 6 cm), respectively (Fig. 10A-F). They are dominated by recentmost cohorts younger than 10 years."*

349: it seems odd that shells with periostracum preservation should be negatively correlated with pyrite linings as one would suspect both might indicate higher rates of burial and reduced decay.
Response: This was our mistake, the frequencies of pyrite-lined valves correlate positively with the frequencies of valves with periostracum correlate positively (negatively with the frequencies of valves without any periostracum). We have revised this sentence as follows by revising "without any relicts": *"First, per-increment frequencies of pyrite-lined valves rank correlate negatively with the frequencies of disarticulated shells (Fig. 11A), with the frequencies of valves without any relicts of periostracum or conchiolin layer (Fig. 11B-C),..."*

385: this result: increased borings in the HST vs. TST seems paradoxical as sedimentation rates are normally predicted to increase into the later HST. Any explanation?
Response: The temporal dynamic in accommodation/sediment supply ratio in the NE Adriatic with low sediment input (with the exception of sites close to river input) and sediment winnowing (and shedding towards deeper basinal part) is complex and sediments deposited during the latest highstand phase were at some locations affected by strong winnowing (related to the counterclockwise current system that fully developed in the northern Adriatic Sea during the highstand phase), leading to very thin/condensed sediments (and the input of clastic was partly compensated by in situ production of heterozoan carbonate particles). At regional scales, the highstand phase is thus represented by a thin condensed wedge – that is locally even thinner than the transgressive portion. However, the transgressive units tend to show retrogradation at large scales, whereas the

thin HST units tend to show aggradation. In Methods, we have added this information that can clarify this complexity: "*We note that the net sedimentation rates at Piran and Brijuni (affected by negligible clastic sediment input and by significant contribution of in situ heterozoan carbonate production) were very slow and did not increase relative to the condition during the transgressive phase (it did not lead to the formation of prograding sediment bodies during the highstand phase)."*

Is it also possible that anthropogenic activity is related to increased rates of runoff and therefore, faster burial of organisms?

Response: This scenario is possible to some degree at Pirand and Brijuni where the 210Pb profiles uppermost 10-20 cm show that the 20^th^ century sediments , but long-term estimates of sediment accumulation rates do not indicate this scenario at Po and at Panzano. In Methods, we have expanded our description of temporal variability in sedimentation rate within sites as follows: "*Upcore changes in median shell age show that sedimentation rates moderately oscillated through time and do not show any increase in the uppermost levels that correspond to the late 20th century. The within-site variability in sedimentation rates is smaller than the marked variability among sites. Sedimentation rates fluctuated between ~1 and 2.4 cm/y during the 20th century at Po sites (Tomašových et al., 2018) and between ~0.2-1 cm/y over the past 500 years at Panzano (Gallmetzer et al., 2017; Tomašových et al., 2017)."*

Lines 443-445. This is a very interesting finding in line with observations of iron sulfide blackened shells in ancient assemblages in which there is a strong positive correlation between other taphonomic indicators of long residence time and darkening: Kolbe, S., Zambito, IV, J.J., Brett, C.E., Wise, J.L., Wilson, R.D., 2011. Brachiopod shell discoloration as an indicator of taphonomic alteration in the deep-time fossil record, Palaios 26: 682-692.

Response; We have added to the Discussion: *"A similar relationship with darkened specimens enriched in minerals possessing iron sulfides being more damaged by disarticulation, bioerosion and encrustation in contrast to specimens less affected by discoloration was observed by Kolbe et al. (2011) in Ordovician brachiopods."*

480-onward. The result that shells of the same age may or may not show pyritization does not seem necessarily to support the contention that the pyritization occurred gradually during normal burial rather than during burial events. It is certainly possible that pulses of burial could entomb not only live or recently dead individuals, but many others that had died and decayed prior to the event. Pyrite would be localized in those that were buried with soft tissues intact whereas the "dead shells" would show little tendency toward sulfate reduction or pyrite formation.

Response: We expect that this scenario with burial pulses would actually generate two distinct age distributions of valves with and without pyrite – with valves without pyrite characterized by older age (and thus slower burial rate), i.e., they spend longer time close to the sediment-water interface or within the mixed layer than living or recently-dead shells. To clarify our reasoning, we have added this statement in the Discussion: "*A single episodic burial pulse that mixes living or recently-dead shells (with decaying biomass and potential for framboid formation) with older shells (without biomass) will generate one age distribution of valves with pyrite linings dominated by younger cohorts and another age distribution of valves without pyrite linings dominated by older cohorts whereas Under mixing, age distributions will be smoothed by stochastic movement of valves, but age distributions of valves wit pyrite linings* *should be steeper and their median ages should be still lower, in contrast to our observations both at Po and Panzano."*

When episodic burial occurs frequently, temporal accuracy of dating methods can affect this inference. However, this scenario with episodic burial would also propagate to generally higher sedimentation rate in the upper parts of sediment cores at Po and Panzano where pyrite-lined valves are more frequent – but net sedimentation rates do not increase upwards.

