



A brittle star bed from the Miocene of Patagonia, Argentina

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As a consequence of the extremely poor fossil record of brittle stars, every new discovery is important. The Miocene example studied herein involves the recently described species *Ophiocrossota kollenbergorum* Caviglia, Martínez & del Río recovered from the Chenque Formation of southeastern Argentina. The information used here is derived from unpublished data and a new record from two discrete, thin, monospecific patches. The main taphonomic features of the patches, namely the presence of specimens concordant with bedding planes, (with either aboral or oral side upwards), and the good preservation of the delicate discs (ca. 6 mm wide on average), and the preservation of un-oriented arms complete with fragile tips (not wider than 0.2 mm), point to a suddenly buried census assemblage. Although broken or isolated arms were found, this is attributed to the erosive environmental conditions of the abrasion platform where the studied exposure is located today. Size frequency distributions suggest that both patches were buried at different seasons. Observed densities are 77 and 143 individuals/m², and distances between individuals are random. The arm length/disc diameter ratio indicates that *Ophiocrossota kollenbergorum* may have been an epifaunal surface dweller. No signs of predation (such as regenerated arms), were identified. □ *Ophiocrossota kollenbergorum*, *ophiuroids*, *taphonomy*, *palaeoecology*, *Miocene*, *Argentina*

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Brittle star beds are presently known throughout the world (Aronson 1992), yet only a few Recent populations have been properly studied, for example: *Ophiothrix fragilis* (Abildgaard in O.F. Müller 1789) (e.g. Vevers 1952; Warner 1971; Holme 1984); *Ophiothrix oerstedii* (Lütken 1856) (Aronson & Harms 1985); *Ophiocomina nigra* (Abildgaard in O.F. Müller 1789) (Wilson *et al.* 1977); *Ophiura sarsii* Lütken 1855 (Fujita & Ohta 1990; Piepenburg & Schmid 1997); *Ophiopecten sericeum* (Forbes 1852) (Piepenburg & Schmid 1997); *Ophiacanta bidentata* (Retzius 1805) (Piepenburg & Schmid 1997); and, *Amphiura filiformis* (O.F. Müller 1776) (e.g. Duineveld & van Noort 1986; Rosenberg *et al.* 1997). Equally, fossil brittle star beds are very scarce. Aronson (1989, 1992) listed up to 28 autochthonous shallow-water fossil aggregations, including only 7 from the Cenozoic. Recently, some *in situ* accumulations of Triassic brittle stars have been reported (Radwański 2002; Twitchett *et al.* 2005; Zatoń *et al.* 2008). This poor fossil record may be a consequence of the low preservation potential of this group (Schäfer 1972; Ausich 2001), or, in the case of Cenozoic occurrences, by the effects of the Mesozoic Marine Revolution, and its consequent reduction of ophiuroid aggregations by the increasing predation pressure (Aronson 1987, 1989, 1991, 1992). As a consequence, every new discovery of a brittle star bed not

only constitutes an important input to taphonomy and palaeoecology, but also represents a contribution to test Aronson's hypothesis.

The highly fossiliferous Neogene marine sedimentary sequence exposed along the littoral coast of Patagonia, a region situated in southernmost tip of South America, offers a unique opportunity to improve our knowledge of high-latitude invertebrate biotas. The goal of the present paper is to discuss the results of a taphonomic and palaeoecological analysis carried out in the recently described ophiuroid *Ophiocrossota kollenbergorum* Caviglia *et al.* 2007, a species recovered from the basal horizons of the Miocene Chenque Formation (Santa Cruz Province, Argentina).

Geographical and geological setting

The Chenque Formation consists of a 500-m thick siliciclastic and pyroclastic sequence, composed of five shallowing-upwards parasequences well exposed at the type locality of the formation in the surroundings of the city of Comodoro Rivadavia, San Jorge Basin, northern Santa Cruz Province (Bellosi 1995). The lowermost parasequences I and II are highly tuffaceous, and are characterized by several fossiliferous beds that yield a rich molluscan fauna belonging to the

