

A Discrete Classification Procedure Applied to Encrusted Ammonite Conches—A Contribution to Taphonometrics

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Received: 27 October 2009 / Accepted: 4 April 2010
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Abstract Oyster encrustations on shells of the Albian (Cretaceous) ammonite species *Knemiceras persicum* (Iran) and *K. syriacum* (Lebanon) are analysed by discrete discriminant analysis, a method based on distributional difference in qualitative characters appropriate for greatly unequal sample sizes. The two localities, which are approximately coeval and separated by a distance of 2000 km, are shown to have different taphonometric backgrounds, as manifested in the mode of occurrence and preservation of the encrustations.

Keywords Epizoans · Ammonites · Discrete discrimination · Cretaceous · Albian · Middle East · Taphonometrics

1 Introduction

A problem occurs in interpreting the post-mortem history of cephalopod shells concerns, whether the fossils occur in situ or transported after death by water currents. A useful indicator of this problem is the presence of epizoans such as oysters and other encrusters on the shell. Kennedy et al. (2009) have given a detailed taxonomic and variational study of two species of *Knemiceras* from the Middle East, *Knemiceras persicum* Collignon (Iran) and *Knemiceras syriacum* (von Buch; Lebanon) to which the reader is referred for details bearing on the collections studied in this note and for stratigraphical analyses of the occurrences. The ammonites found in both places are remarkable in that a high percentage of conches bear epizoans, mainly oysters (Fig. 1).

The material studied in this paper comes from beds of Albian age (Kennedy et al. 2009). Encrusted *Knemiceras syriacum* (von Buch) from Jebel Liban were first reported by Hyatt (1903). The Iranian *Knemiceras* were originally thought to belong to

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48 **Fig. 1** *Knemiceras persicum*
49 Collignon. Example of oyster
50 encrustations (left valves) on the
51 left flank of a specimen, with
52 half of the body chamber
53 preserved, from the Albian
54 (Lower Cretaceous) Kazhdumi
55 Formation, Hamuran, Iran.
56 (N. B. The left valve is always
57 the encrusting one in oysters.)
58 Oxford University Museum
59 KY15 (specimen diameter =
60 150 mm). Collector: Peter Kent



63
64 *K. syriacum*, but Collignon (1983) proved this to be unlikely. Reyment and Kennedy
65 (1991) could verify Collignon's opinion by multivariate morphometric analysis. Both
66 occurrences are of a kind that is relatively rare among ammonites of the Cretaceous,
67 and inasmuch as the taphonomic relationships of the two sequences seem, at first
68 sight, to be similar, it becomes a matter of palaeoecological interest to put this im-
69 pression to the test.

70 The categories of shells occurring in the collections are:

- 71 (1) One flank only encrusted by oysters (and very occasionally, barnacles and ser-
72 pulids), with or without encrusts on the venter.
73 (2) Both flanks encrusted with or without encrusts on the venter.
74 (3) No encrusted shells.

75 The first case derives from oyster spat having settled on stranded shells. The second
76 case represents encrusting organisms having settled on nekroplanktonically trans-
77 ported shells, on living shells fouled in life, or on reworked moulds (Reyment 2008).
78 Two possible examples of the fouling of living individuals were observed in the Per-
79 sian material, an indication of which is that the orientation of the length axis of the en-
80 crusting organism runs parallel to the tangent of the direction of coiling. The species
81 of oysters forming the encrusts is *Exogyra* cf. *ardennuensis* d'Orbigny, according to
82 Collignon (1983). The Russian palaeontologist J.A. Efremov coined the term Taphon-
83 omy in 1940 for the study of burial, sedimentation, and preservation of animals and
84 plants. The statistical analysis of such data requires special methods encompassing
85 factors not usually considered to form a united whole in neontological work. It is for
86 this special aspect of palaeobiometry that I here coin the term 'taphonometrics'.
87
88

89 2 Statistical Analysis of the Oyster Encrustations

90 2.1 Hypothesis of Equal Frequencies

91
92 Suppose that we have a set of observed frequencies F_1, F_2, F_3, \dots . A standard chi-
93 squared test may be used to decide whether these frequencies differ significantly from
94

Table 1 Allocation rule results for the encrustation states for Lebanon and Iran

State	Π_1 Observed Lebanon (n_j)	Π_2 Observed Iran (m_j)	Rule-value (formula (2))	Allocation
1 0 0	6	7	1.000	Π_1
1 1 0	6	16	1.011	Π_1
1 1 1	6	42	1.024	Π_2
Sum	18	65		

Cut-off value for allocation rule = 1.018 (expression (3) in text)

Key:

