The molluscs of the "Falunière" of Grignon (Middle Lutetian, Yvelines, France): quantification of lithification bias and its impact on the biodiversity assessment of the Middle Eocene of Western Europe

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ABSTRACT

Lithification is stressed as a major bias for the palaeobiodiversity evaluation. Although this bias is often discussed in the literature, it has rarely been quantified. This work offers a first estimation of diagenesis impact over mollusc diversity record for a single bed of the "Falunière" of Grignon (middle Lutetian, France). This bed possesses the particularity of displaying two lithological facies: one lithified and the other unlithified, both from a same taphocoenosis. Mollusc diversities of three unlithified and three lithified samples have been compared (1453 specimens among 131 species). The comparison was made possible by the construction of rarefaction curves extrapolated for 30 samples and the introduction of two indexes: the eDG (extrapolated Diagenesis Gap) that gives a value of diversity loss between two facies and the STD (sampling/diagenesis bias threshold) that gives the threshold (in number of samples) after which eDG can be estimated. The analysis reveals that nearly 80% of species richness is not recorded in the lithified facies, and that loss can reach 100% for species smaller than 2 mm. The bias linked to specimen sizes is discussed, both for large and small shells. The

differences of biodiversity recorded among litholofacies have also been approached at regional level by the comparison of taxon associations from lithified and unlithified lithologies from the middle Eocene of Paris Basin (Lutetian: Vanves, Nanterre, Damery, Ferme de l'Orme, Chaussy, Grignon and Villiers-Saint-Frédéric; Bartonian: Baron), Aquitaine Basin (Bartonian: Blaye and Gironde) and Italy (Lutetian: San Giovanni Ilarione, Verona). A revaluation of biodiversity estimates of San Giovanni Ilarione that consider lithification bias suggests that the Tethyan regions housed similar or higher species richness than the Paris Basin during the Lutetian, which does not agree with a raw data comparison but which would better fit with the hypothesis of a biodiversity hotspot in the western Tethys. Any future comparisons of the biodiversity from distinct regions or time intervals have to consider the conditions of preservation and the lithification bias.

RÉSUMÉ
Les mollusques de la « Falunière » de Grignon (Lutétien moyen, Yvelines, France) : quantification du biais d'induration et son impact sur l'évaluation de la biodiversité à l'Éocène moyen en Europe occidentale.
L'induration des sédiments est un problème majeur pour l'évaluation de la paléobiodiversité. Bien qu'abondamment discutés dans la littérature, les biais liés à l'induration ont rarement été quantifiés. Ce travail propose une première estimation de l'impact lié à la diagenèse sur l'enregistrement de la diversité malacologique pour un niveau de la Falunière de Grignon (Lutétien moyen, France). Ce niveau a la particularité de présenter deux faciès lithologiques : un meuble et un lithifié issus d'une même taphocénose. La diversité des mollusques de trois échantillons meubles a été comparée à celle de trois échantillons indurés représentant en tout 1453 individus, répartis dans 131 espèces. Cette comparaison a été réalisée grâce à la construction de deux courbes de raréfaction extrapolées pour des jeux de 30 échantillons et le calcul de deux indices : le eDG (extrapolated Diagenesis Gap) qui donne une valeur de perte de la biodiversité entre les deux facies et le STD (sampling/diagenesis bias threshold) qui donne le seuil (en nombre d'échantillons) à partir duquel peut être calculé le eDG. L'analyse de la différence de richesse obtenue révèle une perte de près de 80 % de l'enregistrement de la paléobiodiversité dans le faciès induré. Cette perte peut aller jusqu'à 100 % pour les espèces de taille inférieure à 2 mm. Les problèmes d'enregistrement liés à la taille des spécimens sont discutés aussi bien pour les grandes que pour les petites coquilles. Le problème de l'enregistrement de la biodiversité malacologique en fonction de la lithologie est aussi abordé à l'échelle régionale par la comparaison de données bibliographiques pour des sites à lithologie indurée ou non, provenant du Bassin parisien et datés du Lutétien (Vanves, Nanterre, Damery, Ferme de l'Orme, Chaussy, Grignon et Villiers-Saint-Frédéric) ou du Bartonien (Baron), du Bartonien du Bassin d'Aquitaine (Blaye et Gironde) et du Lutétien d'Italie (San Giovanni Ilarione). Une réévaluation de la biodiversité en tenant compte des biais d'induration semble indiquer une richesse faunique équivalente, voire supérieure de la région téthysienne (San Giovanni Ilarione) par rapport au Bassin de Paris, ce qui ne correspond pas aux données disponibles mais serait plus en accord avec les hypothèses de point-chaud de la biodiversité dans l'ouest de la Téthys. Dans l'avenir, les comparaisons de biodiversité entre intervalles de temps ou régions distinctes devraient tenir compte des conditions de préservation et d'induration.

INTRODUCTION

The biodiversity recorded in the fossils is affected by a number of phenomena linked to sedimentary processes. Among them, the lithification bias is potentially one the most prominent, but also one of the less known (Hendy 2009, 2011). The paleobiodiversity of marine invertebrates collected from Cainozoic rocks is directly linked to the degree of lithification. Unlithified sediments hold a much higher diversity than the lithified ones, supposedly due to an easier sample processing (Alroy *et al.* 2008). Unlithified sediments do not occur frequently in geological series older than the Cretaceous and almost all Palaeozoic rocks found in the world are strongly lithified, which limit the recovered paleobiodiversity at individual sites and the estimates of global diversity (Hendy 2011). The expected impact of diagenesis is likely to increase with the number of

diagenetic transformations, and consequently with the age of the geological units, with loss of biodiversity at each step (Bush & Bambach 2004; Behrensmeyer *et al.* 2005).

The relationship between lithification and sampled paleobiodiversity is not straightforward. The change of sediment into rock is a by-product of diagenesis, and diagenetic processes may have distinct incidence on paleobiodiversity estimates according to their timing and intensity. Usually, the diagenetic processes lead to progressive loss of information, by destruction of the organic remains. Shells and skeletons are rarely in chemical equilibrium with the interstitial fluids of the sediment, which lead to dissolution (Chave 1967; Lawrence 1968; Brachert & Dullo 2000). Dissolution can start as early as death of an organism and its burial into the sediment (Hecht 1933; Aller 1982). The propensity of individual shell to dissolution depends on its size, microstructure and mineralogy (Martin

FIG. 1. — Geological and paleogeographical localisation of the "Falunière" of Grignon (Yvelines, France): **A**, geological map of the studied area (modified after Cavelier & Feugueur 1967); **B**, paleogeographic map of the Paris Basin in correspondence of the deposition of the "Banc à verrins" (unit 5b) and the lower part of the "Vergelé" (modified after Gély 2008a).

1999). In the case of molluscs, the selective loss of aragonitic shells is recognized as a major factor of biases in biodiversity estimates, so that the number of shells collected might be reduced to 1% of the initial taphocoenosis (Cherns & Wright 2000, 2009; Wright *et al.* 2003). Only an early lithification and mineralisation of organic parts warrant the preservation of most of the biological and ecological information held in

the taphocoenosis (Tomašových & Schlögl 2008). How to recover the information remains a major problem faced by palaeontologists. The methods developed to describe the diversity of fossil forms will depend on initial shell mineralogy, size range, the degree of rock lithification, the mineralogy of cements and sedimentary grains, etc. The variety of preservation conditions and the variety of investigation methods

add to the difficulty of biodiversity comparison among sites, paleoenvironmental conditions, geological history of a sedimentary basin, or global estimates across geological times.

Opportunities to compare the biodiversity of one taphocoenosis under different conditions of preservation are extremely rare. The quantification of biases associated with sediment lithification is only possible where a single shell bed was exposed to varied diagenetic conditions. A part of the section of the "Falunière" of Grignon (bed 5b, see Fig. 2) allows a comparison of a single Eocene taphocoenosis of molluscs preserved under two lithologic facies. Burial was very limited, sands remain soft, and dissolution and diagenetic alteration of the shells are minimal. From place to place, the soft calcareous sand is lithified into calcareous sandstone. Lithification represents the most recent diagenetic event and did not alter drastically the preservation of the shells. The comparison of diversity recovered from lithified and unlithified samples is a direct evaluation of experimental/analytical biases implied by sediment lithification, combined to limited diagenesis. In usual conditions, environment and ecology controls on living communities of organisms, sedimentary dynamics and prediagenesis taphonomic phenomenon have an impact on the composotion of fossil assemblages and the biodiversity estimates. Grignon offers the opportunity to investiate the single effects of lithification at the local scale, prior to selective dissolution. The consequences of lithification biases on the measures of biodiversity are quantified at fine scales (sample, bed). Comparisons at wider scales (among rock facies, stratigraphical units, localities or regions) cannot objectively segregate the respective ecological, taphonomic and diagenetic control of fossil assemblages. However, lithification is considered a sufficiently prominent factor to significantly impact the biodiversity estimates among fossil collections, which has consequences when mixing or comparing data from varied lithologies in the exploration of large scale biodiversity patterns. Western Europe is understood as a biodiversity hotspot for molluscs during the Lutetian (Merle 2008b; Huyghe *et al.* 2012). Most of the richest shell beds occur within unlithified sands, a condition most favourable for recovery of past biodiversity (Hendy 2009). In this paper we compare values of biodiversity of Lutetian shell beds sampled at different sites from both lithified and unlithified, carbonate and silicoclastic sediments, in order to evaluate whether the biases observed at a local scale might be sufficient to explain paleobiodiversity patterns at a regional scale. To do so we compare Grignon to a wide range of well-studied Bartonian and Lutetian localities from the Paris basin, the Aquitaine Basin, and San Giovanni Ilarione (Veneto Basin, Italy), a locality with outstandingly rich mollusc fauna derived from lithified carbonates.

GEOLOGICAL SETTING

The "Falunière" of Grignon is located in the Paris Basin, and is a classical locality of the Lutetian stage (Fig. 1A). During this period, Grignon was on the south-western border of the basin, close to the seashore and the Bray anticline (Fig. 1B and Gély 1996, 2008a). The sediments are typical of marine coastal environments, with evidences of tidal, storm and lagoonal deposits, in warm carbonate-rich waters (Gély 1996). Biostratigraphic data indicate a middle Lutetian age for these deposits, (Aubry 1985), confirmed by correlation with Gély's parasequences A6 to A10 (Gély 1996). During the Lutetian, the basin was connected to the Atlantic Ocean though the English channel (Gély 1996, 2008a). The area of Grignon emerged by the end of the Eocene and middle Lutetian sediments are today covered by only a few meters of upper Lutetian and Quaternary deposits. The Paris Basin is an intracratonic basin which has undergone limited tectonic activity since the Middle Eocene (Cavelier & Pomerol 1979; Brunet & Le Pichon 1982; Guillocheau *et al.* 2000). The sub-aerial diagenesis of Lutetian sediments remained extremely limited.