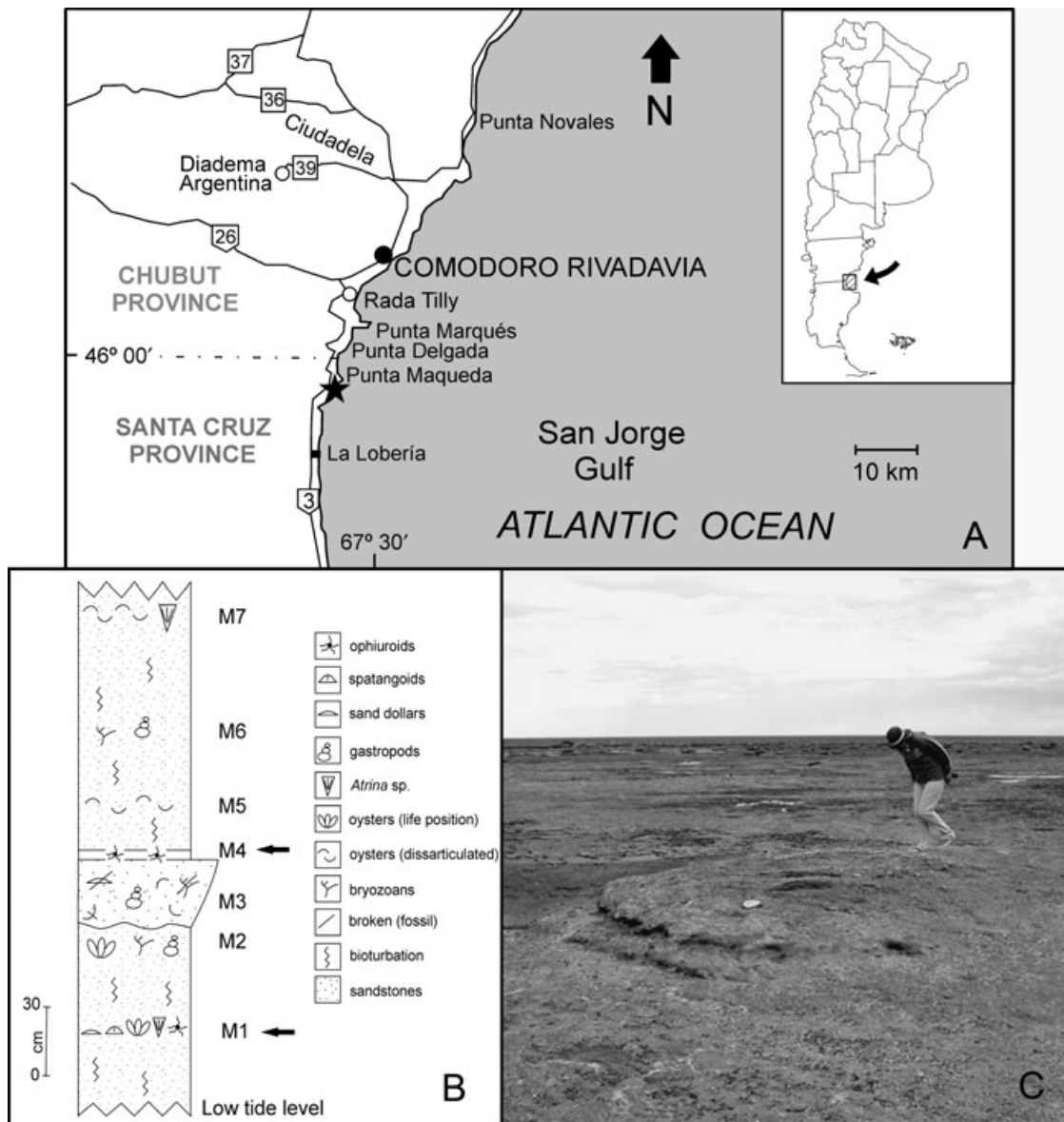


Fig. 1. Geographic location (A), stratigraphical section (B), and a view during low tide (C), of the studied outcrop.

Jorgechlamys juliana–*Reticulochlamys borjasiensis* assemblage (del Río 2004). Molluscs dominate the invertebrate assemblage, but ophiuroids and asteroids, as well as irregular echinoids, are especially abundant in thin horizons that are sparsely distributed throughout Parasequence I.

Two thin beds yielding brittle stars were recovered from an outcrop of about 1200 m² located 2 km south of Punta Maqueda (= Punta Peligro) situated on the recent abrasion platform that is only visible during low tides, and is subject to high energy erosive conditions (Fig. 1A–C). These beds are correlated with the basal section exposed at Punta Maqueda (Parasequence I) and are dated as Early Miocene on the basis of palynology (Bellosi & Barreda 1993).

These fossiliferous sedimentary rocks were deposited in a distal, lower shoreface environment dominated by a low hydraulic energy regime and affected by sporadic weak storm.

The lithological section (Fig. 1B) consists of 2.4 m thickness of highly bioturbated, grey-greenish, fine- to very fine-grained sandstones where seven fossiliferous beds are recognized. Five of them represent thin, autochthonous assemblages composed of monospecific aggregations, and two (M1 and M4 in Fig. 1B) correspond to the brittle stars patches studied herein. The lower bed (M1) is characterized by different groups in life position represented by separate patches of brittle stars (CR1), schizasterids, *Amplaster* sp. and *Abertella* sp., bunches of oysters and clusters

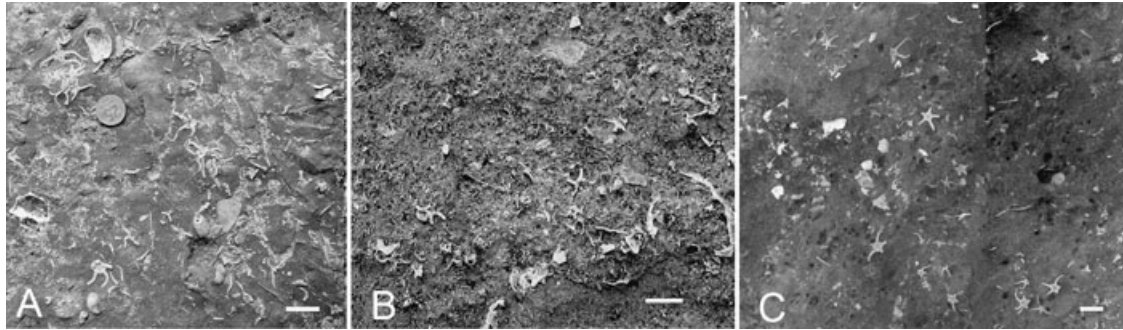


Fig. 2. The studied patches of *Ophiocrossota kollenbergorum*. A, CR1; B, CR2; C, CR3. Scale bars represent 25 mm.

of *Atrina* sp. (a species with a very fragile shell), and octocorals. The uppermost brittle star bed (CR2) was recovered from an extremely thin horizon (M4) resting on a 30-cm thick, time-averaged accumulation (M3) that varies laterally from highly broken, eroded, encrusted and bored gastropods, bivalves, bryozoans and echinoids, to densely packed turritellid accumulations with a well-marked bidirectional orientation, to extensive patches of stacked articulated and entire specimens of *Atrina* sp.

Material and methods

The material analysed was recovered from two isolated patches, CR1 (50 cm × 35 cm; Fig. 2A) and CR2 (100 cm × 40 cm; Fig. 2B) and also from taphonomic data obtained from a patch that no longer exists (CR3; Fig. 2C; mentioned by Caviglia 1978, and personal communication, 2007).

