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Extinction Events Among Jurassic Bivalves*

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Abstract: Generic/subgeneric level data on bivalves from the Jurassic Proto-Atlantic record three regional extinction events, at the end of the Pliensbachian, beginning of the Callovian and Tithonian stages. The extinction at the Tithonian is the most important in terms of magnitude and duration. These extinctions can correlate with sea-level changes and associated environmental deterioration. The end-Pliensbachian extinction, related to anoxia caused by a sharp rise of sea level, selectively eliminated infaunal bivalves. In the Callovian event, which was linked to a regional regression, the selection against infaunal group occurred only in mid-latitude area. Tithonian event was a result of extreme and prolonged regression and lacked the selective extinction of infaunal bivalves.

Keywords: extinction; Jurassic bivalves; Proto-Atlantic

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1 Introduction

Two extinction events among Jurassic organisms, at the end of the Pliensbachian and Tithonian stages, were confirmed at family level by Sepkoski et al[1]. Using species-level data of the molluscs, Hallam[2] demostrated that marine invertebrate mass extinctions at these times occurred on a regional, not a global scale. He estimated that 84% of species became extinct in West Europe in the end-Pliensbachian extinction, which was considered the most important of the whole Jurassic. However, no detailed studies on the Jurassic extinctions at the generic level were published up to date. Selective extinction has been recognized in some events, such as the end-Triassic extinction[3]. It remains to be examined in detail if any selectivity existed in the extinctions within the Jurassic, in spite of Hallam's suggestion based on species data[2]. The proposed causal mechanism for Jurassic extinctions — sea-level changes and associated habitat reduction or deterioration — also needs to be tested by providing more evidence.

The generic/subgeneric data on bivalves from the Jurassic Proto-Atlantic show that striking decline in diversity ocurred in the Toarcian, Callovian and Tithonian[4]. This suggests that a third extinction could exist at the end of the Bathonian or beginning of the Callovian, in addition to the extinctions

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at the end of the Pliensbachian and the Tithonian. The taxonomic data on bivalves from the Proto-Atlantic involving these three phases, which have been compiled[4], will be used here. The aim of the present study is threefold: first, to confirm the Jurassic extinctions among marine bivalves at the generic/subgeneric level; secondly, to examine the ecological selectivity in the extinctions; and thirdly, to discuss causal factors of these extinctions and selection patterns.

2 Bivalve data

Based on the systematically compiled Jurassic bivalve data[4], the extinction frates of selected regions in the Proto-Atlantic for the end-Pliensbachian, Callovian and Tithonian were calculated and shown in Table 1.

(1) **Pliensbachian:** The bivalve extinction event can be to various extent recognized in all seven regions. From Greenland, 45% genera/sugenera went extinct by the end of the Pliensbchian. The 22% extinct taxa include 14 infaunal genera/subgenera (53% of infauna) and 8 epifaunal genera/subgenera (42% of epifauna). Northern England, northern France and southwestern France recorded the most pronounced loss of bivalves, respectively with 77.5%, 100% and 85.7% of genera/subgenera becoming extinct. In the northern England, the 31 elimilated genera/subgenera include 21 (84%) infaunal and 10 (66.7%) epifaunal elements. The data from southern England show a disappearence of 32 genera/subgenera (53.3%) of the Plienbachian bivalves, with the loss of 22 (66.7%) infaunal elements and 8 (36.3%) epifaunal elements. In Morocco, the 35 (59.3%) extinct genera/subgenera include 19 (67.8%) infaunal taxa and 14 (50%) epifaunal taxa. Portugal was less affected by this extinction event, with 34.6% bivalves going disappeared.

Tab. 1 Genera/subgenera extinction rates of Pliensbachian, Callovian and Tithonian bivalves in the Proto-Atlantic

Regions	Late Pliensbachian	Early Callovian	Early Tithonian
E-Greenland	22/49= 45%	2/23= 8.6%	5/29= 17.2%
N-England	31/40= 77.5%	12/34= 35.3%	34/34= 100%
S-England	32/60= 53.3%	59/98= 60.2%	18/65= 27.7%
N-France	16/16= 100%	49/54= 90%	82/122= 67.2%
SW-France	24/28= 85.7%	32/57= 56.1%	38/38= 100%
Portugal	9/26= 34.6%	5/24= 20.8%	49/91= 53.8%
Morocco	35/59= 59.35%	36/72= 50%	16/44= 36.4%