We ultimately prefer the scenario without rapid burial (and we find it useful to attempt to use the alternative represented by low bioirrigation, even when conceptually these two scenarios are not mutually not exclusive) because individual flood events occur at decadal scales (thus infrequent relative to ages of pyrite-lined valves that seem to form annualy), their frequency did not change during the 20th century, and the mixing that still occurs would make the initial phase of rapid burial ultimately unimportant because shells reworked up would be oxidized. We have revised and expanded this part in the *Discussion* as follows: "*Distinct layers deposited by major decadal floods preserved in cores at Po prodelta (Tesi et al., 2012; Tomašových et al., 2018) may have triggered episodic burial of benthic communities, but similar flood-event layers were not detected at Panzano. However, first, the major discharge events that lead to the deposition of flood deposits occur at decadal scales at Po prodelta (seven events during the 20th century, Zanchettin et al., 2008), whereas age distributions of pyrite-lined valves indicate that pyrite linings form almost every year. The frequency of flood events did not increase during the 20th century, in contrast to the increasing frequency of pyrite-lined valves. Second, pyrite-lined valves younger than 10 years old occur in the uppermost 5-10 cm of the mixed layer close to the sediment-water interface. Their high abundance in the uppermost zones indicates that they do not represent transient valves that were just recently exhumed from deeper zones. Although mixing after the deposition of thin flood layers can rework some subset of valves upward, exhumation of initially-buried valves to oxic conditions would lead to removal of pyrite linings. Third, equally-old valves with and without pyrite linings occur at similar depths and age distributions of pyrite-lined valves and valves without pyrite at Po and Panzano are similar (Fig. 9A-F), indicating that valves with and without pyrite were buried below the mixed layer at the similar rate. A single episodic burial pulse that mixes living or recently-dead shells (with decaying biomass and potential for framboid formation) with older shells (without biomass) will generate one age distribution of valves with pyrite linings dominated by younger cohorts and another age distribution of valves without pyrite linings dominated by older cohorts whereas Under mixing, age distributions will be smoothed by stochastic movement of valves, but age distributions of valves wit pyrite linings should be steeper and their median ages should be still lower, in contrast to our observations both at Po and Panzano. Although multimodal whole-core age distributions and stratigraphic changes in abundance indicate that input rates of V. gibba were not constant over the duration of core deposition at all sites (especially increasing in abundance after~1950 AD, Tomašových et al., 2018), the burial-rate parameter based on the exponential model (assuming the temporally-constant input of V. gibba) can be realistic when based on the topcore increments characterized by yearly to decadal time averaging at Po and Panzano (i.e., these increments were deposited after the mid-20th century increase in dominance by V. gibba). The pyrite framboids thus did not preferentially form within valves that were rapidly buried deeper in sediments (either by new* *sediment deposition or by burrowers) as predicted by the obrution scenario and rather precipitated in near-surface sediment levels naturally inhabited by V. gibba."*

559 - this observation (of loss of Fe from sediments under persistent anoxia) is very important, as it may help explain the absence of pyritized fossils in truly black, laminated sediments that we have documented repeatedly (see Brett, C.E., Dick, V.B. and Baird, G.C.,1991. Comparative taphonomy and paleoecology of Middle Devonian dark gray and black shale facies from western New York. In Landing, E. and Brett, C.E., eds., Dynamic Stratigraphy and Depositional Environments of the Hamilton Group in New York Pt. II. State Museum Bulletin 469, p. 5â'36.) One implication is that, while eutrophication and increased organic matter may enhance pyrite formation up to a point (because of lower benthic O_2 and reduced bioirrigation); too much OM may shut down the process.

Response: We note that another subset of this dynamic is that mixing of particles by burrowers (i.e., the subset of bioturbation that does not necessarily irrigate the sediment) enhances the development of the suboxic iron-rich zone. To follow this comment, we have expanded the Discussion in 5.2 as follows: At the end of section 5.2., we have revised our discussion of anoxic scenario, as follows: *"If the nutrient-fueled eutrophication or other sources of sediment organic enrichment lead to permanent anoxia of bottom waters and high sulfate reduction, the concentrations of pyrite framboids within shells will be prohibited because sulfide production by bacterial sulfate reduction in organic-rich sediments can exceed in-situ availability of reactive iron oxides, H_2S diffuses and precipitates elsewhere (Raiswell and Berner, 1985; Schenau et al., 2002; Raiswell et al., 2008; Farrell et al., 2009). Iron limitation can be driven by iron bounded to framboids linked to disseminated organic matter under high sediment organic enrichment but also to release of ferrous iron from sediments to water column (if water column is not sulfidic, Pakhomova et al., 2007). In addition, as mentioned above, mixing of sediments by burrowers that underlies the iron-based redox shuttle is aborted under anoxic conditions, and iron-limitation in pore waters is thus further enhanced by the lack of bioturbation. The absence of pyrite linings in anoxic sediments documented in the deep-time stratigraphic record (e.g., Brett et al., 1997) indicates that in marine environments with persistent bottom-water anoxia, the window for the early and rapid formation of pyrite linings (e.g., within shells of nektonic groups as cephalopods that fell on the anoxic seafloor) will be closed when organic matter degradation in surface sediments leads to the excess of hydrogen sulfide."*

570: forgive my ignorance, but I do not understand your use of **hysteresis** here. Perhaps explain a bit.