Patches were sampled and photographed in the field; photographs were subsequently analysed in laboratory using ImageTool (Wilcox *et al.* 2002). Normality of size–frequency distributions was checked using the Shapiro-Wilk test, and comparisons between samples were determinate by Mann-Whitney and Kolmogorov-Smirnov tests. Statistical analysis and graphs were calculated using the PAST software (Hammer *et al.* 2001). Information about the mineral composition was obtained by means of scanning electron microscopy photographs and energy dispersive spectrometer (EDS) coupled with the scanning electron microscopy (Facultad de Ciencias, Montevideo).

Taphonomy and palaeoenvironment

Results

Ophiuroid concentrations occur in the sedimentary rock as surficial, thin (1–2 cm thick) discrete patches,

with no isolated specimens between them. Specimens are extremely fragile with tiny plates well preserved and composed of recrystallized calcite with low Mg content. Arms do not show any preferred orientation (Fig. 4A–D), are complete, and some even retain their very delicate tips, which are no wider than 0.2 mm (Fig. 3A). As shown in Fig. 3A–E, specimens are represented by: discs with their five arms complete or nearly complete; discs with some arms broken; discs where only base of arms have been preserved; five or four arms from the same individual preserved *in situ*, but without the discs; and, isolated complete arms. With the exception of only one specimen obliquely placed, the remaining individuals were found in a horizontal position, parallel to the bedding plane, and with either up or down (oral-aboral) facing position (but according to results of Fisher's exact test, only CR2 has an equal proportion of both positions) (Figs 5, 6).

Discussion and interpretation

The taphonomic aspects described in the previous discussion indicate that both patches suffered sudden burial and, as it will be discussed in the succeeding discussion, they are interpreted as census assemblages (*sensu* Hallam 1972; see also Kidwell 1998).

Echinoderms begin to disarticulate between 30 min and 48 days after death (Blyth Cain 1968; Schäfer 1972; Allison 1990), and as already stated, arms and discs are complete, and extremely delicate parts are finely preserved (i.e. arm tips). Moreover, it is not probable that the loss of some elements of the brittle stars (see the five types of preservation in previous discussion) can be attributed to environmental energy during the burial process, or to a long residence time on the sea bottom after death. On one hand, arms do not show a preferred orientation, discarding the possible presence of one or two-directional currents, and the absence of isolated plates in the sediment indicates that no disarticulation happened before or during

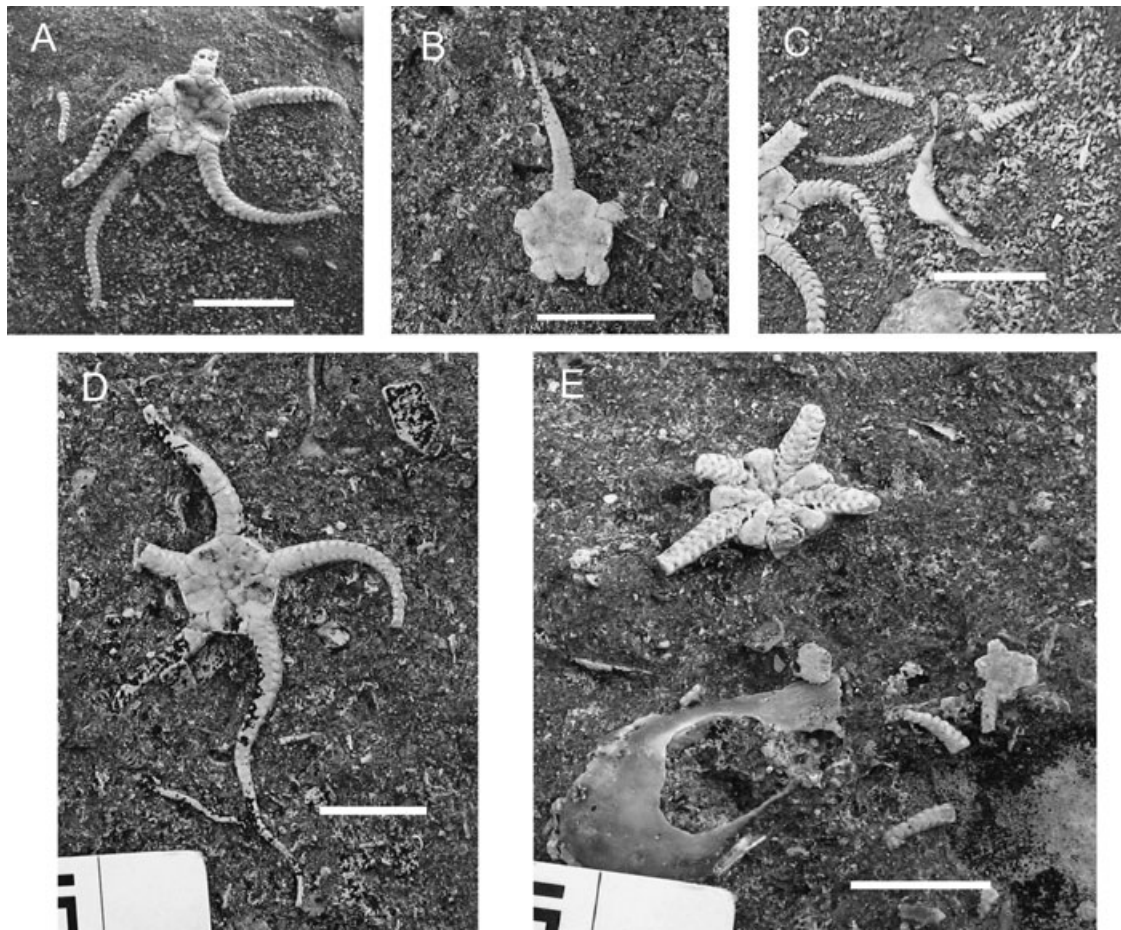


Fig. 3. A, *O. kollenbergorum* specimen preserved with four arms (CR2). B, disc with only one arm with its delicate tip preserved (CR1). C, arms preserved without the disc (CR2). D, preservation of extremely delicate arm tip (CR1). E, disc without arms and arms without disc, preserved side by side (CR1). Scale bars represent 10 mm.

