

## Gastropod evidence against the Early Triassic Lilliput effect: REPLY

REPLY: doi:10.1130/G31765Y.1

Arnaud Brayard<sup>1</sup>, Alexander Nützel<sup>2</sup>, Andrzej Kaim<sup>2,3</sup>, Gilles Escarguel<sup>4</sup>, Michael Hautmann<sup>5</sup>, Daniel A. Stephen<sup>6</sup>, Kevin G. Bylund<sup>7</sup>, Jim Jenks<sup>8</sup>, and Hugo Bucher<sup>5</sup>

<sup>1</sup>UMR 5561 CNRS Biogéosciences, Université de Bourgogne, 21000 Dijon, France

<sup>2</sup>Bayerische Staatssammlung für Paläontologie und Geologie, 80333 Munich, Germany

<sup>3</sup>Instytut Paleobiologii PAN, PL-00-818 Warsaw, Poland

<sup>4</sup>UMR 5125 CNRS PEPS, Université Lyon 1, 69622 Villeurbanne Cedex, France

<sup>5</sup>Paläontologisches Institut und Museum, Universität Zürich, 8006 Zurich, Switzerland

<sup>6</sup>Department of Earth Science, Utah Valley University, Orem, Utah 84058, USA

<sup>7</sup>Spanish Fork, Utah 84660, USA

<sup>8</sup>West Jordan, Utah 84084, USA

We are pleased that our study prompted Fraiser et al. (2010) to abandon their previous concept of a global Early Triassic “Lilliput effect” that extended from the Griesbachian to at least the Smithian (e.g., Fraiser and Bottjer, 2004). As far as we know, their view that the Lilliput effect was restricted to just the first two Early Triassic conodont zones is expressed in their Comment for the first time. Indeed, Twitchett’s (2007) conclusion cited in Fraiser et al. (2010) explicitly assumed that “pre-extinction sizes are not commonly recorded until at least the Middle Triassic” (p. 132). Additionally, Twitchett concluded that “all animal groups suffered a size reduction after the Late Permian extinction event” (p. 143), a conclusion that is contradicted by the well-known normal size of ammonoids. Furthermore, the distinction between a Lilliput phase spanning the earliest Triassic zones and a subsequent phase spanning the rest of the Early Triassic with still-reduced body size is arbitrary.

Even Twitchett (2007) stated that the Lilliput effect *sensu stricto* is not applicable for gastropods at the Permian-Triassic boundary because boundary-crossers have not yet been reported among gastropod species. The Lilliput effect *sensu lato* has been considered by various authors (including our opponents; e.g., Twitchett, 2007), based on the comparisons of size distributions of pre- and post-crisis gastropod faunas (without discrimination of taxa). In this case, it is irrelevant whether newly originated taxa are included because such comparisons argue on the class and sample level. On that basis, a small body size was suggested to be typical for Gastropoda during the entire Early Triassic (e.g., Fraiser and Bottjer, 2004).

The dominance of small gastropods is not unique to the Early Triassic; this size class is largely dominant in Recent normal marine faunas (Bouchet et al., 2002; 71.4% of the species are <19 mm) and most fossil faunas throughout the Phanerozoic. It is only the apparent lack of very large gastropods in the Early Triassic which is remarkable. This alleged small maximum size of Early Triassic gastropods also plays an important role in the papers of Fraiser and Bottjer (2004, p. 267) and Twitchett (2007, his table 1). The discovery of gastropods that are twice as large (~100 mm) as previously known is relevant. Gastropods with a size of 20–40 mm have repeatedly been reported from Early Triassic faunas, including the Griesbachian (Brayard et al., 2010), not only in high latitudes (as argued by Fraiser et al., 2010) but also in low latitudes (37-mm-wide *Naticopsis* from Oman, a large size for gastropods; only ~10% of Bouchet et al.’s [2002] species show adult size >37 mm).

The largest known gastropod ever (*Syrinx aruanus*) mentioned by Fraiser et al. (2010) is a recent neogastropod, a group originating in the

Cretaceous and whose members reach large sizes. Such gastropods were not present in the Early Mesozoic. Using *Syrinx* as a reference, the vast majority of Phanerozoic gastropod faunas would fall into the Lilliput category. Moreover, the absence of “giant” taxa in the Early Triassic fossil record may well be a preservation artifact due to the generally poorly documented fossil record of that time interval.