Description of the section

The studied section is located on the property of Agro-Paris-Tech site de Grignon (INAPG), near the town of Thiverval-Grignon (Yvelines, France) (Fig. 1A), about 45 km westward from Paris. Under the name of Grignon were included up to five fossil sites (Fritel 1910; Abrard 1925), among which only the "Falunière" remains today.

The "Falunière" of Grignon section is around 12 m thick, but only its upper 7 m (eastern and western fronts) are easily observable (Fig. 2). This section is described in Gély (1996), Merle & Courville (2008), Huyghe *et al.* (2012) and Guernet *et al.* (2012), among the most recent works. A synthesis of the stratigraphic and sedimentological results is shown in Figure 2. The "Falunière" is a remarkable section due to its very high mollusc species richness (Merle & Courville 2008), rising interest since the early days of geology (Lamarck 1802-1809; Cuvier & Brongniart 1811). Sampling was carried out in a pit dug in the northern end of the "Falunière", within unit 5b of Guernet *et al.* (2012), displaying two lithofacies: an unlithified one representing most of the bed and a less common one which is lithified. The unit 5b is known also as the *Campanile giganteum* keyhorizon, corresponding to the "banc à verrins" bed observed in a great part of the Paris Basin and in the neostratotype section of Saint-Vaast-les-Mello (Blondeau 1965; Merle 2008a). In comparison, a lower species richness of mollusc is reported for the two sections selected as neostratotypes of the Lutetian stage at St-Vaast-les-Mello and St-Leu-d'Esserent, fifty kilometers NE to Grignon (Blondeau & Cavelier 1962; Blondeau 1964).

MATERIAL AND METHODS

Sampling

Three unlithified bulk samples, labelled US 1-3, were collected using a trowel along the total extension of the accessible outcrop (around 2.5 m: Fig. 3). Three similar lithified samples were collected along the same bed, labelled LS 1-3.
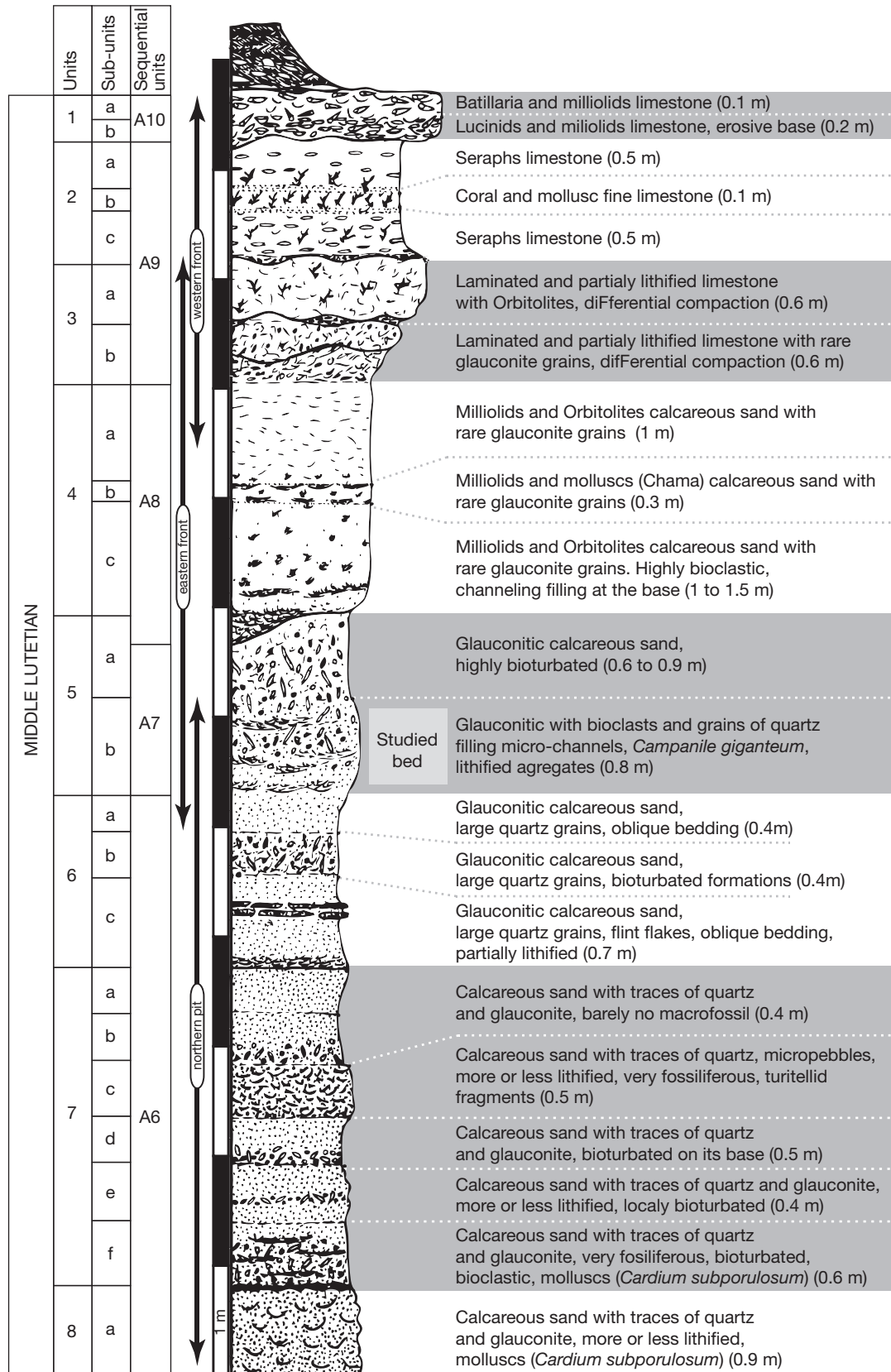
Units	Sub-units	Sequential units		

The figure shows a stratigraphic column with the following lithologic descriptions (from top to bottom):

MIDDLE LUTETIAN

- Unit 1, sub-unit a — A10: Batillaria and milliolids limestone (0.1 m)
- Unit 1, sub-unit b — A10: Lucinids and miliolids limestone, erosive base (0.2 m)
- Unit 2, sub-unit a — A9: Seraphs limestone (0.5 m)
- Unit 2, sub-unit b — A9: Coral and mollusc fine limestone (0.1 m)
- Unit 2, sub-unit c — A9: Seraphs limestone (0.5 m)
- Unit 3, sub-unit a — A9: Laminated and partialy lithified limestone with Orbitolites, diFferential compaction (0.6 m)
- Unit 3, sub-unit b — A9: Laminated and partialy lithified limestone with rare glauconite grains, difFerential compaction (0.6 m)
- Unit 4, sub-unit a — A8: Milliolids and Orbitolites calcareous sand with rare glauconite grains (1 m)
- Unit 4, sub-unit b — A8: Milliolids and molluscs (Chama) calcareous sand with rare glauconite grains (0.3 m)
- Unit 4, sub-unit c — A8: Milliolids and Orbitolites calcareous sand with rare glauconite grains. Highly bioclastic, channeling filling at the base (1 to 1.5 m)
- Unit 5, sub-unit a — A7: Glauconitic calcareous sand, highly bioturbated (0.6 to 0.9 m)
- Unit 5, sub-unit b — A7: **Studied bed** — Glauconitic with bioclasts and grains of quartz filling micro-channels, *Campanile giganteum*, lithified agregates (0.8 m)
- Unit 6, sub-unit a: Glauconitic calcareous sand, large quartz grains, oblique bedding (0.4m)
- Unit 6, sub-unit b: Glauconitic calcareous sand, large quartz grains, bioturbated formations (0.4m)
- Unit 6, sub-unit c: Glauconitic calcareous sand, large quartz grains, flint flakes, oblique bedding, partially lithified (0.7 m)
- Unit 7, sub-unit a — A6: Calcareous sand with traces of quartz and glauconite, barely no macrofossil (0.4 m)
- Unit 7, sub-unit b — A6: Calcareous sand with traces of quartz, micropebbles, more or less lithified, very fossiliferous, turitellid fragments (0.5 m)
- Unit 7, sub-unit c — A6: Calcareous sand with traces of quartz and glauconite, bioturbated on its base (0.5 m)
- Unit 7, sub-unit d — A6: Calcareous sand with traces of quartz and glauconite, more or less lithified, localy bioturbated (0.4 m)
- Unit 7, sub-unit e — A6: Calcareous sand with traces of quartz and glauconite, very fosiliferous, bioturbated, bioclastic, molluscs (*Cardium subporulosum*) (0.6 m)
- Unit 8, sub-unit a: Calcareous sand with traces of quartz and glauconite, more or less lithified, molluscs (*Cardium subporulosum*) (0.9 m)

(Labels on the column: western front, eastern front, northern pit; scale bar 1 m)

Fig. 2. — The "Falunière" of Grignon section, after Guernet *et al.* (2012) for the section profile, lithologic units and sub-units and descriptions, Gély (1996) for the sequential units and Huyghe *et al.* (2012) for the correlation of sequential and lithologic units.

Fig. 3. — View as of February 2013 of unit 5b ("Falunière" of Grignon, Lutetian, Yvelines, France) with indications for the samplings. Notebook scale: 20 cm.

PREPARATION

The three unlithified samples have been put into hot water for three hours before being divided in different size classes by sieves with mesh of 5 mm, 2 mm and 1 mm. The residue of each sieve has been labelled with the sample number and the mesh size, and then dried off in the oven for 12 hours. All identifiable bivalve and gastropod shells were extracted under binocular microscope. The three lithified samples have been brushed under hot water in order to remove traces of unlithified sediment, and then put in the oven for 12 hours.

Sifting was not possible and mechanical extraction was unpractical for lithified sediment samples. To circumvent this problem, we established a photographic mapping and a microscopic surface survey of all lithified samples. The observed specimens were named and assigned to a granulometric class according to the mesh size of sieves used for unlithified sample. Size classes were assigned to fossil molluscs by measuring the longest dimension of their shells. This generally corresponded to the distance between the anterior and posterior edges for the bivalves, and the distance between the anterior and posterior end for the gastropods.

SPECIES IDENTIFICATION

Specimens were identified at the species level whenever possible, based on the photographic atlas "Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris" by Cossmann & Pissarro (1904-1913), with taxonomy updated by Le Renard & Pacaud (1995), Courville *et al.* (2012) and Caze *et al.* (2012). Some cryptic species were identified using the methodology of Caze *et al.* (2010, 2011) by revealing the residual colour patterns under UV

light (λ = 3600 Å) (Fig. 4). All shells were identified under binocular microscope.