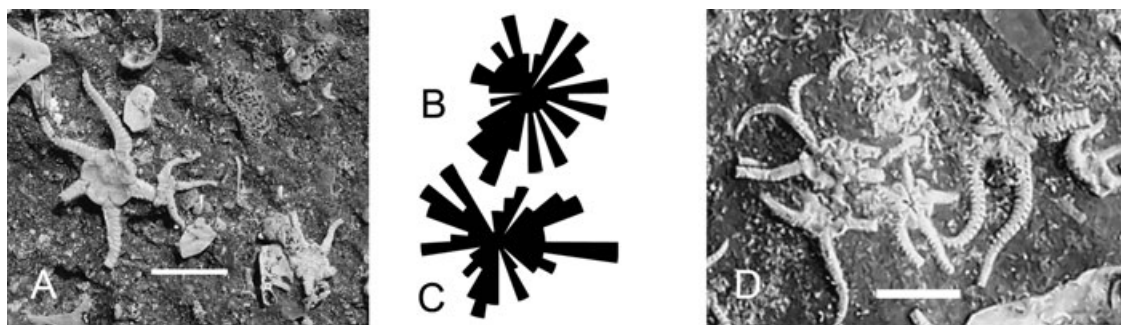


Fig. 4. A, specimens (CR1) showing arms without a preferred orientation. Scale bars represent 10 mm. B, rose diagram concerning arm orientation at CR1. C, rose diagram showing arm orientation at CR2. D, some specimens at CR2 showing arms without a preferred orientation. Scale bars represent 10 mm.

burial. On the other hand, although relationship between oral/aboral orientation has been interpreted by Twitchett *et al.* (2005) as evidence of transport prior to burial, in Recent populations individuals are commonly found living in any of the both positions (e.g. Fell 1961; Hendler *et al.* 1995; Vevers 1952), and

this is a proper interpretation for fossil species (e.g. Kesling & Le Vasseur 1971; Blake 1975). Although even weak storms can overturn the ophiuroids, the most parsimonious explanation for the presence of oral/aboral orientation seems to be that brittle stars were buried in life position. In addition, high-energy



Fig. 5. Specimens with oral or aboral side upwards, preserved side by side (CR2). Diameter of coin 24 mm.

conditions on the recent abrasion platform would be the responsible mechanism for the breakage of specimens after exhumation, and for the complete destruction of the CR3 patch mentioned by Caviglia (1978), which according to photographs and field works, seems to have been removed during the last 30 years. It can be also argued that the recent high-energy conditions have selectively removed some specimens from our patches, distorting the original population structure, but the taphonomic evidence already discussed suggest that specimens have been only slightly eroded, and have a good state of preservation.

Time-averaging is a common process recorded in death assemblages of hard, durable skeletons such as those belonging to brachiopods and bivalves, making it difficult to recognize the original living community (Fürsich & Aberhan 1990; Kidwell & Flessa 1996; Carroll *et al.* 2003; Kowalewski & Bambach 2003; Barbour Wood *et al.* 2006; among others). In the present analysis, time-averaging is rejected, because the skeletons of the studied ophiuroids are so fragile that, if they had not been immediately buried below the taphonomic active zone, they would have been completely destroyed in a very short time. Hence, both

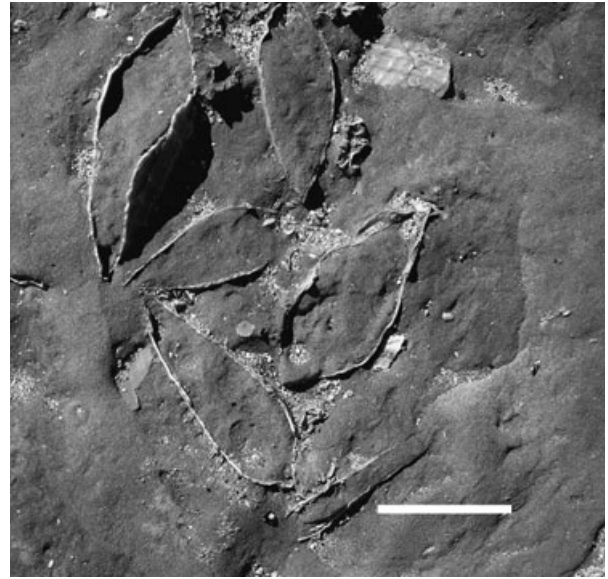


Fig. 7. Cluster of very delicate shells of *Atrina* sp. preserved *in situ*. Scale bars represent 50 mm.

patches represent a snapshot (census assemblages) of the populations at a given time, and may be ideally identical to the original life assemblage, allowing reliable palaeoecological studies (see succeeding discussion).

According to the preceding discussion and other geological data, the Patagonian Miocene populations of *O. kollenbergorum* inhabited well-oxygenated waters upon a substrate affected by episodic weak storms that suddenly buried the ophiuroids, keeping them away from conditions that lead to subsequent breakage (an obrution event *sensu* Brett 1990).