(2) **Callovian:** The data from southern England, northern France, southwestern France and Morocco show a striking decrease in genera/subgenera numbers. In southern England, of 98 genera/subgenera recorded from the Bathonian, 59 (60.2%) disappeared well before the beginning of the Callovian. These 59 disappeared genera/subgenera include 42 infaunal elements (75%) and 10 epifaunal elements (31.2%). The data from northern France show a loss of 100%. In southwestern France, 56.1% of Bathonian bivalves did not move into the Callovian. From Morocco 36 of 72 taxa (50%) became extinct. 24 of 46 infaunal genera/subgenera (52.2%) and 13 of 26 epifaunal genera/subgenera (50%) were involved. Of those extinct bivalves, Tethyan elements were dominant.

(3) **Tithonian:** Because of the lack of marine shelf habitats during regression, Jurassic bivalves completely disappeared from northern England and southwestern France during the Tithonian. Northern France and Portugal also show a significant loss of bivalves. From northern France 82 of the 122 gener-

a/subgenera (67%) became extinct, with the disappearence of 52 infaunal elements (66.7%) and 30 epifaunal elements (68%). Portugal showed weaker response to the previous two extinction events, but got a sharp loss of 49 genera/subgenera (53.8%) during this phase. The 49 extinct taxa include 22 of the 45 infaunal bivalves (49%) and 27 of the 45 epifaunal bivalves (60%). Bivalve faunas from southern England were little affected at the beginning of the Tithonian, just with a loss of 27.7% taxa. By the end of the Tithonian, however, nearly a half of the standing bivalves, including 14 infaunal elements (45.2%) and 14 epifaunal elements (48.3%), became extinct. Greenland showed the same case as southern England. During the early Tithonian only 5 of the 29 genera/subgenera went disappeared, but 19 elements failed to persist to the end of the stage.

3 Discussion

The data presented above indicate that three regional extinction events among Jurassic bivalves can be recognized at the generic/subgeneric level, at the end of the Pliensbachian, beginning of the Callovian (probably end of the Bathonian) and Tithonian stages. Of them, the Tithonian extinction is the most profound. It lasted a longer time than the other two extinctions. A pronounced elimination of bivalves were recorded from the whole Proto-Atlantic area. Although some regions such as Greenland were little affected at the beginning of the event, they got a striking loss of bivalves by the end of the Tithonian. Within the Proto-Atlantic, 63 genera/subgenera (about 40% of the standing bivalves) became extinct at the beginning of the Tithonian and 41 genera/subgenera failed to survive the end of the Tithonian. The Pliensbachian extinction is second in importance. Extinction phenomenon in bivalves can be observed from most regions. The Callovian event is smaller in scale and less important than the other two extinctions. Striking changes among bivalves only took place in southern England, northern France, southerwestern France and Morocco. The rest regions were little affected during this event.

It has been proposed that there is a correlation between sea-level changes and faunal extinctions[2, 5]. Both regression and sharp transgression may result in increasing faunal extinction rates. This is so far a reasonable and acceptable hypothesis for the Jurassic extinctions. The Pliensbachian extinction was related to a rise of sea level, which caused the widespread development of anoxia of bottom waters. Such anaerobic or near-anaerobic conditions were not favourable for benthic organisms and led to eliminating a number of bivalves. By the Late Toarcian, with environmental amelioration, bivalves recovered and new elements appeared in some regions, especially in Portugal, where thus occurred an increase in diversity.

The Callovian extinction was bound up with regression on a regional scale. The event was recorded well in southern England, France and Morocco. During the Callovian, which was marked by a withdrawal of the Tethys, a number of Tethyan bivalves disappeared from these regions and migrated back south. Owing to its geographical location, Portugal held these Tethyan elements and showed an increase in diversity. During the same time, the Boreal Sea spread southwards, which was favorable for the dispersal of Boreal bivalves. As a result, bivalve diversity in Greenland and northern England raised.