CONSTRUCTION OF THE DATABASE

A database was constructed by counting the number of specimens for each species (Appendix 1). Number of gastropods was equated to the number of apices (Gitton *et al.* 1986), unless rare cases when the number of specimens was unequivocal even in the absence of preserved apices, like for specimens of *Athleta* (*Volutopupa*) *citharoedus* (Holten, 1802). Bivalve specimens with articulated valves are extremely rare at Grignon, therefore abundance was equated to the highest number of left or right valves, or umbos in case of fragments. For equivalve species such as *Glycymeris* spp. or *Limopsis* (*Pectunculina*) *granulata* (Lamarck, 1805) the total number of specimens was obtained dividing the total number of valves by two (Gitton *et al.* 1986).

COMPARISONS OF BIODIVERSITY
AMONG LITHIFIED AND UNLITHIFIED SAMPLES

For practical reasons, we compared standardised abundances from sieved bulk samples with standardised abundances from surfaces of lithified samples. Varied biodiversity estimates are calculated: the number of shells and the number of species sampled in each sample, three distinct metrics of evenness (Simpson Index, Pielou's evenness, equitability), and the expected number of species for a sample of 30 shells (Std30) (Hammer & Harper 2006). Since species richness is a function of sample size, we used rarefaction to compare samples of different size. The main goal of this method is to study the effect of samples size
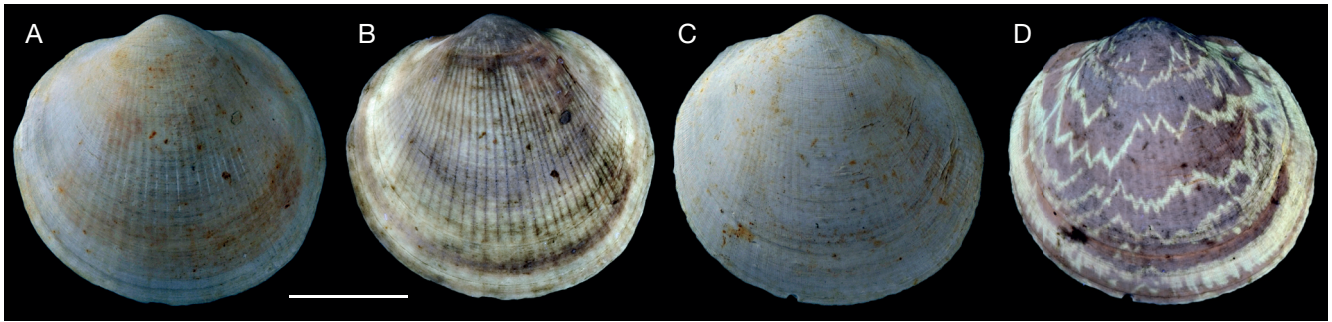
Fig. 4. — Comparison of two species of *Glycymeris* Da costa, 1778 under natural light (**A, C**) and under UV light (**B, D**): **A, B**, *Glycymeris pulvinata* (Lamarck, 1805) right valve (external view), MNHN.F.A25067 (Faullummel coll.), Grignon (Yvelines, France); **C, D**, *Glycymeris dispar* (Defrance, 1826) left valve (external view), MNHN.F.A26015, Grignon (Yvelines, France). Scale bar: 2 cm. Photo: P. Loubry.

over the counting of species, or to compare the counting of species within sample of different sizes (Hammer & Harper 2006). Rarefaction curves standardise values of species richness from several samples of different sizes by bringing it to the size of the smallest sample, assuming that, independently from their size, samples contain sufficient information to estimate taxonomic richness (Vavrek 2011). Recent versions of rarefaction statistics (Colwell *et al.* 2012) allow extrapolating the shape of the rarefaction curve to the theoretical maximal richness of a batch of samples for a predetermined number of specimens or samples. For this study, rarefaction curves and estimates of the taxonomic richness are determined using the EstimateS V9.1 software (Colwell 2013). The rarefaction curves are computed following a sample-based resampling mode, and are prolonged analytically for a higher number of samples than actually processed. The expected number of species S (est) is extrapolated using equation 18, and confidence intervals (95% Lower and upper Bounds) using equation 19 from Colwell *et al.* (2012). Values of taxonomic richness estimated at curve plateau are used to compare species richness between lithified and unlithified samples, the difference reflecting the lithification bias. For each analysis, a minimal threshold or STD (sampling / diagenesis bias threshold) of samples was estimated after which both curves reach a plateau. The value is indicative of the lithification bias, independently of sampling.

Assuming that the unlithified conditions represent the optimal conditions for sampling, the lithification bias is measured as the difference between the maximal taxonomic richness estimated for unlithified and lithified facies. We introduce the "index of extrapolated Diagenesis Gap": eDG. This estimator corresponds to the mean loss of richness (in percent) between the two facies.

ABBREVIATIONS
US   unlithified samples;
LS   lithified sample;
MNHN.F   Muséum national d'Histoire naturelle, Paris. Collection de Paléontologie;
STD   sampling/diagenesis bias threshold;
eDG   extrapolated Diagenesis Gap;
INAPG   Institut national agronomique Paris-Grignon.

RESULTS

SEDIMENTOLOGICAL ANALYSIS

The sediment of the unit 5b is a calcareous sand containing numerous mollusc remains, with rare occurrence of corals, annelids and bryozoans. Quartz and glauconite account each for 10% of the clasts. Where lithified, the soft sediment is transformed into a bioclastic grainstone (Fig. 5). The cementation is unevenly distributed, and a high porosity remains. The cements are made of a single type of tiny, calcite crystals (microspar). In thin section, the microstructure of the shells is well preserved, and no coating of the grains by fringes of minute prismatic calcite crystals was observed. Calcite often seals the cracks produced to the shells by sediment compaction. Shell residual colour pattern under UV light is similarly visible in both facies (Fig. 6). Yet, some shells from lithified facies appear to be slightly powdery in surface, which could reflect partial dissolution. This is of very little incidence for identification of larger shells, but it obviously prevent some small shells to be analyzed properly.

Actualistic comparisons suggest that the mollusc fauna is mainly composed of endobenthic suspension feeders from a largely barren soft bottom (e.g., *Glycymeris* Da Costa, 1778, *Limopsis* Sassi, 1827, *Pitar* Römer, 1857, *Sigmesalia* Finlay & Marwick, 1937 and *Haustator* Monfort, 1810). There is no obvious change in shell assemblages and sedimentary compounds among samples. The two distinct lithofacies sample shells from the same original taphocoenosis.

Several diagenetic pathways can lead to the formation to such heterogeneous facies, but the hypothesis of a recent lithification is more likely. There is no clear evidence of an early diagenesis hold in marine conditions. The sediment remained under its sandy state and the late lithification may be caused by phreatic diagenesis. Today, the piezometric level of the area still temporarily reaches the studied bed, bringing dissolved carbonates from lower limestone. The heterogeneities of the sand and the low quantity of dissolved carbonates from underneath may have prevented the entire lithification of the bed. A similar diagenesis is assumed at Fleury-la-Rivière, where a water source induced lithification of the Lutetian shells beds that can be observed in the outcrops of the geosite "La Cave aux Coquillages" (Merle & Courville 2008).

TABLE 1. — Biodiversity metrics for all unlithified (**US**) and lithified (**LS**) samples collected in unit 5b, "Falunière" of Grignon (Yvelines, France). Simpson, evenness and equitability indices were calculated with Past (Hammer & Harper 2006). Std30 is the expected biodiversity for a sample of 30 shells given by the rarefaction curves. There is no value for the sample LS1 [2-1mm] because no specimen was found in this size range. *, indicates non-significant values due to a too small number of specimens. The bottom values give the values for all unlithified (**USt**) and lithified (**LSt**) samples treated altogether.

Samples	Species	Specimens	Simpson index	Evenness	Equitability	Std30
US1	91	554	0.96	0.43	0.81	19
US1 > 5 mm	21	39	0.93	0.81	0.93	18
US1]5-2mm]	48	178	0.94	0.55	0.85	18
US1]2-1mm]	60	337	0.94	0.43	0.79	17
US2	59	358	0.92	0.41	0.81	17
US2 > 5mm	12	16	0.90	0.91	0.96	–
US2]5-2mm]	35	110	0.91	0.55	0.83	16
US2]2-1mm]	36	232	0.90	0.47	0.79	14
US3	73	380	0.95	0.5	0.84	19
US3 > 5mm	32	65	0.95	0.77	0.92	20
US3]5-2mm]	40	149	0.95	0.67	0.89	18
US3]2-1mm]	39	166	0.90	0.49	0.81	16
LS1	10	13	0.89	0.95	0.97	–
LS1 > 5mm	7	9	0.84	0.94	0.97	–
LS1]5-2mm]	4	4	0.75	1*	1*	–
LS1]2-1mm]	0	0	–	–	–	–
LS2	21	54	0.89	0.68	0.87	15
LS2 > 5mm	16	37	0.88	0.72	0.88	14
LS2]5-2mm]	9	14	0.85	0.86	0.93	–
LS2]2-1mm]	3	3	0.67	1*	1*	–
LS3	31	92	0.94	0.73	0.91	18
LS3 > 5mm	24	71	0.93	0.74	0.90	16
LS3]5-2mm]	12	16	0.91	0.94	0.98	–
LS3]2-1mm]	3	5	0.56	0.86	0.87	–
USt	129	1292	0.95	0.39	0.76	19
LSt	37	159	0.94	0.66	0.89	18

BIODIVERSITY ESTIMATES

The whole samples allowed us to identify 1771 shells (umbos or apices, see Methods) belonging to 1453 individuals from 131 species of molluscs (Appendix 1). Table 1 gives standard biodiversity indices for all individual samples and for all lithified and unlithified samples treated together. For initial samples representing the same volume, the number of specimens recovered from lithified samples is only 12% of the number for unlithified samples (Table 1). The number of sampled taxa is consistently lower in lithified samples. The similar values of the Simpson index (0.95 for US and 0.94 for LS) and equitability (0.76 for US and 0.89 for LS) for the two types of samples (Table 1) suggest that comparisons of these metrics remains possible between lithified and unlithified samples. The evenness is quite different (0.32 for US and 0.66 for LS).

Bivalves and gastropods are affected in a similar way (Fig. 7). Loss of biodiversity during lithification appears strongly dependant on the size of identifiable species (Fig. 7), with 100% of adult species under 2 mm found in sandy samples being absent in lithified ones. The same tendency can be observed for the 2-5 mm size class, where 86% of mollusc species have not been found in lithified samples. Differences in species richness are lowest for larger species, with 63% of molluscs >5 mm found in sand samples being present also in lithified samples. The differences noted for the larger size classes could be due only to a sample size effect, as the standardized values are not significantly distinct. Rarefaction curves (Fig. 8) allow a comparison of species richness between lithified and unlithified sediments, for gastropods, bivalves and their sum.