Taphonomic conditions of contemporaneous assemblages also point to a quiet environment, only affected by weak storms, as shown by numerous patches of oysters and echinoids (schizasterids) in life position, and concentrations of *Atrina* sp. (Fig. 7) associated laterally with CR2, as well as other accumulations

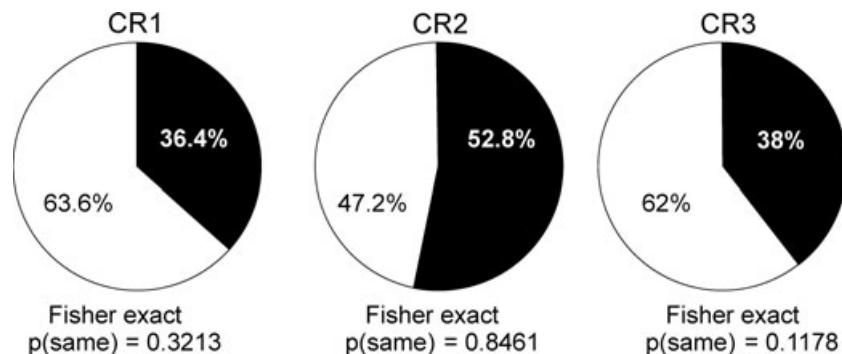


Fig. 6. Percentages of specimens with oral side (white) and aboral side (black) upwards, and results of Fisher's exact test.



Fig. 8. Heavily encrusted gastropod preserved along with ophiuroids (CR1). Scale subdivided in millimetres.

made up of not more than three species of gastropods and octocorals, with no evidence of either transport or a prolonged residence on the substrate.

In the case of CR1, the brittle star patch rests on a previously time-averaged assemblage of echinoids, gastropods and bivalves that shows clearly a long residence on the substrate with broken, encrusted, bored and highly abraded specimens (Fig. 8), indicating that these time-averaged assemblages were suddenly buried with the living brittle star population.

Population structure and dynamics

Taking into account the particular framework of a palaeoecological study, the existence of well-preserved census assemblages allowed the study of different aspects of the population structure and dynamics, discussed in the succeeding paragraph.

Size

One of the most easily captured properties of fossil assemblages is the size–frequency distribution, a property that has been estimated for fossil and death assemblages in different groups (e.g. mammals, Kúrtén 1953; brachiopods, Richards & Bambach 1975; molluscs, Cummins *et al.* 1986; trilobites, Sheldon 1988; echinoids, Dodd *et al.* 1985; Nérandaeu 1991) but there are few studies on ophiuroids (Kesling & Le Vasseur 1971; Twitchett *et al.* 2005; Zatoń *et al.* 2008).

Basic statistics regarding size are shown in Table 1. Figure 9 shows that small sizes are not represented (less than 2 mm in CR1, less than 3 mm in CR3 and less than 5 mm in CR2), a usual problem in putative fossil populations (Olson 1957; Hallam 1972; Richards & Bambach 1975; Dodd *et al.* 1985; amongst others).

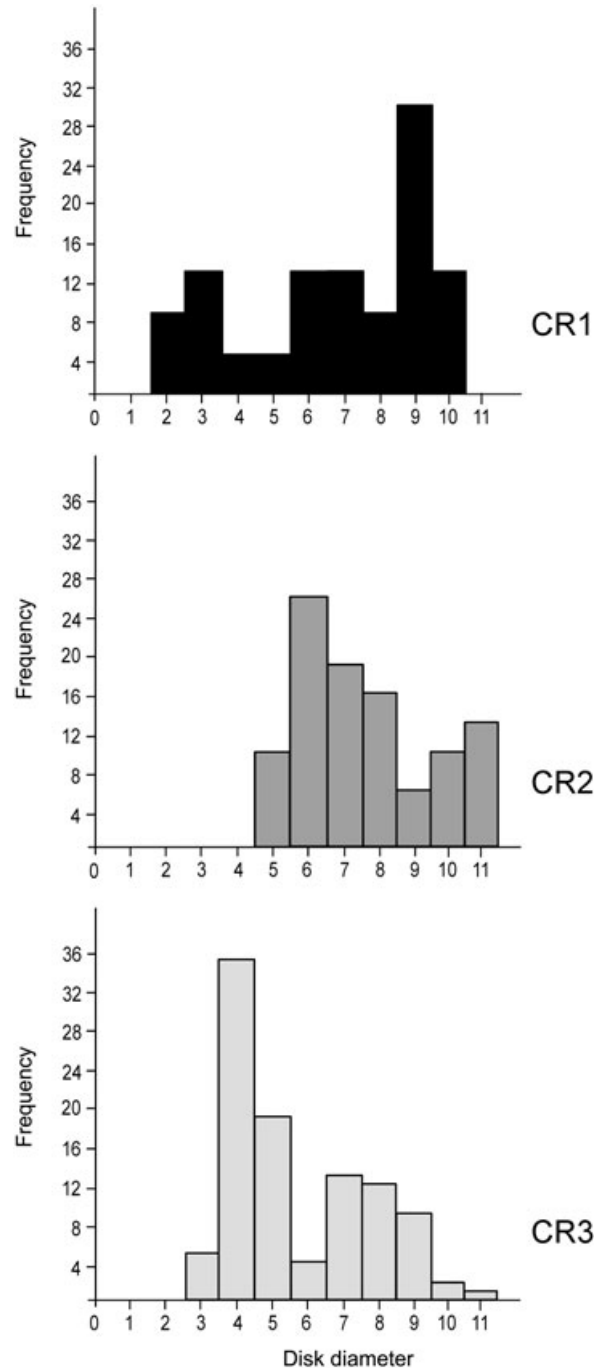


Fig. 9. Histograms showing size frequencies at each patch.

Hallam (1972) and Dodd *et al.* (1985) stated that the apparent lack of juveniles can be caused by factors such as collection failure, transport by currents, mechanical destruction, dissolution, migration, predation, different habitat of juveniles and adults, or even by growth and mortality rates. In the present example, with the exception of growth and mortality rates as the possible explanation for the absence of

Table 1. Results of normality tests and basic statistics.