Response: Hysteresis corresponds to non-linear ecosystem dynamic that generates alternative stable states under the same environmental conditions. We have added parenthetically into the Discussion: "*... can remain in a hysteresis state (non-linear ecosystem dynamic that generates alternative community states occur under the same environmental conditions, Duarte et al., 2015). For example, ecosystems subjected to eutrophication shift to a new state under some specific nutrient loading, but when recovering from eutrophication, the pre-eutrophication state is not established until the nutrient loading is reduced to a much lower level relative to the level that forced the shift initially. Some observations of recentmost oligotrophication in the northern Adriatic Sea (Mozetic et al.; Djakovac et al., 2012, 2015)* *coupled with the continuing dominance of V. gibba in soft-bottom habitats indicate that the soft-botom communities, initially disturbed by high frequency of hypoxic events, is to some degree in hysteresis (Tomašových et al., 2020).”*

577: it is not intuitive that large size would be associated with lowered oxygen levels (resulting from eutrophication); in many cases low oxygen has been attributed to stunting and diminutive organisms. Apparently in Varicorbula the stunting affect is offset by increased growth. Presumably this is well documented; a reference might be useful.
Response: The increase in size reflects the indirect effect of ecological release coupled with higher tolerance of V. gibba to short-term hypoxic or anoxic events. V. gibba is also negatively affected by anoxia, but this species is able to grow to larger sizes in the wake of those events, in contrast to conditions without any hypoxic events.

613: but why do these bivalves not open shortly after death? If they are not buried rapidly (episodically) then how do they come to remain tightly closed?
Response: Of course, shells buried themselves during their life, but we refer to the absence of additional postmortem burial. We assume that these shells were located in the uppermost sediment zones in the upper 3 cm after their death, i.e., at their living locations. *V. gibba* possesses a relatively small internal ligament that, as in other members of the superfamily Myoidea, generates a small opening moment that is not sufficient to open valves against the sediment pressure (Trueman, 1954, Yonge, 1982).

Line 635: this also contrasts with nanopyrite infillings that seem to increase together with other signs of degradation with residence time.
Response: yes, we have modified this sentence to:*“Pyrite-lined valves thus represent a unique type of alteration that contrasts with other types of alteration (including the frequency of stained valves with nanopyritic inclusions) whose incidence increases with residence time in the taphonomic active zone”*

Illustrations are fine and require no modification.

References I have gone through and highlighted all that appear to be correctly cited; most are fine but there are a number of minor problems:
The following are **slightly out of alphabetical order:** Briggs et al. 1991., Boyle, Bjereskov, Degobbis. Meysman, Schieber 2012 (should come before Schieber and Baird)
Response: Fixed

Wrong date
Brush et al. 2020 (2021 intext) **Fixed to 2021**
Kralje et al. 2019 (2020 in text) **Fixed to 2019**
Slagter et al. 2021 (2020 intext) **Fixed to 2021**
No date (in ref list) Hunda et al. [2006] **Fixed**

In reference list but apparently not referenced in text:
Aller, 1982 **Added to main text**
Arcon et al. 1999 **Added to main text**
Clark ad Lutz, 1980 **Removed**

Eliott et al. 2007 **Added to main text as Elliott**
Faganeli et al 1985 **Added to main text**
Palinkas et al. 2007 **Added to main text as Palinkas and Nittrouer 2007**
Powell and Stanton 1985 **Removed**

Cited in text but not in reference list:
Alvizi et al. 2016 **Added to main text**
Stanton and Powell, 1985 **Removed from the main text**
Wignall et al., 2010 **Added to main text as Bond and Wignall 2010**

Need to designate a and b references in text:
Tomašovych 2019 a vs. b
Response: Fixed

Overall: this is an excellent paper, which needs only minor revision for publication. The paper provides much new data and reaches important conclusions regarding the little known phenomenon of early diagenetic pyritization; it has important implications for sedimentation rates and rates of bioirrigation, for the taphonomy of exceptional fossils, and potentially for conservation paleobiology and evidence for anthropogenic effects. The results will be of interest to geochemists, sedimentologists, taphonomists, paleobiologists and perhaps conservation paleobiologists. I strongly recommend publication with slight correction.