STDs and eDGs are given in Table 2. Considering the molluscs within the total size range of the study (Fig. 8I), the lithification bias accounts for the loss of 71% of species (131 species) one third being gastropods (85 species, Fig. 8G).

DISCUSSION

Relevance of local fossil assemblages for biodiversity estimates: the imprint of lithification bias.

SAMPLING EFFORT, LITHOLOGY AND THE RELEVANCE OF BIODIVERSITY COMPARISONS

The samples collected at Grignon are extremely rich with up to more than 554 identifiable shells in one litre of sand (e.g., US1, Table 1). The richness and abundance of species varies highly among samples, especially between lithified and unlithified lithologies. However, considering all size classes together, the individual rarefaction curves are grossly similar among the six samples, whatever the lithification mode. Either the equitability, or the recovered diversity for a standardized number of shells do not differ significantly between lithified and unlithified processed samples. Only the eveness index seems to be altered by lithification bias. A sample of one litre of sand is far from recovering the predicted number of species preserved in the bed. A comprehensive coverage of species richness (within 95% confidence interval) would require the analysis of 10-15 litres of sand, which would correspond to 4300-6460 shells. Increasing
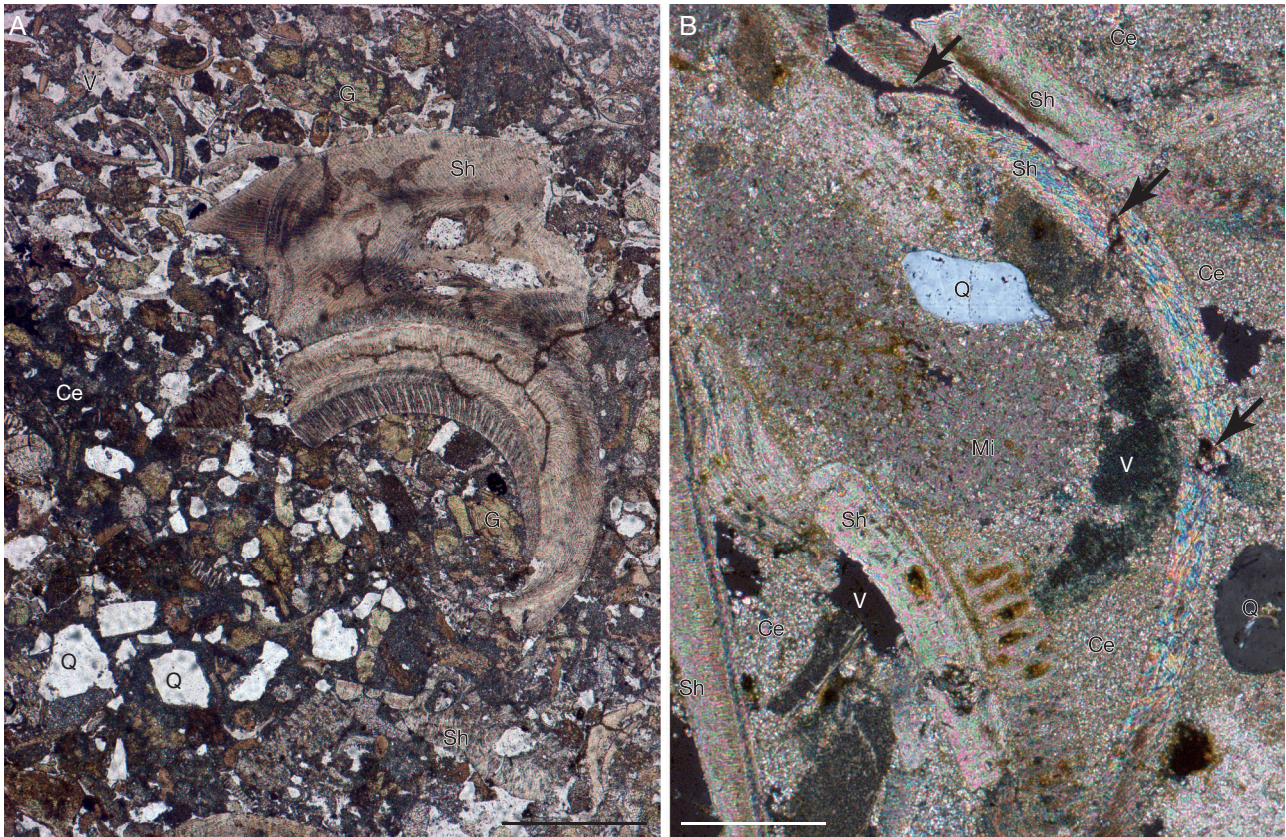
FIG. 5. — Thin section (MNHN.F.A51274) of a lithified sample from unit 5b at the "Falunière" of Grignon (Yvelines): **A**, general view showing the composition of bioclasts, glauconite, quartz grains and microspar; **B**, detail on the homogeneous microspar indicating a single cement generation, and some shell broken during burial. Abbreviations: **Ce**, microsparitic cement; **G**, glauconitic grain; **Mi**, micritic grain; **Q**, quartz grain; **Sh**, shell or shell fragment; **V**, voids; **arrows**, shell fractures. Scale bars: A, 1 mm; B, 250 µm. Thin section: S. Morel; photo: L. Villier.
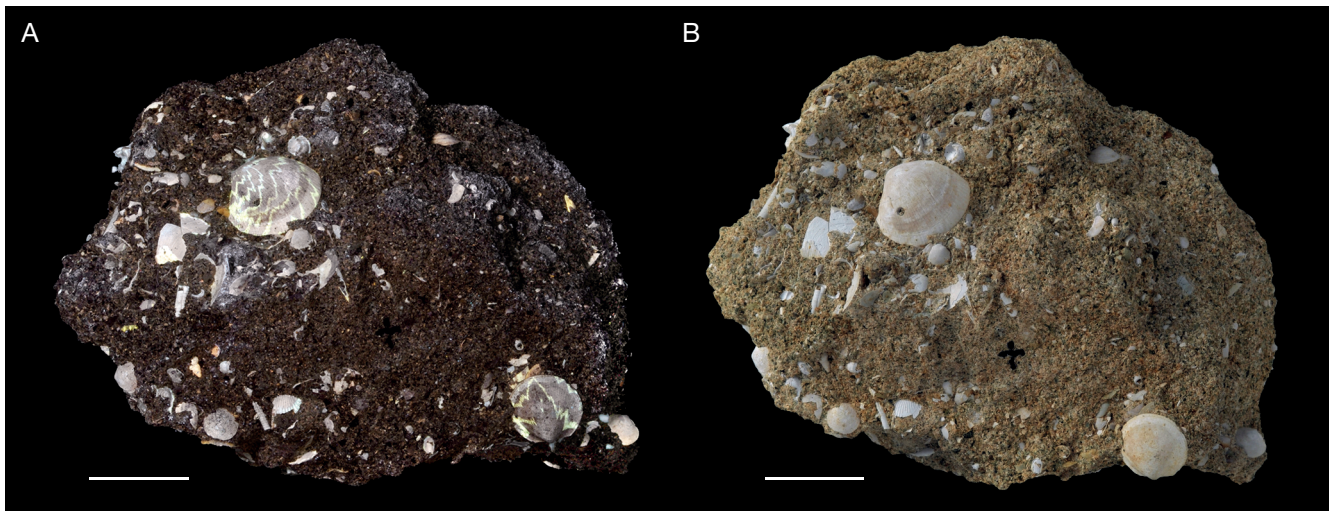

FIG. 6. — From the unit 5b of the "Falunière" of Grignon (Yvelines), a lithified sample (LS 2, MNHN.F.A51273) under UV light showing residual colour patterns on shells (**A**) and in natural light (**B**). Scale bars: 2 cm. Photo: P. Loubry.

the amount of processed material changes our perception of biodiversity properties. The size of the samples traditionally used for paleoecological studies (100-200 specimens) would always underestimate the actual species richness and overestimate evenness.

Obvious differences in diversity appear when all available data for a given lithology are combined. Three litres of unlithified sand provides nine times more identifiable specimens than a similar volume of lithified sandstone (159 vs 1292), and 3.5 more species (129 vs 37). For a

TABLE 2. — Diagenesis Gaps (**eDG**) in percent and number of species for gastropods, bivalves and the combination of both considering three size ranges (>5 mm,]5-2],]2-1] mm), and value for the minimal number of samples required to reach the extrapolated number of species (**SDT**).

Size range		eDG		STD
		%	nbr of species	nbr of samples
> 5 mm	Gastropoda	65	50	31
	Bivalvia	26	5	5
	Gastro. + Bivalv.	49	33	14
]5-2] mm	Gastropoda	59	51	20
	Bivalvia	48	14	14
	Gastro. + Bivalv.	59	66	12
]2-1] mm	Gastropoda	73	85	15
	Bivalvia	76	45	13
	Gastro. + Bivalv.	75	131	13

similar effort of field sampling, the unlithified rocks are much more productive. If the only reason for the differences between the two facies was the sampling effort, then the rarefaction curves should tend to the same asymptotic number of species, which is not the case. The rarefaction curve for lithified samples bent to a plateau while those of unlithified samples continue rising (Fig. 8I), hens other factors (e.g., lithification) should be considered. The evenness and equitability increase significantly in lithified samples, which suggest the selective loss of rare species. The lithified blocks sample grossly the same species each, whereas the diversity of unlithified samples is more diverse, including varied suites of rare taxa. The deficit of species in lithified samples reaches 71% of the diversity housed in unlithified sand, but is reduced to 50% for the species larger than 5 millimetres. Thus, the unrecovered species are mostly small and rare species. Other attempts to measure lithification biases on biodiversity estimates obtained similar values, with unlithified sediments sampling about two times more species than lithified rocks (Alroy *et al.* 2008; Hendy 2009; Sessa *et al.* 2009).

The lithification biases are often understood as driven by the selective loss of aragonitic shells (Cherns & Wright 2000, 2009). The taphonomic analysis of Grignon suggests that the shells available in both lithified and unlithified sands sample displays the same initial biodiversity, without selective loss of aragonitic shells in lithified rocks. Differences in species count among lithified and unlithified samples derive mostly from sample processing, which has been assumed by former authors (Kowalewski *et al.* 2006), but remained unquantified. This factor affects biodiversity estimates to a comparable degree to that of other taphonomic biases. This should be considered in further analyses of biodiversity patterns, when mixing data from sites with different diagenetic histories.

