Discussion

Further comments on the origin of oysters

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In his comment to our recent paper (Márquez-Aliaga et al. 2005), Hautmann (2006) raises two interesting questions: (a) the ambivalent attachment to the substrate recognized in the species cristadiformis Schlotheim, 1820 and spondyloides Schlotheim, 1820, which we include into the Ostreoidae genus Umbrostrea, is in conflict with the sinistral attachment usually recognized as an autapomorphy of the group and (b) antimarginal ribs are not valid as a character linking Prospondylus acinetus Newell and Boyd, 1970 and early oysters (our proposal of derivation), because they appear in several unrelated families of bivalves. Moreover, Hautmann (2005), finds additional difficulties in accepting our hypothesis of descent of oysters from the Prospondylidae because, contrary to the latter group, (c) oysters, in general, do not develop a pallial line; (d) the resilifer of the right valve is in high relief and flanked by two depressions and the ligamentary area of the left valve impresses such shape; (e) the microstructure of the inner shell layer of prospondylids (crossed-lamellar) is different from that of early oysters (probably nacreous); (f) too few data are known from the internal morphology of the Japanese and Chinese forms, which we attribute to Prospondylidae gen. indet., to be considered the closest to earliest oysters.

While acknowledging Hautmann for his constructive critique, we would like to additionally comment on some of them while disagreeing with others:

(a) Recognition of autapomorphies permits the clear-cut definition of clades. Our proposal to include ambivalent forms in Ostreidae somehow alters the present-day well-defined concept of oysters. We adopted our position by taking into consideration that it does not affect the accepted monophyly of the clade (but see Malchus, 1990, regarding Cenozoic Lophinae) and the lack of knowledge on the evolution of oysters through the Permian–Triassic transition. Future progress in this subject will allow more formal aspects generic and familial assignment for these early oysters.

(b) Antimarginal ribs were recognized in several bivalve families, but we also established the clear morphogenetic difference between the antimarginal ribs of oysters, plicatulids and dimyids, which affect the whole shell thickness, and those of other bivalves, in which ribs are restricted to the...
outer shell layers (Checa and Jiménez-Jiménez 2003, p. 147). We determined that ribs of oysters, plicatulids and dimyids basically form by a process of folding of the mantle margin and that these groups are the only ones among present-day bivalves sharing that morphological, as well as morphogenetic, trait. Differences in the microstructure and hinge-ligament structure allow us to also differentiate two independent clades (Ostreidae and Plicatulidae+Dimyidae). Recognition of an oyster-like ribbing pattern in *Prospondylus acinetus* and other indeterminate Late Permian Prospondylidae link these groups with oysters (see additional data in Márquez-Aliaga et al., 2005). Without further explanation, Hautmann (2005) disregards the relevance of antimarginal ribs in bivalve evolution.

(c) We thank Hautmann for attracting our attention to this point. Certainly the transition from *P. acinetus* to early oysters involved loss of the pallial attachment. This transition covered a wide time span and there are surely species involved, which are yet to be discovered. Liberation from its attachment to the shell margin enables the oyster mantle to extend or contract to a high degree, which might be useful for, e.g., the periodic secretion of the extensive lamellae usually found on both valves. As mentioned by Hautmann, *P. acinetus* still shows a pallial line, but we want to stress that it is very internal within the shell (see Newell and Boyd, 1970, Fig. 20C). Internalization of the pallial line in *P. acinetus* (and in the Prospondylidae, in general) may represent a first step towards the acquisition of a widely extensible mantle, enabling this and other species of the Prospondylidae to secrete their extensive shell lamellae. Nakazawa and Newell (1968) recognized adductor muscle imprints, but no traces of a pallial line in some specimens of *Lopha? murakamii* (which we instead assign to Prospondylidae and find to be intermediate between *P. acinetus* and oysters). Therefore the pallial attachment might have already been lost in these Late Permian forms.

(d) In general this is a highly variable character in oysters. In our collection of Cenozoic oysters, the resilifer of the right valve varies from elevated to flat to depressed within single species (Fig. 1A, B). This change in shape also affects the lateral elevations of the resilifer. The resilifer of the left valve is always depressed. Interestingly, good examples of right valves with depressed resiliifers can be appreciated in the specimens of *Umbrostrea emamii* figured by Hautmann (2001, Plate 6, Fig.13, Plate 8, Figs. 2, 4, 5, 7). In view of this highly intraspecific variability, we find the alivincular-arcuate ligamentary area of Hautmann (2004) hardly tenable as an autapomorphy of oysters. Additionally, the right resilifer of the recent gryphaeid genus *Neopycnodonte* is always low relief (Fig. 1C).

(e) This aspect was discussed at length in our original paper. In short, the only reliable data on the microstructure of the Prospondylidae come from two species of the Triassic genus *Newaagia* (Carter, 1990; Hautmann, 2001). The statement that “prospondylids also differ in the crossed-lamellar layer microstructure of their inner shell layer from Triassic ostreids, in which the aragonitic shell layer was probably nacreous” Hautmann (2005) is based on the assumptions that (1) the microstructure of *Newaagia* represents the general condition in Prospondylidae (note that Carter, 1990, related *Newaagia* with pectinoideans, rather than with the Pseudomonotidae) and (2) the same applies to the Carnian specimen UNC.

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Fig. 1. Examples of depressed resiliifers of the right valve in Neogene oysters and gryphaeids. (A) *Ostrea lamellosa* Brocchi, Lower Pliocene, El Alquián, Almería, Spain. (B) *Hyotissa hyotis* (Linnaeus), Lower Messinian, La Mela, Almería, Spain. (C) *Neopycnodonte navicularis* (Brocchi), Lower Pliocene, El Alquián, Almería, Spain. Specimens reposited in the Departamento de Estratigrafía y Paleontología, Universidad de Granada; scale bars = 1 cm.
13497b of Carter (1990) with regard to early oysters. More data are still needed to make this a useful character in ostreid phylogeny. 

(f) From the exterior of the valves we concluded that both the Late Permian specimens from Japan described by Nakazawa and Newell (1968) as *Lopha?* and the Dzulfian Chinese specimens classified as *Enantiostreon* by Xu (1976) were dextrally attached to the substrate from early postlarval stages and had a typical oyster-like rib pattern. This alone certifies intermediate placement between *P. acinetus* and oysters.

Finally, Hautmann (2005) states that we prefer derivation of the Ostreidae, instead of the Plicatulidae, from the Prospondylidae. Obviously, the two possibilities are not mutually exclusive. We do not understand why he goes into the origin of the Plicatulidae, because this is briefly alluded to in the introduction of our paper with reference to a previous report (Checa et al., 2003) in which we advanced preliminary results of an ongoing research. To sum up, we confidently placed both the species *flabellum* (formerly an *Enantiostreon*), from the Ladinian of Spain, and, most likely, also *matercula* (previously within *Placunopsis*), from the Lower Muschelkalk of Germany within the plicatulid genus *Pseudoplacunopsis*. Accordingly, the record of this genus and family can be extended back to the Anisian (see also Checa and Jiménez-Jiménez, 2005) and thus predates the early records of *Eoplicatula* (Carnian) and *Persia* (Upper Norian), the latter being considered by Hautmann (2001) as the proplaculid closest to the Plicatulidae. Besides the fact that prospondylids never developed plicatulid-like crura, Hautmann’s (2001) sequence *Persia*-like ancestor-*Eoplicatula*-*Pseudoplacunopsis* cannot hold.

**References**