	CR1	CR2	CR3
Range	2–10 mm	5–11 mm	2–11 mm
Mean	6.88	7.64	5.73
Median	7	7	5
Standard error	0.532	0.346	0.2
Standard deviation	2.608	1.893	1.989
Skewness	-0.5067	0.4646	0.6175
Kurtosis	-1.2117	-1.0893	-0.8629
Shapiro-Wilk W	0.8869	0.9011	0.8766
Shapiro-Wilk Probability	0.009617	0.007659	0.000001306

Table 2. Results of Mann–Whitney and Kolmogorov–Smirnov nonparametric tests.

Mann–Whitney		
CR1 vs. CR2	T = Ub: 341	P = 0.4484
CR2 vs. CR3	T = Ub: 769.5	P = 1.885 E-05*
CR1 vs. CR3	T = Ub: 923.5	P = 0.04421*
Kolmogorov–Smirnov		
CR1 vs. CR2	D: 0.247742	P = 0.316941
CR2 vs. CR3	D: 0.493226	P = 1.0075 E-0.5*
CR1 vs. CR3	D: 0.31	P = 0.0332583*

small-sized individuals, the remaining factors must be discarded, as the material was carefully collected, the sedimentological data indicate low-energy environmental conditions at the time of deposition and, furthermore, the preservation of very small (up to 0.6 mm) ossicles at the tip of the arms (much smaller than the missing small discs), show that mechanical destruction or dissolution must be also rejected. Néranda (1991) found spacial segregation between juvenile and adult individuals of the Cenomanian echinoid *Mecaster grossouvrei*, but in examples studied here, no patches of juveniles of *Ophiocr. kollenbergorum* were found. Finally, as will be discussed in succeeding sections, there is no evidence of predation.

Size distribution of the populations is not normal (Table 1). We checked the differences among them using nonparametric tests: the Mann–Whitney, which compares the medians; and the Kolmogorov–Smirnov, which compares the structure of distributions. Results of both tests (Table 2) show that CR1 and CR2 are not statistically different, but both are significantly different from CR3, the patch measured by Caviglia (1978, and personal communication, 2007; see previous discussion), pointing to a case of ‘operator error’ (Rothfus 2004). The mode falls at different sizes in the three populations (CR1 = 9 mm, CR2 = 6 mm, CR3 = 4 mm) and, also, the less common size is different among them (CR1 = 4–5 mm, CR2 = 9 mm, CR3 = 6 mm).

Table 3. Arm length/disc diameter (specimens selected by chance from CR1 and CR2).

Arm length	Disk diameter	al:dd
22.3	10.1	2.2
20.6	10.1	2.0
15.4	10.1	1.5
20.3	8.9	2.3
18.5	8.9	2.1
16.1	6.6	2.4
8.6	6.6	1.3
12.8	5.0	2.6
17.1	9.3	1.8
19.8	9.0	2.2
6.8	3.3	2.0
6.0	2.7	2.2
10.2	5.8	1.7
13.3	4.2	3.2
10.8	4.1	2.7
11.1	5.8	1.9
16.0	9.0	1.8
18.0	9.0	2.0
17.0	10.0	1.7
19.0	11.0	1.7
22.0	11.0	2.0
15.0	7.0	2.1
22.0	11.0	2.0
	averages	
15.6	7.8	2.1

What do these distributions imply? Recent ophiuroids have different population structures related to time (recruitment periods), depth trends or density-dependent factors (e.g. Fujita & Ohta 1990; Piepenburg & Schmid 1997). In the present case, depth and density factors can be rejected because, as has been already discussed, the studied populations lived at the same depth, and density was not significantly different among the three patches (see succeeding discussion); but recruitment period is a reasonable argument to justify the presence of different snapshots of populations at different moments of the year.

Mode of life

According to Twitchett *et al.* (2005), the arm length/disc diameter (al:dd) ratio indicates the mode of life of Recent ophiuroids; burrowing brittle stars have the highest ratios (al:dd > 9), epifaunal surface dwellers have the lowest (al:dd < 5) and crevice dwellers are placed between them. As the average ratio of *O. kollenbergorum* is 2.1 (Table 3), this species must be considered as an epifaunal surface dweller.

Density

Density of individuals/m² was calculated as an average of about 18 m² in CR3 (45 ind/m²), and as an extrapolation from patches CR1 (0.175 m²) and CR2 (0.4 m²)

(143 ind/m², and 77 ind/m² respectively). They are not uncommon values, according to those reported in the literature for recent ophiuroids, particularly when comparing them with those taxa that are epibenthic shallow water inhabitants, as we have interpreted *O. kollenbergorum* to be. Among them, there are *Ophiothrix oerstedii* with a mean density of around 50 ind/m² in a saltwater lake (Aronson & Harms 1985), and *Ophiocomina nigra* and *Ophiothrix quinque maculata* with more than 100 ind/m² (Wilson et al. 1977; Stachowistch 1979). *Ophiothrix fragilis* has been reported from 340 ind/m² (Vevers 1952) to 1330 ind/m² (Warner 1971), but in this species juveniles live above the adults (Morgan & Jangoux 2004). Like *O. kollenbergorum*, *Ophiocomina nigra*, *Ophiothrix quinque maculata* and *Ophiothrix fragilis* form discrete patches.

Inter-individual distance

Inter-individual distances are at random, and vary from specimens touching each other to those separated by lengths that comprise many equivalent radiuses. However, overall distribution of brittle stars in the patch is rather homogenous (it is not distinguished between a more densely 'packed' central zone and a loosely 'packed' peripheral one or halo). Patches present an average surface covering around 10–12%.

Biological interactions: predation

Predation on fossil ophiuroids was reviewed by Aronson (1987, 1989, 1991, 1992), who proposed an increase of predation upon brittle stars in Cenozoic times, a process with roots in the 'Mesozoic Marine Revolution'. As in the Chenque Formation, where repaired arms from complete or partially broken specimens or from isolated arms have not been recorded, it can be assumed that these populations were not predated, although potential predators, such as sea stars, were found nearby. Brittle stars may have been eaten entirely, but this assertion can not be tested with the available evidence.