SELECTIVE LOSS OF INFORMATION
ON SMALLER TAXA IN LITHIFIED SAMPLES

Although species with shell smaller than five millimetres are present, they are hardly identified in lithified samples.

Small specimens have been observed in all samples but, due to their inclusion into rocks, we were unable to provide identification at the species level (Fig. 9B). Only molluscs outcropping in an ideal orientation (ventral view for gastropods and internal view for bivalves) may have a chance to be identified, indeed, the powdery nature of the shells prevents us from any manipulation which would have irrevocably damaged them. In this study all the specimens smaller than two millimetres in lithified sample were juvenile belonging to species whose adults were present in larger size classes. That is why the Figure 7 does not count species smaller than 2 millimetres. Thus, the lower size class does not add a single species to the list for the lithified samples. Even considering an extensive sampling and a careful survey of lithified blocks, the expected species number to be counted remains less than 50% of the actual diversity of the species included in the size range between two and five millimetres. The selective loss of small forms is an usual suspect in issues with analyses of fossil biodiversity (Cooper *et al.* 2006; Kowalewski *et al.* 2006; Sessa *et al.* 2009; Cherns & Wright 2011). Two approaches were used to cope with the lithified biases in biodiversity comparisons, among fossil levels:

1) a size of five millimetres seems to be a threshold below which the measures and comparisons of biodiversity become difficult (Kowalewski *et al.* 2006; Sessa *et al.* 2009). Even in the Recent, the diversity of small molluscs is often underestimated (Bouchet *et al.* 2002) and the size distribution patterns of species across oceans remain unclear pending a revaluation of the actual diversity of small forms (Kantor & Sysoev 2005). Small forms can represent more than 50% of the extant species (Bouchet *et al.* 2002) and small species likely represent a high part of the post-Palaeozoic mollusc diversity (Cherns & Wright 2011). The selective loss of the shells smaller than five millimetres in lithified rocks prevents direct comparisons of diversity from lithified and unlithified collection records, and between past and modern ecosystems. Several studies exclude small shells to increase robustness of statistical comparisons, assuming that it will not dramatically blur our perception of ecological and evolutionary patterns (Kowalewski *et al.* 2006; Bush *et al.* 2007).

and 2) the large scale analyses of fossil diversity requires the joint analysis of data describing groups of organisms and collection levels with varied conditions of preservation. The reduction of the unevenness of the fossil record in time and space became a central issue in investigation of the large scale biodiversity patterns. The analytical standardization of the sampling efforts is expected to reduce the biases (Alroy *et al.* 2001). However, lithification biases cannot be compensated by simply adjusting the sample size and all available data cannot yet be mixed in large scale analyses. The most direct way to avoid the lithification effect remains to compare samples that experienced similar taphonomic loss of data, either in favouring, or discarding, unlithified fossil collections (Hendy 2011) or collection of exceptional preservation (Cherns *et al.* 2008). As an example, Alroy *et al.* (2008) excluded species lists derived from level of exceptional preservation and from unlithified sediments
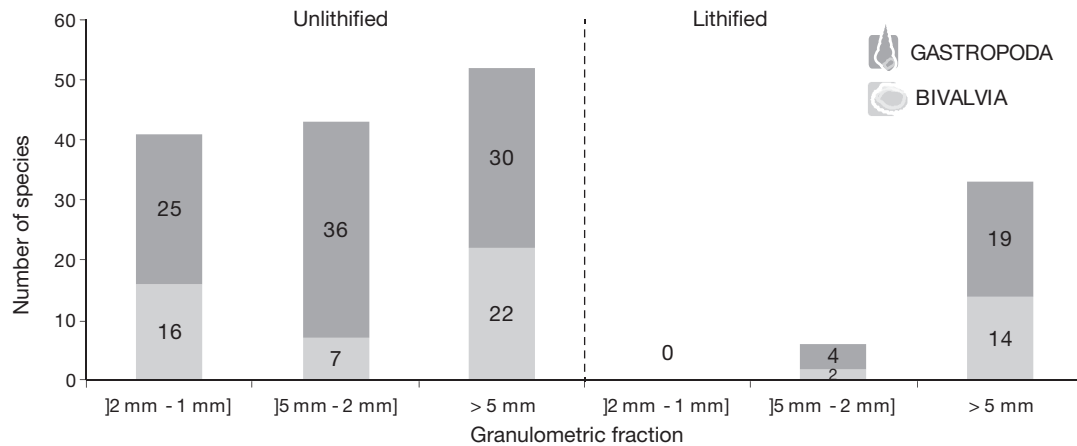
FIG. 7. — Number of mollusc species (gastropods and bivalves) as a function of their granulometric fraction and the kind of samples (unlithified versus lithified lithofacies) for the bed 5b of the "Falunière" of Grignon.
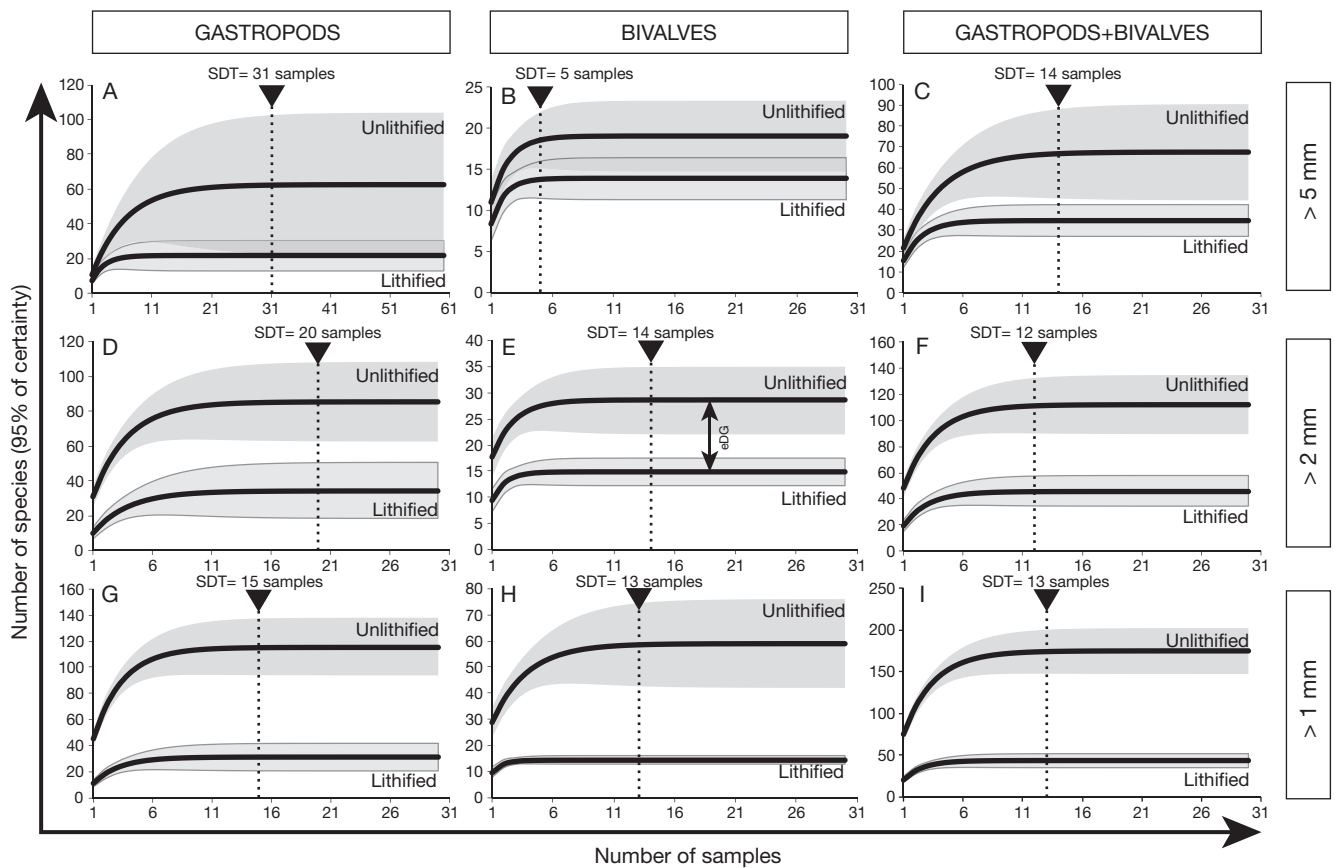

FIG. 8. — Sample-based rarefaction curves, plotted for gastropods (**A, D, G**), bivalves (**B, E, H**) and their sum (**C, F, I**), considering three cumulated size classes (> 5 mm: A-C; > 2 mm: D-F; >1 mm: **G-I**). Dotted lines represent the sampling/diagenesis bias threshold (**SDT**) for each analysis. A graphic representation of the variables used in the definition of the extrapolated Diagenesis Gap (**eDG**) is given on the diagram E.

that cannot be easily compared with more common fossil collections. Lithification and other taphonomic biases are usually selective and their effect can be predicted for given local conditions, at least qualitatively. A method considering taphonomic and lithological properties of local fossil collections should improve comparisons of localities and reliability of biodiversity signals derived from aggregation of large, uneven datasets.

A REMAINING PROBLEM WITH LARGE TAXA

Koumac (New Caledonia) is a Recent Pacific locality in which the high mollusc's diversity is homogeneously described for all shell sizes. The specimens larger than five millimetres represent around half of the species diversity (Bouchet *et al.* 2002), while this is only 20% at Grignon. This low number of large taxa is unexpected as the selective loss of smaller forms would increase the relative frequency of larger forms

(Hendy 2011). At least three hypotheses can explain the low frequency of larger shells at Grignon:

1) in theory, large taxa often belong to the rare taxa and their sampling is subdued to an extensive sampling effort. Larger shells have usually low populations densities compared to smaller forms. A long life and low rate of juvenile production reduce their chances to be transferred in dead shell assemblages, which reinforce their rarity in shell assemblages. Most of the largest taxa known at Grignon are uncommon and are only sampled pending the processing of large amount of sand or selective search. Even their juvenile stages are encountered at a low frequency. Usual standardized sampling processes used in palaoecological and paleobiodiversity studies remain inaccurate at collecting the largest forms;

2) in lithified facies, the diversity of the largest shells is over-estimated in comparison to that of unlithified facies. Large specimens are genuinely easily identifiable, but they are also more likely to be shattered during sediment compaction. In lithified facies, most of the fragmented shells can be identified at species level and considered in biodiversity estimates (Fig. 9). In unlithified sediments, the fragments of shells will usually be mixed during processing of the sediments and they have limited chances to be taken into account for biodiversity estimates. The lithification does not affect large and small shell in a similar manner, but the number of large taxa will be underestimated in unlitified samples, compared to the smaller ones;

and 3) shell size distributions of molluscs vary in time and space. The low number of large shells reflects the initial conditions and can be investigated on macroevolutionary and macroecological perspectives.

