Proceedings of the Iowa Academy of Science

Volume 83 | Number Article 5

1976

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Jacobs, Stephen E. (Department of Geology, University of Nebraska, Lincoln, NE). *Neochonetes granulifer,* an Explosive opportunist from the Stull Shale (Upper Pennsylvanian) in Southwestern Iowa. Proc. Iowa Acad. Sci. 83(1): 20-22, 1976.

The brachiopod *Neochonetes granulifer* (Owen) is inferred to be an "opportunistic species" of the Stull Shale Member, Kanwaka Formation (Upper Pennsylvanian) in southwestern Iowa. The "opportunism" of this species is restricted to Horizon B of the Stull, but this restriction is evidently masked by the abnormally high number of *N. granulifer* in Horizons C and D, its shells inferred to have been reworked from B. The presence of this species as an opportunist is characteristic of the high physiological stress on the community of Horizon B as evidenced by the low brachiopod (and overall) diversity.

Neochonetes granulifer satisfies most of Levinton's (1970) criteria for recognition of "explosive opportunists," primarily by its sudden "population explosion" in a narrow stratigraphic range, its dominance of the fauna by 95%, the poor sorting of its shell size fractions, and its presence in a relatively young, low diversity-community.

INDEX DESCRIPTORS: Stull Shale, *Neochonetes granulifer.*

MacArthur (1960) first pointed out the distinction between opportunistic and equilibrium species. He states that opportunistic species possess relative abundances that are independent of the community structure, whereas equilibrium species show a dependence.

Levinton (1970) has ventured further to discuss the paleoecologic significance of opportunistic species in the fossil record. He states that they are essentially non-resource limited and characterized by "very high fecundity, short generation time," and "high intrinsic rates of population increase" (Levinton, 1970, p. 69). Equilibrium species, however, are resource limited and are characterized by their populations approaching the carrying capacity of the environment (Levinton, 1970). From another view, those species which are primarily adapted to unstable "physically controlled" communities of low diversity are eurytopic and those adapted to stable "biologically accommodated" communities of high diversity are stenotopic (Sanders, 1968).

The present study proposes to show that *Neochonetes granulifer* (Owen) behaves like an "explosive opportunist" at Folsom, Iowa according to Levinton's criteria discussed below. *N. granulifer,* a chonetid (see Fig. 1), is one of the most abundant brachiopod species in the Pennsylvanian of the midcontinent region of the United States. In the Stull Shale of Nebraska and Iowa it is most abundant in the doubly reoccurring *Crurityris-(Neochonetes)* Assemblages (Jacobs, 1973). The estimated number of individuals of *N. granulifer* ranges, in general, from about 10 to 250 (for size, *i.e.,* valve length, fractions greater than 2 mm. per 1 kilogram of rock sample). However, in the *Neochonetes* (opportunistic) Community, which is a part of the above assemblages, at Folsom, Iowa the estimated number of *N. granulifer* is 1625 (Table 1) (actually about 3500 individuals for all size fractions) (Jacobs, 1973, p. 46).

PALEOECOLOGIC SETTING

As revealed in Table 1, *N. granulifer* behaves strongly like an "explosive opportunist" at Horizon B, but is very rare above and below at Horizons E and A, respectively. Horizon A probably represented a young community with conditions of high physical stress and perhaps slightly reducing as evidenced by the dark gray color of the shale (Fig. 2) and very low biomass (Table 1). Horizon B, subsequently, experienced the sudden explosive proliferation of *N. granulifer*. The high stress on the community of this horizon is indicated by the low brachiopod (as well as overall) diversity. The occurrence of almost all light-weight shell forms, in turn, suggests a very "soupy" substrate. Rudwick (1970, p. 90) has suggested that the ability of chonetid brachiopods to appear in such large numbers may reflect their so-called ability to resist sedimentation in "soupy" environments by assuming a "quasi-nektonic" mode of life.

The number of *N. granulifer* decreases drastically upward in Horizons C and D to a virtual absence in Horizon E. The still relatively large number of individuals, 138 in C and 70 in D, is abnormal, because at the same horizons elsewhere *N. granulifer* numbers less than 30. The