The reported maximum sizes of Permian (but *not* Late Permian) and Middle Triassic gastropods does exceed that of Early Triassic gastropods, but this might be a purely stochastic effect due to the rather low Early Triassic species diversity (<100 species known) and specimen abundance. Usually, log-normal size distributions are highly right-skewed, making larger species much rarer than smaller ones (independent of species’ relative abundance, negatively correlated with body size). We ran sub-sampling Monte Carlo analyses of Bouchet et al.’s (2002) size distribution of 2581 extant mollusc species based on random generation of sets of 100 species (ca. Early Triassic gastropod diversity; 10<sup>6</sup> iterations). Under a conservative hypothesis of equal sampling probability of each species, the probability distribution of the largest sampled size class turned out to be: [41–88 mm] = 13.6%, [89–190 mm] = 62.7%, and >200 mm = 23.7%, clearly compatible with the largest Early Triassic gastropods found by us.

Concerning our sampling strategy, we carefully sampled, bed by bed, several sections representing ~80 m of well-calibrated Smithian strata. It is trivial that any type of surface collection method is biased because small species are underrepresented. The purpose of our paper was not to estimate the full size distribution, but rather to document large gastropods and to correct the underestimated maximum shell size of Early Triassic gastropods. Our previous and new collections yielded several hundred gastropods (much more than most previously published assemblage); the largest is 103 mm high.

Incidentally, the 27200 cm<sup>3</sup> bulk samples mentioned by our critics is not impressive; it corresponds to a 2.72-cm-thick layer covering 1 m<sup>2</sup>, probably not really representative for 120 m of strata from 3750 km<sup>2</sup> as indicated by them. The sampling method of Fraiser and Bottjer (2004) was obviously also biased because they failed to find large gastropods although they worked in the same area as we did. Some of their material is derived from high-energy deposits (e.g., tempestites) and is size-sorted. We do not exclude that size reduction affected some Early Triassic clades, e.g., in heterodont bivalves (see Hautmann and Nützel, 2005). However, previous claims that the Lilliput effect *sensu lato* was a global phenomenon during the entire Early Triassic that influenced all animal groups (Twitchett, 2007) are unconvincing: the importance of the Lilliput effect on Early Triassic faunas, if any, has been clearly overestimated.

### REFERENCES CITED

- Bouchet, P., Lozouet, P., Maestrati, P., and Heros, V., 2002, Assessing the magnitude of species richness in tropical marine environments: Exceptionally high numbers of molluscs at a New Caledonia site: *Linnean Society Biological Journal*, v. 75, p. 421–436, doi:10.1046/j.1095-8312.2002.00052.x.
- Brayard, A., Nützel, A., Stephen, D.A., Bylund, K.G., Jenks, J., and Bucher, H., 2010, Gastropod evidence against the Early Triassic Lilliput effect: *Geology*, v. 38, p. 147–150, doi:10.1130/G30553.1.
- Fraiser, M.L., and Bottjer, D.J., 2004, The non-actualistic Early Triassic gastropod fauna: A case study of the Lower Triassic Sinbad Limestone member: *Palaios*, v. 19, p. 259–275, doi:10.1669/0883-1351(2004)019<0259:TNETGF>2.0.CO;2.
- Fraiser, M.L., Twitchett, R.J., Frederickson, J.A., Metcalfe, B., and Bottjer, D.J., 2010, Gastropod evidence against the Early Triassic Lilliput effect: Comment: *Geology*, doi:10.1130/G31614C.1.
- Hautmann, M., and Nützel, A., 2005, First record of a heterodont bivalve (Mollusca) from the Early Triassic: Palaeoecological significance and implications for the “Lazarus problem”: *Palaeontology*, v. 48, p. 1131–1138, doi:10.1111/j.1475-4983.2005.00505.x.
- Twitchett, R.J., 2007, The Lilliput effect in the aftermath of the end-Permian extinction event: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 252, p. 132–144, doi:10.1016/j.palaeo.2006.11.038.