BIODIVERSITY ASSESSMENT AND LITHIFICATION BIAS

The impact of the lithification may have tremendous consequences on the evaluation and comparisons of the paleobiodiversity, at local, regional, or larger scales according to the uneven distribution of lithification conditions in time and space. At the regional scale, we have compared the biodiversity of Grignon's bivalves and gastropods with values encountered at four Lutetian outcrops from the Paris Basin, bearing shell beds of calcareous sand (Villiers-Saint-Frédéric, Chaussy, La Ferme de L'Orme and Damery) and values encountered at two fossiliferous outcrops of lithified limestone (Nanterre and Vanves). Then we have made comparisons of mollusc species richness measured at Baron (Oise), a Bartonian outcrop of the Paris Basin bearing a sandy facies, with values measured at the Bartonian of the Blaye area, in the Aquitaine Basin, which bears a lithified limestone (Calcaire de l'Octroi). At an even larger scale, we have compared mollusc species richness measured at Grignon with values measured at a famous Italian Lutetian locality, San Giovanni Ilarione (Verona, Veneto Basin), in which the molluscs were collected in lithified, or partially lithified limestone.

COMPARISON BETWEEN GRIGNON AND FRENCH LUTETIAN LOCALITIES BEARING UNLITHIFIED LIMESTONE

The whole inventory of Grignon gives 506 species of gastropods and 282 species of bivalves (Merle & Courville 2008, modified). With its outstanding mollusc richness, this historical and well known locality contributes to consider the Lutetian from the Paris basin as a hotspot of paleobiodiversity for which 1550 species of gastropods and 540 species of bivalves are recorded (Merle 2008b). The inventory of Grignon is mainly based on two rich beds, the Campanile giganteum bed (unit 5, Fig. 2) and the Calcaire à Orbitolites bed (units 4, 3, 2, Fig. 2). The other localities display very similar paleoenvironmental (shallow marine waters) and geological characters (Campanile giganteum bed and Calcaire à Orbitolites bed). The locality of La Ferme de l'Orme (Yvelines, Beynes city), known since about a century and a half (Goubert 1863), exposes the upper part of Calcaire à Orbitolites. The inventory (Merle & Courville 2008) gives 286 species of gastropods and 101 species of bivalves (Fig. 10). Molluscs found in the Calcaire à Orbitolites at Chaussy (Yvelines) were first studied by Deshayes (1795-1875). The total species richness amounts to 424 species of gastropods and 80 species of bivalves (Fig. 10; see Le Renard 2014). The Campanile giganteum bed and the Calcaire à Orbitolites outcrop also in the locality of Villiers-Saint-Frédéric (Yvelines; see Goubert 1863), with a total of 624 species of gastropods and 164 species of bivalves for both units (Fig. 10; Le Renard 2014). The locality of Damery (Marne), with exposures of the Campanile giganteum bed, was made known by the naturalist Guettard (1751), bearing 137 species of gastropods and 29 species of bivalves (Le Renard 2014). The richness documented for individual locality show a large variation (between around 140 and 620 species), depending of different parameters not further discussed here (e.g., number of shell beds, extension of the outcrop, research effort, selective sampling of gastropods or bivalves). However, the three localities geographically close to Grignon (Yvelines, west of the Paris Basin) share very high species richness. The species richness at Grignon is even exceeded by that at Villiers-Saint-Frédéric, where it peaks to 620 species of gastropods. The lowest value is obtained at Damery (east of the Paris Basin), but this result could due to local paleoenvironmental effects (muddy facies, Merle & Courville 2008). Thus, the species richness found at Grignon is not exceptional at a regional scale, or at least is comparable to specie richness in shoreface calcareous sand from other localities of the middle Lutetian of the Paris Basin.

COMPARISON BETWEEN GRIGNON AND FRENCH LUTETIAN LOCALITIES BEARING LITHIFIED LIMESTONE

The Lutetian of the Paris basin is famous for its lithified limestone, which was used during many centuries for Paris monuments construction such as Notre-Dame-de-Paris cathedral (Gély 2008b, de Wever *et al.* 2008). The lithified limestone, mainly represented by the Campanile giganteum bed (also called "banc à Verrins" by the quarrymen) and the Calcaire à Orbitolites (also called Lambourdes and Vergelé) occurs in many localities of the Paris Basin, including Paris and its

FIG. 9. — Shells preservation from lithified samples (unit 5b, "Falunière" of Grignon, Yvelines, France): **A**, sample LS3 showing a fragment of the species *Athleta* (*Volutopupa*) *citharoedus* (Holten, 1802), MNHN.F.A51275; **B**, sample LS1 showing an unidentifiable fragment of bivalve, MNHN.F.A51276. **White arrow** shows the aragonitic shell of the gastropod. **Black arrow** shows a bivalve bearing remains of its shell and a part of its internal mold. Scale bars: 2 cm. Photo: M. Sanders.

neighbourhood, the neighbourhood of Creil, Oise, in the Northwestern part, and in neighbourhood of Reims, Marne, in the easternmost part of the basin. The two neostratotypes, Saint-Vaast-les-Mello and Saint-Leu-d'Esserent (Oise) displays this facies (Blondeau & Cavelier 1962; Blondeau 1964). Although the lithified limestone can be observed in many localities of the Paris basin and was studied by numerous geologists since the 18th century, it very weakly contributed

to the knowledge of the mollusc diversity. An indication of this weak contribution is that no species from the lithified limestone was presented in the monographs by Lamarck, Deshayes and Cossmann. Inventories of molluscs are also few and it is only in the thesis of Abrard (1925) that several molluscs lists are presented. The most complete lists are those from the quarries of Vanves and Nanterre near Paris which exposed the Campanile giganteum bed and the Calcaire à Or-

FIG. 10. — Comparison of species richness from Middle Eocene French and Italian sites displaying lithified and unlithified facies (all localities are Lutetian, except Baron, Blaye and Gironde which are Bartonian).

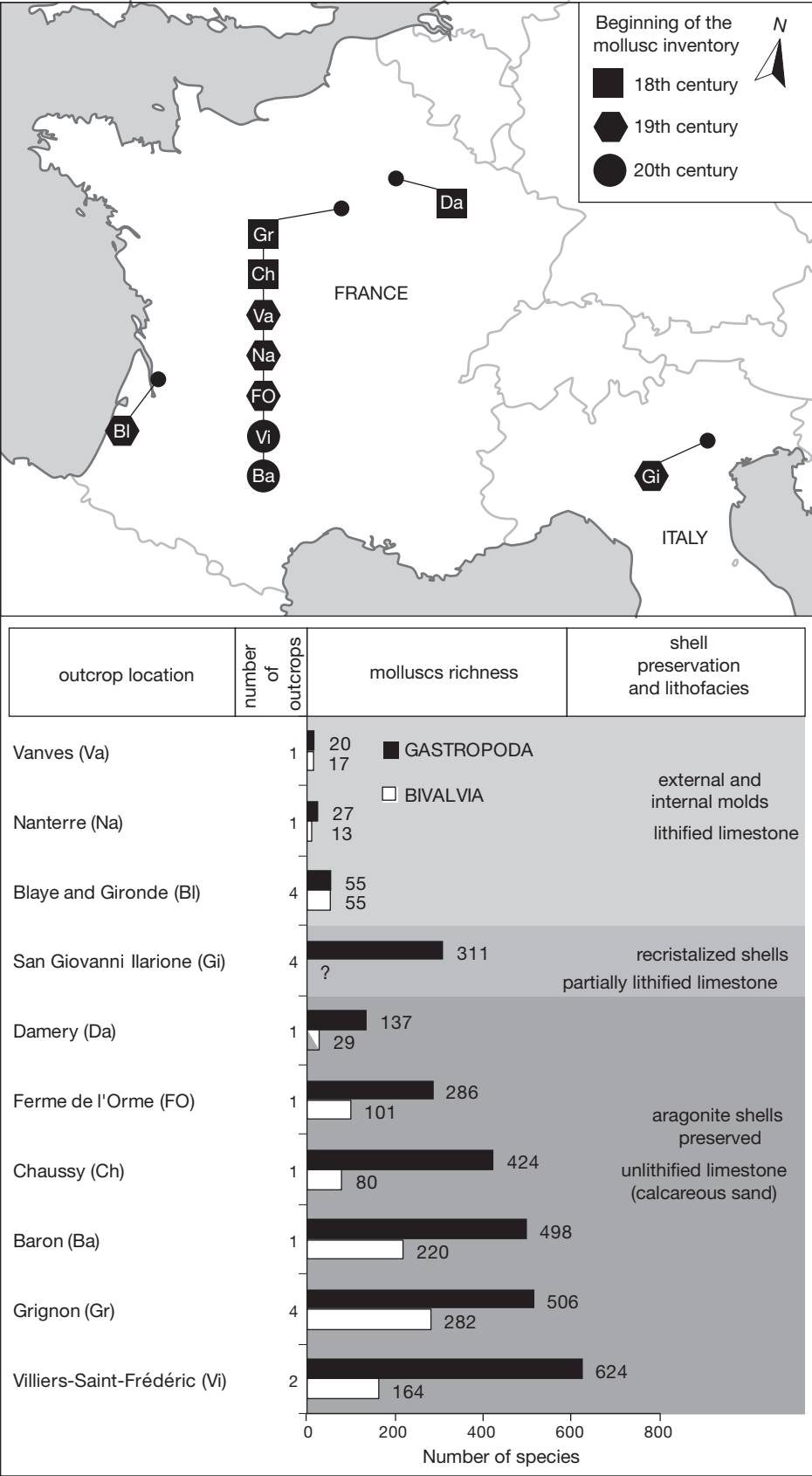FIG. 11. — **A**, Lithified sample from the Lutetian of San Giovanni Ilarione (Italy) (MNHN.F.B21800) suggesting the difficulty to determine species (mostly Mytilidae Rafinesque, 1815); **B**, **C**, difference of preservation between two Rimellidae Stewart, 1927 from Grignon (**B**, an aragonitic shell of *Rimella fissurella* (Linnaeus, 1767) MNHN.F.A51277) and San Giovanni Ilarione (**C**, a recrystallized shell of *Ectinochilus retiae* (De Gregorio, 1880) MNHN.F.A51278). Scale bars: 2 cm. Photo: G. Doitteau.

bitolites. At Vanves (Fig. 10), Abrard (1925) cited 20 species of gastropods and 17 species of bivalves, whereas at Nanterre (Fig. 10) he cited 27 species of gastropods and 13 species of bivalves. The limited research effort may partially explain these low values, similar to those found in our samples from the lithified Campanile giganteum bed of Grignon, in which we counted 26 species of gastropods and 13 species of bivalves for three samples. The consistently low values of lithified samples in stratigraphically equivalent levels of a region demonstrate the negative impact of the lithification of sediments for the evaluation of the paleobiodiversity. It emphasize the contrast of species richness between both types of lithofacies, whom we were able to determine in the level 5b of the "Falunière" of Grignon.