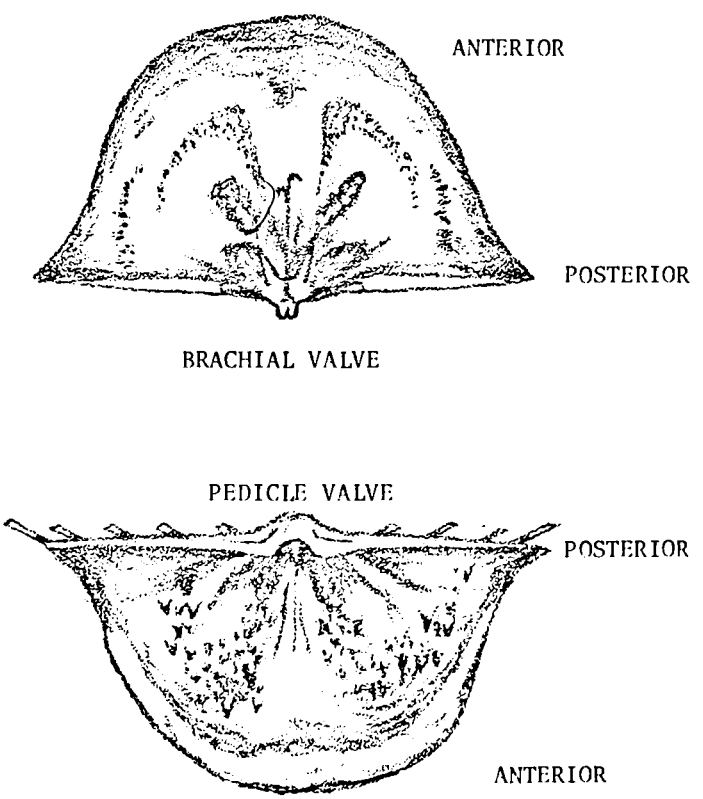

Figure 1: Diagram of *Neochonetes granulifer* (Owen) (x 2). Adapted from Pabian (1970).

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Table 1: FAUNAL DISTRIBUTION DATA

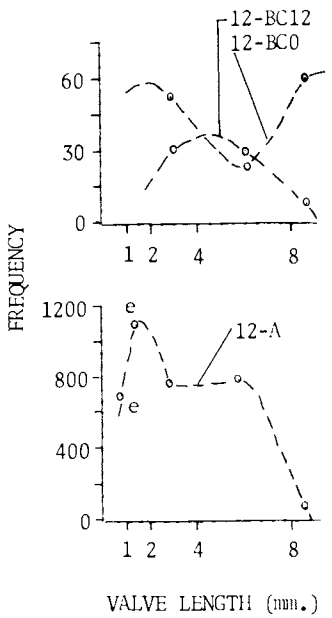
HORIZON	SAMPLE[a] NO.	TOTAL BIOMASS (gm./1 kg. sample) (e=estimated)	BRACHIOPOD[e] DIVERSITY INDEX VALUES	TOTAL NO. OF N. GRANULIFER INDIVIDUALS (>2 mm. per 1 kg.)	DISART. VALVE RATIO: DISART./ART.	OPPOSITE VALVE RATIO: BRACH./PED.	N. GRANULIFER SIZE FREQUENCY DISTRIBUTIONS (e=estimated)
F	12-BC35	33.00(e)	1.75	35	0.67	0.57	
E	12-BC24	63.00(e)	1.43	2	–	–	
D	12-BC12	62.00(e)	1.41	70[d]	0.89	0.52	
C	12-BC0	72.00(e)	1.25[b]	138[d]	0.83	0.44	
B	12-A	102.79	0.24	1625	2.21	0.87	
A	12-E	2.95	1.51[c]	8	1.67	0.80	

a = sample numbers from Jacobs (1973). b = value lowered by current activity.

c = non-representative value; sample size too small.

d = pre-burial number was probably much lower.

e = Shannon-Wiener information function values



unusually large number has, thus, apparently masked the evidence of pre-burial opportunism restricted to Horizon B and can perhaps be explained by the following hypotheses: (1) the unusually high *N. granulifer* density in Horizons C and D is due to some element of the physical environment specially preferred by the genus; (2) the transportation of *N. granulifer* shells from another contemporaneous locality; and (3) the erosion of *N. granulifer* shells from pre-existing rocks at the same locality.

The first hypothesis cannot explain the preference of *N. granulifer* for Horizon C, because in fact Horizons C, D, and E comprise a lithologically uniform interval of calcareous mudstone intercalated with argillaceous limestone lenses (Fig. 2), a uniform environment, in which one might expect a corresponding uniform distribution of *N. granulifer*, as Table 1 shows to the contrary.

The second hypothesis, first of all, requires the existence of another locality to provide a large enough source for *N. granulifer* (much greater than 100 individuals per kilogram of rock sample) to yield the number of individuals transported to Folsom at Horizons C and D. However, such a source area is not evident at other studied localities at the same horizons, for they contain less than 30 individuals, as mentioned above. The second requirement is that the shells of *N. granulifer* should be fragmented and disarticulated; this claim, too, is contradicted by the observation of shells greater than 4 mm. (valve length) being almost all unbroken and yielding, as Table 1 shows, a low disarticulated to articulated shell ratio of 0.83. Although a low opposite valve ratio of 0.44 suggests perhaps local transportation, such a value is not surprising for a "mixed assemblage" (see below): Thus, the second hypothesis appears untenable.