Thus, Aronson's rule is not fulfilled in our example, and in the shallow environment of the Chenque Formation, physical factors appear to have controlled the brittle star populations.

Conclusions

The studied brittle star beds are census assemblages and constitute snapshots of the Miocene living populations. *Ophiocrossota kollenbergorum* was an epifaunal suspension feeder that lived in moderately

dense patches, in shallow, usually quiet waters with low sedimentation rate, occasionally disturbed by storms. The populations were not affected by heavy predation and had some seasonal(?) recruitment period(s).

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References

- Allison, P.A. 1990: Variation in rates of decay and disarticulation of Echinodermata: implications for the application of actualistic data. *Palaíos* 5, 432–440.
- Aronson, R.B. 1987: Predation on fossil and Recent ophiuroids. *Paleobiology* 13, 187–192.
- Aronson, R.B. 1989: A community-level test of the Mesozoic Marine Revolution theory. *Paleobiology* 15, 20–25.
- Aronson, R.B. 1991: Predation, physical disturbance and sublethal arm damage in ophiuroids: a Jurassic–Recent comparison. *Marine Ecology Progress Series* 74, 91–97.
- Aronson, R.B. 1992: Biology of a scale-independent predator-prey interaction. *Marine Ecology Progress Series* 89, 1–13.
- Aronson, R.B. & Harms, C.A. 1985: Ophiuroids in a Bahamian saltwater lake: the ecology of a Paleozoic-like community. *Ecology* 66, 1472–1483.
- Ausich, W.J. 2001: Echinoderm taphonomy. In Jangoux, M. & Lawrence, J.M. (eds): *Echinoderm Studies vol. 6*, 171–227. Balkema, Rotterdam.
- Barbour Wood, S.L., Krause, R.A., Kowalewski, M., Wehmiller, J. & Simões, M.G. 2006: Aspartic acid racemization dating of Holocene brachiopods and bivalves from the southern Brazilian shelf, South Atlantic. *Quaternary Research* 66, 323–331.
- Belloso, E. 1995: Paleogeografía y cambios ambientales de la Patagonia central durante el Terciario Medio. *Boletín de Informaciones Petroleras* 44, 50–83.
- Belloso, E. & Barreda, V.D. 1993: Secuencias y palinología del Terciario Medio en la Cuenca San Jorge, registro de oscilaciones eustáticas en Patagonia. *12º Congreso Geológico Argentino y 2º Congreso de Exploraciones de Hidrocarburos* 1, 78–86.
- Blake, D.B. 1975: A new West American Miocene species of the modern Australian ophiuroid *Ophiocrossota*. *Journal of Paleontology* 49, 501–507.
- Blyth Cain, J.D. 1968: Aspects of the depositional environment and palaeoecology of crinoidal limestones. *Scottish Journal of Geology* 4, 191–208.
- Brett, C.E. 1990: Ostrution deposits. In Briggs, D.E.G. & Crowther, P.R. (eds): *Palaebiología: A Synthesis*, 239–243. Blackwell, Oxford.
- Carroll, M., Kowalewski, M., Simões, M.G. & Goodfriend, G.A. 2003: Quantitative estimates of time averaging in terebratulid brachiopod shell accumulations from a modern tropical shelf. *Paleobiology* 29, 381–402.
- Caviglia, S.E. 1978: Presencia del género *Ophiocrossota* (Echinodermata, Ophiurida, Ophiuridae) en el Terciario marino de Patagonia. *Ameghiniana* 13, 331–332.
- Caviglia, S.E., Martínez, S. & del Río, C.J. 2007: A new Early Miocene species of *Ophiocrossota* (Ophiuroidea) from southern Patagonia, Argentina. *Neues Jahrbuch für Geologie und Paläontologie* 245, 147–152.
- Cummins, H., Powell, E.N., Stanton, R.J. & Staff, G. 1986: The size-frequency distribution in palaeoecology: effects of taphonomic processes during formation of molluscan death assemblages in Texas Bay. *Palaentology* 29, 495–518.
- del Río, C.J. 2004: Tertiary Marine molluscan assemblages of Eastern Patagonia (Argentina): a biostratigraphic analysis. *Journal of Paleontology* 78, 1097–1122.