COMPARISON BETWEEN GRIGNON AND FRENCH BARTONIAN LOCALITIES

In the Paris basin, the Bartonian is the second richest stage regarding mollusc diversity, with around 1,000 recorded gastropod species (Merle 2008b: figs 83, 84). The richest localities from the Paris Basin correspond to the "Auversian" sands (Auversian facies of former authors), contemporaneous with the early Bartonian (Aubry 1985). The Auversian facies outcropping at the quarry of Baron (Oise), from a shallow marine depositional environment (Dolin *et al.* 1980), provides a further useful chance for a comparison with the unlithified Grignon facies. Species richness at Baron includes 498 species of gastropods and 220 species of bivalves (Fig. 10), values comparable to those from the unlithified facies found in the middle Lutetian of Grignon. Unfortunately, there is no known Auversian locality in the Paris Basin with lithified sediments. The species richness of Baron can be compared with

the one of the shallow marine limestone of the Calcaire de l'Octroi located between Blaye and Saint-André-de-Cubzac (Gironde) in Southwestern France. Several papers have been published by Vasseur (1881), Benoist (1887), Fabre (1939), Larroudé (1967), Cossmann (1922) and more recently by Pacaud & Ledon (2010, 2012). A synthetic list from these authors allows to measure a species richness of 55 species of gastropods and 55 species of bivalves (J.-M. Pacaud, written communication), further emphasising the strong loss of species richness in the lithified facies.

COMPARISON BETWEEN GRIGNON AND THE ITALIAN LUTETIAN LOCALITY SAN GIOVANNI ILARIONE (LITHIFIED LIMESTONE)

As seen above, the Lutetian of the Paris Basin displays exceptional species richness in unlithified facies and was recently considered to be a hotspot of the paleobiodiversity (Merle 2008b; Huyghe *et al.* 2012). However, during the Middle Eocene, the Western Tethys displays a paleogeographic position close the equatorial line and a tectonic activity favouring the emergence of archipelagos (Butterlin *et al.* 1993a, b). These features match more with the geographic configuration of the Recent Indo-Pacific marine hotspots (Merle 2008b: fig. 86) than those of the Paris Basin, but sediments in the Western Tethys are usually lithified, leaving a doubt regarding the status of the Paris Basin as richest area of Cenozoic.

San Giovanni Ilarione (Veneto Basin, Italy) belongs to the Western Tethyan realm. As for Grignon, it is a Lutetian locality abundantly studied for its molluscs (Brongniart 1823; De Gregorio 1880; Quaggiotto & Mellini 2008). Both localities correspond to carbonate environments. In addition, the Italian gastropods fauna is in many ways similar to that of Grignon,
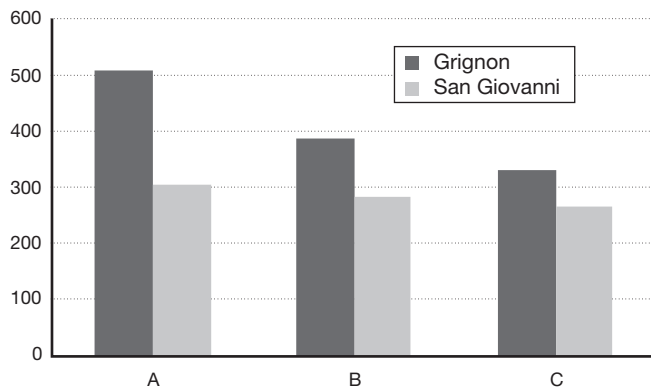
Fig. 12. — Comparison of the species richness between Grignon (Lutetian, Paris Basin, France) and San Giovanni Ilarione (Lutetian, Veneto Basin, Italy): **A**, raw species richness (difference in favour of Grignon: 201 species, 39.7%); **B**, species richness of 49 shared families including small forms (difference in favour of Grignon: 104 species, 28.8%); **C**, species richness of 43 shared families excluding small forms (difference in favour of Grignon: 62 species, 18.8%). It shows that the species richness of shared families excluding small forms minimizes the effect of lithification bias.

with 114 shared species. Grignon is located at higher latitude in the Paris Basin which is open towards the Atlantic Ocean and the paleotemperature reconstructions (mean annual temperatures between 20 and 23°C) indicate a cold Eocene interval (Huyghe *et al.* 2012, 2015). However, for Kantor & Sysoev (2005), the species size frequency distribution may not vary regarding the latitudinal gradient (e.g., England vs New Caledonia). Then we assume that initial molluscan diversity had likely the same size structure in San Giovanni Ilarione and Grignon. The strongest difference is that Grignon is mostly constituted of unlithified limestone, whereas San Giovanni Ilarione displays lithified or partially lithified rocks (Fig. 11 A).

The inventory for San Giovanni Ilarione gives 305 marine gastropod species (bivalves have not been revised yet) within 62 families (Quaggiotto & Mellini 2008), but the species richness does not excess Grignon's (506 species). The raw difference of species richness between Grignon and San Giovanni Ilarione represents 201 species (or 39.72%). Among the 62 families, 49 are shared between both localities, where they are represented by 388 species at Grignon and by 284 species at San Giovanni Ilarione. If the comparison is reduced to the shared families, Grignon is then 104 species richer (or 26.80%). However, among these shared 49 families, six (Tripanaxidae Gougerot & Le Renard, 1987, Rissoidae Gray, 1847, Actaeonidae d'Orbigny, 1843, Marginellidae Fleming, 1928, Cylichnidae Adams & Adams, 1854 and Buccinidae Rafinesque, 1845) are represented by smaller species at Grignon (58 species) than at San Giovanni Ilarione (16 species). As smaller species are prone to lithification bias, we have excluded from comparisons these six families. Then, the species richness of the 43 remaining families remains still lower at San Giovanni Ilarione (268 species) than at Grignon (330 species), but the difference represents only 62 species (or 18.79%). Thus considering a comparison only based on the shared families and excluding the smaller species, the lithification bias could be minimized (Fig. 12).

On the other hand, if lithification biases would have the same effects at San Giovanni Ilarione and Grignon, we would expect an underestimation of the species diversity at San Giovanni Ilarione. Considering a rough correction of San Giovanni Ilarione biodiversity following the eDG values measured at Grignon, then the estimation of San Giovanni's species richness would reach 670 species for a size over 2 mm (Fig. 8D); the 268 known species representing only 40% of the potential biodiversity. This value exceeds both the amount of gastropods found in Grignon (506 species) or Villiers-St-Frédéric (624 species). Although sampling bias would be minimal for extensively studied localities like Grignon and San Giovanni Ilarione, the reliability of corrected richness remains unclear without direct testing of sampling artifacts on the taxonomic inventory, and without considering the selective loss of smaller taxa through lithification bias.

Using the different approaches seen above, the values suggest that the raw difference of species richness currently measured at San Giovanni Ilarione and Grignon (305 versus 506) is misleading. All evidence suggests that the Veneto molluscs were possibly as or more diverse than those of the Paris Basin, which would be more congruent with patterns of latidunal biodiversity gradients described for living molluscs (Roy *et al.* 2004), and with the hypothesis of a biodiversity hotspot in the western Tethys during the Eocene for the Foraminifera (Renema *et al.* 2008).

CONCLUSION

The recovered number of species in lithified samples from the bed 5b of the "Falunière" of Grignon is by 70% lower than that of unlithified samples. The bias increases with decreasing size, smaller shells being more difficult to isolate and identify on the surface of lithified samples. In modern seas, most of mollusc diversity is constituted by small and rare species. The difficulties to account for specimens smaller than 5 millimetres certainly have a tremendous effect over fossil biodiversity as shown at the regional scale. And it may have blurred our evaluation of the main malacological hotspots from the Middle Eocene. As shown, the Veneto Basin may have displayed a similar or a much greater diversity than the Paris basin and this need further investigation. Only the best conditions of preservation of fossils offer the opportunity for direct comparisons of paleontological with recent assemblages of taxa. The high difference of diversity accessible from lithified and unlithified samples and the reconstructed biodiversity patterns over time and space. Whether we can identify lithification bias, its consideration into analyses of past biodiversity patterns remains rather difficult. Lithified carbonates are more common in the tropical belt, which could lead to an underestimate of tropical diversity compared to that of temperate environments. The amount of unlithified lithofacies is virtually null before the Cretaceous period, and increases progressively to reach 40% of the fossil collections in the Neogene. The problem can

be mitigated by excluding records from unlithified rocks in the reconstruction of the history of marine invertebrate biodiversity during the Phanerozoic. A method for comparison or correction of biodiversity signals that account for the heterogeneity of rock records over time and space is still to be elaborated.

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APPENDIX 1. — Results of the counting by species (presented by systematic order) for the six samples (US1-3 and LS1-3) from the unit 5b of the Lutetian from Grignon (Yvelines, France).