Therefore, the third hypothesis, the erosion of *N. granulifer* shells from pre-existing rocks at the same locality seems most feasible. Evidence to support this viewpoint is the underlying *Neochonetes* Community of Horizon B yielding 1625 individuals for size fractions greater than 2 mm. per kilogram of rock sample, thus, providing the most likely source for the 138 individuals of *N. granulifer* in Horizon C. In addition, Horizon C represents a "mixed assemblage," containing well-sorted *N. granulifer* shells of greater than 8 mm. (see Table 1), evidence which further strengthens the hypothesis that these shells were reworked (Jacobs, 1973, p. 72-3; Fagerstrom, 1964).

The cessation of opportunism for *N. granulifer* at the base of Horizon C in southwestern Iowa can certainly be attributed to the highly ameliorating conditions as evident by the high brachiopod diversity and by the relatively high diversity of morphologic and ecologic groups, as well as the number of individuals, of bivalves and gastropods. These high diversities, in turn, strongly indicate a more "biologically accommodated" benthic environment, with the prominence of large infaunal bivalves suggesting a firm enough substrate to support the heavy shells.

CRITERIA SATISFIED FOR OPPORTUNISM

Of those criteria for recognition of "explosive opportunists" listed by Levinton (1970, p. 76), the following are satisfied by *N. granulifer:*

(1) The random orientation (convex side of valves facing up or down stratigraphically as observed in the field) and lack of size sorting of specimens in Horizon B (see Table 1), particularly on individual bedding surfaces.

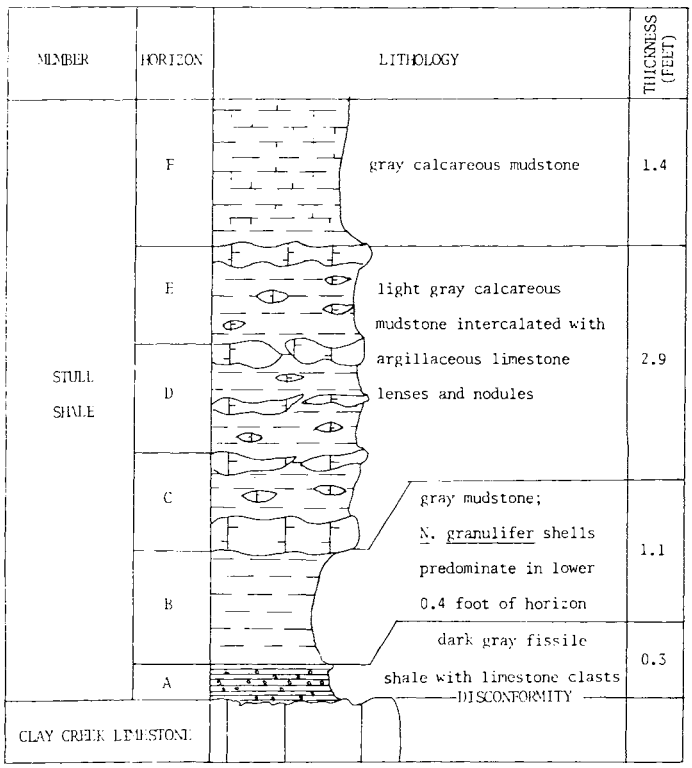


Figure 2: Stratigraphic column of the lower Stull Shale in southwestern Iowa[1].

(2) Aggregation of the sessile *N. granulifer* in clusters.

(3) *N. granulifer* is virtually restricted, pre-burially, to Horizon B indicating a brief invasion.

(4) *N. granulifer* dominates its community by comprising about 95% of all the estimated brachiopod individuals (as well as the entire fauna).

(5) The presence of *N. granulifer* in a young "physically controlled" community is evident by the very low brachiopod diversity index value (Sanders, 1968) (see Table 1), that species' sudden appearance in a horizon overlying the poorly fossiliferous shale of Horizon A, and the base of Horizon B lying only 0.3 foot above a disconformity at the base of the Stull Shale Member (see Fig. 2).

CRITERIA NOT SATISFIED FOR OPPORTUNISM

The following criteria of Levinton (1970) were, unfortunately, not satisfied for opportunism:

(1) *N. granulifer* is an opportunist in only one distinct faunal assemblage, although this author suspects the existence of other such assemblages above or below the Stull.

(2) Levinton (1970) indicates that the explosive opportunist is extremely abundant in a facies with which it is not usually associated. *N. granulifer*, on the contrary, is still fairly abundant in the Stull at the same horizon at localities other than Folsom, though it is only co-dominant or subordinate in abundance to the brachiopod *Crurithyris planoconvexa* (Shumard).

[1]Locality 12 of Jacobs (1973): Folsom Quarry (active), NW 1/4, SE 1/4, NW 1/4, Sec. 29, T. 73 N., R. 43 W.; Pacific Junction Quad., Mills Co.

ACKNOWLEDGEMENTS

Sincere appreciation and thanks are extended to Dr. J. A. Fagerstrom for his suggestion of this topic and for critically reading the manuscript. Conversations with Dr. B. F. Rowell were also helpful concerning *N. granulifer* populations in the Pennsylvanian.

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