1 0 0 denotes one flank of conch encrusted

1 1 0 denotes one flank of conch and venter encrusted

1 1 1 denotes both flanks of conch and venter encrusted

Π_i ($i = 1$ or 2) indicates the classification of the state according to the discrete discrimination rule of Kameo Matusita

an expected hypothesis. Reyment (1971, Chap. 7) illustrates examples of the test of common occurrence in palaeontology. In the present case, the hypothesis is that all of the encrusting categories recorded occur in equal proportions under the supposition that oyster spat have settled on conches under like conditions at both sites (Table 1). A test of association by chi-squared for the categories is given: one side fouled (1 0 0), one side and venter encrusted (1 1 0), both sides and venter fouled (1 1 1), and shells lacking epizoans (0 0 0). It indicates that the proportions for the Iranian specimens ($\Sigma N = 81$) give a very highly significant value of chi-squared of 32.10 for 3 d.f., with $P < 0.0001$, which indicates that the postulate that the frequencies for all states are equal, is not supported. Granted that about half of the Iranian conches are fouled on all sides (i.e. both flanks and venter), the result is not unexpected and it would seem likely that the majority of the shells were settled upon while floating post-mortem in shallow water. The result for the Lebanese material ($\Sigma N = 27$) yields a non-significant value of chi-squared of 1.000 for 3 d.f., with $P = 0.80$, which may indicate that the material has a mixed origin such as would be found where reworking is an important factor and where nekroplanktonic shells occur jumbled together with shells that were originally settled by epizoans while lying on the sea-floor, before and/or after reworking. These results suggest that the Iranian material is composed mainly of nekroplanktonically transported conches.

2.2 Discriminant Allocation

In many situations, discrete classification rules may be constructed through approximations to, and estimates of, multinomial densities. For the problem considered in this note, a different approach is used, in which likelihood ratios are not used as a foundation for classification, since the data are discrete and depart from a normal model. A problem also arises out of the small size of the Lebanese data set. The chi-squared method may be adversely affected by unequal sample sizes, particularly where one sample is much smaller than the other one; such is the case here. A useful, partly heuristic approach is a procedure based on distributional distance originally

142 proposed by Matusita (1954, 1964) (also, Dillon and Goldstein 1978) for greatly un-
 143 equal sample sizes. The notation of Goldstein and Dillon (1978) is adhered to in the
 144 following.

145 Consider data generated by discrete random variables X_1, X_2, \dots, X_p encompass-
 146 ing distinct values s_1, s_2, \dots, s_p in the sample space consisting of $s = \prod_j s_j$ states
 147 generated by the vector \mathbf{X} which has a multinomial distribution. Let $F_1 = \{p_j\}$ and
 148 $F_2 = \{q_j\}$, denote two discrete distributions defined on the same space. The states
 149 here are the patterns of occurrence of the encrustations as shown in Table 1 (three
 150 states: the state encompassing specimens lacking encrustations is not relevant for the
 151 classification exercise as opposed to the chi-squared model).

152 Matusita's concept of distributional distance relies on a measure of affinity defined
 153 as

$$154 \rho(F_1, F_2) = \sum_{j=1}^s (p_j q_j)^{1/2},$$

155 and a measure of distance between F_1 and F_2 given by

$$156 \|F_1 - F_2\|^2 = \sum_{j=1}^s (p_j^{1/2} - q_j^{1/2})^2,$$

157 for expressing classification rules. The distance $\| \cdot \|$ is a metric with properties that are
 158 not shared by other distributional distances (Dillon and Goldstein 1978, p. 306). An
 159 allocation rule may be expressed as an ordered partition $D = (D_1, D_2)$ of the sample
 160 space. The rule is that D allocates an observation \mathbf{x} to Π_i if $\mathbf{x} \in D_i$, for $i = 1$ or 2
 161 (Goldstein and Dillon 1978, p. 11).

162 If $n < m$ so that $m(n + 1)/n(m + 1) > 1$ and $n_k = 0$ but $m_k \neq 0$, then the rule
 163 allocates the observation to F_1 of the inequality (1)

$$164 (m_k)^{1/2} < \sum_{j \neq k} (n_j m_j)^{1/2} [(m(n + 1)/(n(m + 1)))^{1/2} - 1], \quad (1)$$

165 which is satisfied, if the samples are very unequal in size, and m_k is small in relation
 166 to the other values of the smaller of the samples being compared. The values n and
 167 m constitute the sum of all observations of the states for each of the two samples (n
 168 $< m$). The results summarised in Table 1 place one of the samples with the second
 169 (larger) group (Iran) and two samples with the first group (Lebanon), in accordance
 170 with the allocation model of Matusita (1954, 1964). In other words, both sites contain
 171 shells some of which are thought to have a nekroplanktonic history, but the history
 172 of the Lebanese material bears witness to a more heterogeneous background such as
 173 would result from reworking and renewed burial of the fossils. The way in which (1)
 174 is computed is as follows.