		US1			US2			US3			LS1			LS2			LS3		
		>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1
GASTROPODA																			
Trochidae	*Eumargarita spirata* (Lamarck, 1804)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Calliostomatidae	*Solariella* (*Microgaza*) *solarioides* (Deshayes, 1863)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Solariella sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solariellidae	*Periaulax exisus* (Lamarck, 1804)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turbinidae	*Collonia* (*Cirsochilus*) *grignonensis* (Deshayes, 1863)	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0	0
Phasianellidae	*Tricolia* sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cerithiidae	*Bittium* (*s.str.*) *semigranosum* (Lamarck, 1804)	1	1	5	0	0	5	0	0	5	0	0	0	0	0	0	0	0	0
	Clava (*Semivertagus*) *melanoides* (Lamarck, 1804)	0	3	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0
	Clava (*Semivertagus*) *unisulcata* (Lamarck, 1804)	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	Hemicerithium bernayi (Cossmann, 1889)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Ptychocerithium lamellosum (Bruguière, 1792)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0
	Ptychocerithium sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diastomatidae	*Keilostoma* sp.	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Keilostoma turricula (Bruguière, 1789)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Turritellidae	*Haustator imbricatarius* (Lamarck, 1804)	0	4	51	1	2	25	3	3	12	0	0	0	0	0	1	0	2	0
	Sigmesalia indet. 1	0	3	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
	Sigmesalia multisulcata (Lamarck, 1804)	3	22	0	3	27	53	7	17	42	0	1	0	4	1	0	3	2	1
Ampullinidae	*Crommium acutum* (Lamarck, 1804)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Naticidae	*Amauropsina canaliculata* (Lamarck, 1804)	0	5	1	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0
	Natica epiglottina Lamarck, 1804	0	1	2	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0
	Natica sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	Natica specialis Deshayes, 1864	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Payraudeautia caillati (Deshayes, 1864)	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rissoidae	*Pusillina nana* (Lamarck, 1804)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Rissoina (*s.str.*) *clavula* (Deshayes, 1825)	0	0	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0
Elachisinidae	*Lacunella depressa* (Deshayes, 1861)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tornidae	*Circulus* (*s.str.*) *planorbularis* (Deshayes, 1832)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rimellidae	*Ectinochilus canalis* (Coquebert & Brongniart, 1793)	2	8	2	1	1	1	0	1	4	0	0	0	0	0	0	1	0	0
	Ectinochilus planus Beyrich, 1854	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0
	Rimella fissurella (Linnaeus, 1767)	1	3	0	0	2	0	1	0	0	0	0	0	4	0	0	8	1	0
Seraphsidae	*Seraphs* sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ranellidae	*Sassia* sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Omalaxidae	*Omalaxis bifrons* (Lamarck, 1804)	0	18	31	0	10	14	2	5	17	0	0	0	0	0	1	0	0	1
Xenophoridae	*Xenophora schroeteri* (Gmelin, 1791)	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Epitoniidae	*Amaea* (*Acrilla*) *perangusta* (de Boury, 1914)	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Newtoniellidae	*Laeocochlis* sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Buccinidae	*Suessionia costuosa* (Deshayes, 1864)	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Fasciolariidae	*Clavilithes* (*Clavellofusus*) *parisiensis* (Mayer-Eymar, 1877)	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2	0	0
Muricidae	*Paziella* (*Flexopteron*) *fraterculus* (Deshayes, 1861)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Typhis (*s.str.*) *tubifer* (Bruguière, 1792)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Costellariidae	*Conomitra graniformis* (Lamarck, 1803)	0	1	4	0	1	2	0	1	1	0	0	0	0	0	0	0	0	0
Marginellidae	*Gibberula ovulata* (Lamarck, 1803)	0	6	5	0	7	3	0	2	2	0	0	0	0	0	0	0	1	0
	Microvulina cossmanni (Morlet, 1888)	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Stazzania sp.	0	0	0	0	1	8	1	0	0	0	1	0	0	0	0	0	0	0
	Volvarinella crassula (Deshayes, 1865)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	Volvarinella eburnea (Lamarck, 1803)	0	8	12	0	0	0	0	0	7	0	0	0	0	0	0	0	2	0
Volutidae	*Athleta* (*Volutopupa*) *citharoedus* (Holten, 1802)	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	7	0	0
	Volutocorbis bicorona (Lamarck, 1802)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Olividae	*Amalda* (*Baryspira*) *dubia* (Deshayes, 1830)	0	1	0	0	2	0	0	0	0	0	0	0	1	0	0	2	0	0
	Amalda (*Gracilispira*) *buccinoides* (Lamarck, 1802)	0	0	0	0	2	0	1	1	0	1	0	0	0	0	0	0	0	0
	Ancillarina canalifera (Lamarck, 1802)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Olivancillaria (*Pseudolivella*) *mitreola* (Lamarck, 1802)	0	27	12	1	5	6	1	8	2	0	0	0	2	0	0	9	2	0
	Olivancillaria (*P.*) *parisiensis* (Cossmann, 1889)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conidae	*Conus* sp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Pseudotoma coronata (Lamarck, 1803)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Raphitoma (*s.str.*) *baudoni* (Deshayes, 1865)	0	1	2	0	0	2	1	5	1	0	0	0	0	0	0	1	0	0
	Syphopsis denudata (Deshayes, 1864)	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Borsoniidae	*Domenginella* (*Scobinella*) *lyra* (Deshayes, 1834)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clavatulidae	*Turricula* (*Crenaturricula*) *dentata* (Lamarck, 1804)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Terebridae	*Mirula plicatula* (Lamarck, 1803)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Turridae	*Crassispira* (*Tripia*) *acutangularis* (Deshayes, 1834)	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Crassispira (*Tripia*) *subturrella* (de Boury, 1899)	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
	Drillia sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Eopleurotoma bezanconi (de Boury, 1899)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
	Eopleurotoma bicatena (Lamarck, 1804)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Eopleurotoma decussata (Lamarck, 1804)	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0

Appendix 1. — Continuation.

		US1			US2			US3			LS1			LS2			LS3		
		>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1	>5	5-2	2-1
	Oxyacrum obliterata (Deshayes, 1834)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
	Pseudotoma coronata (Lamarck, 1803)	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
	Turricula crenaturricula (Deshayes, 1834)	0	2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
	Turridae indet. 1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
	Turridae indet. 2	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
	Turridae indet. 3	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	Turridae indet. 4	0	0	1	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0
	Turridae indet. 5	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0
	Turridae indet. 6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Turridae indet. 7	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Turridae indet. 8	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Turridae indet. 9	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cancellariidae	*Unitas separata* (Deshayes, 1864)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Acteonidae	*Acteon* (*s.str.*) *deshayesi* (de Raincourt & Munier-Chalmas, 1863)	0	1	3	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0
Architectonicidae	*Architectonica* sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Nipteraxis plicatum (Lamarck, 184)	0	1	1	0	2	0	1	0	0	1	0	0	0	0	0	3	0	0
Pyramidellidae	*Syrnola* (*Puposyrnola*) *parva* (Deshayes, 1861)	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Syrnola sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ringiculidae	*Ringicula* (*s.str.*) *ringens* (Lamarck, 1804)	0	0	7	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Haminoeidae	*Roxania ovulata* (Lamarck, 1804)	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	1	0
Cylichnidae	*Cylichna* (*s.str.*) *bruguierei* (Deshayes & Milne-Edwards, 1836)	0	2	5	0	0	0	1	2	0	0	0	0	1	0	0	1	0	0

BIVALVIA

		US1			US2			US3			LS1			LS2			LS3		
Nuculidae	*Nucula* (*s.str.*) *parisiensis* Deshayes, 1860	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arcidae	*Arca* sp.	0	0	0	0	0	3	0	0	1	0	0	0	0	0	0	0	0	0
	Barbatia (*s.str.*) *barbatula* (Lamarck, 1805)	2	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
	Barbatia sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Noetiidae	*Scapularca scapulina* (Deshayes, 1805)	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Scapularca sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Striarca (*Arcopsis*) *quadrilatera* (Lamarck, 1805)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Trigonodesma lissa (Bayan, 1873)	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
	Trinacria deltoidea (Lamarck, 1805)	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Glycymerididae	*Glycymeris dispar* (Defrance, 1826)	5	2	0	2	3	0	1	3	0	0	0	0	0	0	0	0	0	0
	Glycymeris pulvinata (Lamarck, 1805)	6	5	0	1	2	0	5	11	0	2	0	0	0	0	0	0	0	0
	Glycymeris sp.	0	0	22	0	0	21	0	0	8	0	0	0	10	4	0	6	0	0
Limopsidae	*Limopsis* (*Pectunculina*) *granulata* (Lamarck, 1805)	2	4	9	0	10	9	3	9	4	0	0	0	2	0	0	2	1	0
Ostreidae	*Cubitostrea plicata* (Solander in Brander, 1766)	2	4	4	1	2	3	3	4	0	0	0	0	1	1	0	1	0	0
Crassatellidae	*Bathytormus lamellosus* (Lamarck, 1805)	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0
	Crassatella sp.	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
	Crassatella sp. 1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Crassatella sp. 2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Crassatina triangularis (Lamarck 1805)	0	2	10	0	2	2	4	8	1	0	0	0	1	1	0	0	0	0
Carditidae	*Cardita* sp.	0	0	37	0	0	14	0	0	7	1	1	0	1	2	0	2	0	0
	Cyclocardia (*Arcturellina*) *elegans* (Lamarck, 1806)	0	4	0	0	4	0	0	9	0	0	0	0	0	0	0	0	0	0
	Cyclocardia (*Arcturellina*) *pulchra* (Deshayes, 1858)	0	0	0	1	1	0	1	2	0	0	0	0	0	0	0	0	0	0
	Venericardia acuticosta Lamarck, 1806	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
	Venericardia imbricata (Gmelin, 1791)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Condylocardiidae	*Condylocardia atomus* (Deshayes, 1858)	0	0	10	0	0	14	0	0	8	0	0	0	0	0	0	0	0	0
Lucinidae	*Parvilucina* (*s.str.*) *pusilla* (Deshayes, 1857)	0	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Montacutidae	*Laubriereia goodallina* Cossmann, 1887	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cardiidae	*Cardium* (*Loxocardium*) *obliquum bouei* (Deshayes, 1858)	1	1	0	1	1	0	2	0	0	1	0	0	2	0	0	1	0	0
	Cardium sp.	0	0	1	0	0	1	1	2	0	0	0	0	2	0	1	5	0	0
	Vepricardium (*s.str.*) *asperulum* (Lamarck, 1805)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Veneridae	*Callista* (*s.str.*) *elegans* (Lamarck, 1806)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Costacallista laevigata (Lamarck, 1806)	0	3	3	0	1	0	0	7	1	1	0	0	3	2	0	7	0	0
	Meroena semisulcata (Lamarck, 1806)	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
	Pitar (*Calpitaria*) *parisiensis* (Deshayes, 1857)	0	3	0	0	0	0	1	3	5	0	0	0	0	0	0	1	0	0
	Pitar sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
	Tivelina gibbosula (Deshayes, 1857)	2	0	1	2	0	2	2	5	1	0	0	0	0	0	0	0	0	0
	Veneridea indet.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Tellinidae	*Tellina* (*Elliptotellina*) *tellinella* (Lamarck, 1806)	0	4	15	0	2	3	0	3	3	0	0	0	0	1	0	1	1	0
Semelidae	*Abra pusilla* (Lamarck, 1806)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Mactridae	*Spisula* (*Austromactra*) *semisulcata* (Lamarck, 1805)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Spisula (*Austromactra*) sp.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Corbulidae	*Caryocorbula striata* (Lamarck, 1801)	3	8	14	0	6	2	4	13	3	0	1	0	1	0	0	2	1	0
	Notocorbula rugosa (Lamarck, 1806)	1	2	0	0	0	1	1	3	0	0	0	0	1	0	0	2	0	0
	Varicorbula minuta (Deshayes, 1824)	0	0	25	0	0	19	0	0	8	0	0	0	0	1	0	0	0	3