The Tithonian extinction event was a result of extreme and prolonged marine regression[2, 6]. Land environment developed in northern England and southwestern France[7], where Jurassic bivalves were completely eliminated. In northern France isolated basins formed and a high energy shore environment influenced strongly by hinterland developed[8], which brought about the disappearence of a number of bivalves. Furthermore, because of the impeded connections between marine basins during times of lowstand of sea level, the bivalves which disappeared from a basin could not be supplied by transport from other basins. In the Lusitanian Basin of Portugal, as a consequence of the regression, salinity deviated increasingly from the normal value[9]. This severe anormal marine condition led to not only the `filtering out´ of stenohaline taxa but also the significant reduction of euryhaline bivalves[10]. Due to the deep-water conditions formed in the Late Jurassic[5], Greenland was less affected by the regression at the beginning of the Tithonian. However, with the prolongation of regression, conditions deteriorated gradually, which made about 35% of the Tithonian genera/subgenera fail to survive the end of the stage.

Based on end-Triassic bivalve data, a pattern of selective extinction of infaunal bivalves was proposed by McRoberts & Newton[3]. The data presented in this study just partly support this pattern. The end-Pliensbachian extinction data reveal a clear ecological selectivity, with a higher magnitude of infaunal extinction. Larval development can account for this selection phenomenon. Different larval types have different responses to anoxia environment. Lecithotrophic larvae develop in bottom waters, which lasts a few hours to a few days. They live with adults in the same environment and both will die in the event of anoxia. All bivalves with lecithotrophic larvae are infaunal. Planktotrophic larvae develop in surface waters, which may last several weeks to months, and are independent of anoxia conditions in bottom waters. Because of their longer pelagic duration, planktotrophic larvae have time to search for suitable habitat area to ressettle. Anoxia caused by a sharp rise of the sea-level during the end-Pliensbachian to beginning of the Toarcian indeed had a greater effect on lecithotrophic larvae. A pronounced decline of the percentage of lecithotrophic bivalves in the Toarcian can be observed in most regions (Fig. 1). This selective elimination of lecithotrophic larvae during the anoxia would in turn result in the increase in extinction rate of infaunal bivalves.

The Callovian extinction data from mid-latitude regions such as southern England show a significantly greater proportion of infaunal bivalve extinction, whereas the data from Morocco show equal extinction rates distributed among infaunal and epifaunal groups. The larvae pattern may also be an explanation for this selectivity related to latitudes. Marine regression and associated habitat restriction or deterioration were more detrimental for lecithotrophic larvae than for planktotrophic larvae[11], mainly because of their different pelagic duration. Environmental conditions, especially temperature, can influence the duration of larvae.

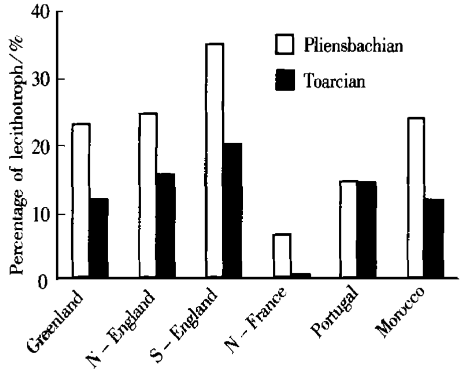

Fig. 1 Percentages of lecithotrophic genera/subgenera during the Pliensbachian and Toarcian in the Proto-Atlantic

The duration of the planktic larval stage can be longer and larvae can be carried further in tropical waters than in temperate waters[11]. This could have helped a number of lecithotrophs survive regression event in Morocco and may be the reason why no selection against infaunal bivalves are found there.

The Tithonian extinction data show little ecological selectivity. This is consistent with the fact that similar extintion rates distributed between lecithotrophs and planktotrophs. This suggests that the selective survivorship of planktotrophs take place only in short-term marine regression but not in extended periods of regression. The Tithonian prolonged regression coupled with environmental deterioration had an equal effect on both lecithotrophs and planktotrophs. The latter probably survived the initial stage, but failed to persist to the end of the event.

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侏罗纪双壳类绝灭事件

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摘　要: 侏罗纪原始大西洋的双壳类数据反映了 3 次区域性海生无脊椎动物绝灭事件, 分别出现于 Pliensbachian 末期, Callovian 初期以及 Tithonian 期. 其中以 Tithonian 事件规模最大, 影响范围最广. 海平面变化以及所伴随的环境恶化是导致绝灭的主要原因.

关键词: 绝灭; 侏罗纪双壳类; 原始大西洋

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