175 Compute firstly the ratio (2)

$$176 \{m_j(n_j + 1)^{1/2} + C\} / \{n_j(m_j + 1)^{1/2} + C\}, \quad (2)$$

177 the operation of which requires finding the constant term C . This is done by comput-
 178 ing the appropriate sum of square roots of the product $n_j m_j$, that is the sum of the
 179

189 square roots of all the states with the exclusion of the state to be allocated. Thirdly,
190 compute a boundary-value (3) for the allocation rule:

$$191 \quad [m(n + 1)/n(m + 1)]^{1/2}, \quad (3)$$

192
193 where n and m retain the same significance as above.

194 A problem that can arise in the statistical analysis of fossil material concerns how
195 is one to handle sparse states and, in particular, the question as to whether all zeros
196 are logically equal. When it comes to the application of statistical methodology to
197 fossils, zero takes on a special significance in terms of the likelihood of turning up a
198 non-zero observation under repeated sampling varying from sampling source to sam-
199 pling source. A qualified zero therefore has a real significance. The case of encrusting
200 organisms with n much smaller than m , is considered here. A zero registered for state
201 j from F_1 could really represent a greater theoretically possible frequency than a very
202 small value recorded in state j from F_2 (Dillon and Goldstein 1978, p. 312). This un-
203 certainty leads automatically to the solution by the full multinomial rule, notably that
204 the non-zero state is referred to F_2 . The rule in Goldstein and Dillon (1978, p. 44),
205 expressed in (1), relaxes the severity of an automatic assignation such as follows from
206 the unqualified application of the full multinomial rule. This result of Goldstein and
207 Dillon has been formally termed the Dillon Goldstein Classification Rule by Pires
208 and Branco (1997).

209 Comparing the two methods used here, the standard chi-squared procedure and a
210 discrete classification method, we see that results obtained by both agree, albeit on
211 different statistical grounds. However, the discrete classification method goes a step
212 further in that it outlines the source of the discrimination by means of an allocation
213 rule. For states 1 0 0 and 1 1 0, the proportions are commensurable with Π_1 . The
214 decision for state 1 1 1 is for allocation to Π_2 . The conclusion is that the taphonomic
215 histories of the two occurrences differ with respect to the mode of occurrence of the
216 encrustations.

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220 3 Conclusions

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222 The results for *Knemiceras* spp. attempt to interpret the differences in the presumed
223 taphonomy of the Iranian and Lebanese ammonite occurrences. A hypothesis as to
224 whether or not the Iranian *Knemiceras* were fouled in life and/or post-mortem must
225 take into account the ecological constraint imposed by the life-history of oysters,
226 particularly the fact that oysters are euryhaline organisms which inhabit a littoral
227 environment. The results of the present study suggest that the environment inhabited
228 by living ammonites was near-shore. Nekroplanktonic shells floating in a near-shore
229 environment would have provided a firm settling ground for oyster spat.

230 As any person with professional sea-going maritime experience will confirm, once
231 a ship starts to lose power seriously, it is time to put it into dry dock for a hull-
232 scraping. Most of the fouling organisms are acquired when in port or riding at anchor.
233 This raises the question as to how the fouling of living cephalopod shells takes place.
234 The energy required to maintain a swimming speed for a heavily encrusted shell is so
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considerable that such a condition would not be sustainable for long by the hosting animal (Reyment 1988). For this reason, it seems likely that encrustation of conches on all sides takes place post-mortem, except in rare circumstances. It is common praxis to treat qualitative data as though they were continuous and to use the Linear Discriminant Function of R.A. Fisher. The LDF does not require normality, but its justification in a likelihood-ratio connection does. The method of distributional distances avoids this difficulty and introduces a taphonomical ingredient to the problem which facilitates interpretation of a complex palaeontological problem.

Once it has been found possible to distinguish between life-assemblages and re-worked assemblages in a particular study, it may be interesting to test the application of a log-linear model to the question of determining the structure of the mixed assembly in more detail if the problem posed in quantifying the different taphonomic origins of the encrustations can be surmounted and the sample sizes are not too divergent (cf. Agresti 2007, p. 329). I thank a referee for suggesting such a possibility.

Acknowledgements I wish to thank Professor W. James Kennedy, Director of the Natural History Museum of Oxford University, Parks Road, Oxford for helping in many ways and for making the facilities of the museum available to me. A research grant from the Dunker Fund of Kungliga Fysiografiska Sällskapet, Lund is gratefully acknowledged.

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