- Dodd, J.R., Alexander, R.R. & Stanton, R.J. 1985: Population dynamics in *Dendroaster*, *Merriamaster*, and *Anadara* from the Neogene of the Kettleman Hills, California. *Palaeogeography, Palaeoclimatology, Palaeoecology* 52, 61–76.
- Duineveld, G.C.A. & van Noort, G.J. 1986: Observations on the population dynamics of *Amphiura filiformis* (Ophiuridea: Echinodermata) in the Southern North Sea and its exploitation by the dab, *Limanda limanda*. *Netherlands Journal of Sea Research* 20, 85–94.
- Fell, H.B. 1961: The fauna of the Ross Sea, 1: Ophiuroidea. *New Zealand Oceanographic Institute Memoirs* 18, 1–124.
- Forbes, E. 1852: Monograph of the Echinodermata of the British Tertiaries. *Monograph of the Palaeontographical Society, London* 6, vii + 36 pp.
- Fujita, T. & Ohta, S. 1990: Size structure of dense populations of the brittle star *Ophiura sarsii* (Ophiuroidea: Echinodermata) in the bathyal zone around Japan. *Marine Ecology Progress Series* 64, 113–122.
- Fürsich, F.T. & Aberhan, M. 1990: Significance of time-averaging for palaeocommunity analysis. *Lethaia* 23, 143–152.
- Hallam, A. 1972: Models involving population dynamics. In Schopf, J.M. (ed.): *Models in Paleobiology*, 62–80. Freeman, Cooper and Co., San Francisco.
- Hammer, Ø, Harper, D.A.T. & Ryan, P.D. 2001: PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4, 9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm
- Hendler, G., Miller, J.E., Pawson, D.L. & Kier, P.M. 1995: *Sea Stars, Sea Urchins, and Allies: Echinoderms of Florida and the Caribbean*, 390 pp. Smithsonian Institution Press, Washington and London.
- Holme, N.A. 1984: Fluctuations of *Ophiothrix fragilis* in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom* 64, 351–378.
- Kesling, R.V. & Le Vasseur, D. 1971: *Strataster ohioensis*, a new Early Mississippian brittle star, and the paleoecology of its community. *Contributions from the Museum of Paleontology, University of Michigan* 23, 305–341.
- Kidwell, S.M. & Flessa, K.W. 1996: The quality of the fossil record: populations, species, and communities. *Annual Review of Earth and Planetary Sciences* 24, 433–464.
- Kidwell, S.M. 1998: Time-averaging in the marine fossil record: overview of strategies and uncertainties. *Geobios* 30, 977–995.
- Kowalewski, M. & Bambach, R.K. 2003: The limits of paleontological resolution. In Harries P.J. (ed.): *Approaches in High-Resolution Stratigraphic Paleontology*, 1–48. Kluwer Academic/Plenum Publishers, New York.
- Kurtén, B. 1953: On the variation and population dynamics of fossil and recent mammal populations. *Acta Zoologica Fennica* 76, 1–22.
- Lütken, C.F. 1855: Bidrag til Kundskab om Slangestjernerne. I. Foreløbig Oversigt over Grønlandshavet Ophiurer. *Videnskabelige Meddelelser fra den Naturhistoriske Forening 1854*, 95–104.
- Lütken, C.F. 1856: Bidrag til Kundskaben Slangestjerner. II. Oversigt over de vestindiske Ophiurer. *Videnskabelige Meddelelser fra den na Turhistorik Forening i Kjøbenhavn 1856*, 1–19.
- Morgan, R. & Jagoux, M. 2004: Juvenile–adult relationship in the gregarious ophiuroid *Ophiothrix fragilis* (Echinodermata): a behavioral and morphological study. *Marine Biology* 145, 265–276.
- Müller, O.F. 1776: *Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae Indigenarum Characteres, Nomina et Synonyma Imprimis Popularium*, i–xxxii +282 pp. Hallagerius, Hauniae [Copenhagen].
- Müller, O.F. 1789: *Zoologia Danica seu Animalium Daniae et Norvegiae rariorum ac minus notorum Descriptiones et Historia. Vol 3*, iv +71 pp. N. Moller, Hauniae [Copenhagen].
- Nérandeau, D. 1991: Lateral variations of size-frequency distribution in a fossil echinoid community and their palaeoecological significance. *Lethaia* 24, 299–309.
- Olson, E.C. 1957: Size-frequency distributions in samples of extinct organisms. *Journal of Geology* 65, 305–333.
- Piepenburg, D. & Schmid, M.K. 1997: A photographic survey of the epibenthic megafauna of the Arctic Laptev Sea shelf: distribution, abundance, and estimates of biomass and organic carbon demand. *Marine Ecology Progress Series* 147, 63–75.
- Radwański, A. 2002: Triassic brittlestar beds of Poland: a case of *Aspiduriella ludeni* (v. Hagenow, 1846) and *Arenorbis squamosus* (E. Picard, 1858). *Acta Geologica Polonica* 52, 395–410.
- Retzius, A.J. 1805: *Dissertatio Sistens Species Cognitas Asteriarum, Quamr. sub Praesidio A.J. Retzii*. Exhibet N. Bruzelius, Lund. 37 pp.
- Richards, R.P. & Bambach, R.K. 1975: Population dynamics of some Paleozoic brachiopods and their palaeoecological significance. *Journal of Paleontology* 46, 167–212.
- Rosenberg, R., Nilsson, H.C., Hollertz, K. & Hellman, B. 1997: Density-dependent migration in an *Amphiura filiformis* (Amphiuridae: Echinodermata) infaunal population. *Marine Ecology Progress Series* 159, 121–131.
- Rothfus, T.A. 2004: How many taphonomists spoil the data? Multiple operators in taphofacies studies. *Palaios* 19, 514–519.
- Schäfer, W. 1972: *Ecology and Palaeoecology of Marine Environments*, 568 pp. Oliver and Boyd, Edinburgh.
- Sheldon, R.W. 1988: Trilobite size-frequency distributions, recognition of instars, and phyletic size changes. *Lethaia* 21, 293–306.
- Stachowitsch, M. 1979: Movement, activity pattern and the role of a hermit crab population in a subtidal epifaunal community. *Journal of Experimental Marine Biology and Ecology* 39, 135–150.
- Twitchett, R.J., Feinberg, J.M., O'Connor D.D., Alvarez, W. & Mccollum, L.B. 2005: Early Triassic ophiuroids: their paleoecology, taphonomy, and distribution. *Palaios* 20, 213–223.
- Vevers, H.G. 1952: A photographic survey of certain areas or sea floor near Plymouth. *Journal of the Marine Biological Association of the United Kingdom* 31, 215–222.
- Warner, G.F. 1971: On the ecology of a dense bed of the brittle-star *Ophiothrix fragilis*. *Journal of the Marine Biological Association of the United Kingdom* 51, 267–282.
- Wilcox, D., Dove, B., McDavid, D. & Greer, D. 2002. *Image Tool for Windows*, v. 3. The University of Texas Health Science Center in San Antonio. <http://ddsdx.uthscsa.edu/dig/itdesc.html>
- Wilson, J.B., Home, N.A. & Barret, R.L. 1977: Population dispersal in the brittle-star *Ophiocomina nigra* (Abildgaard) (Echinodermata: Ophiuroidea). *Journal of the Marine Biological Association of the United Kingdom* 57, 405–439.
- Zatoń, M., Salamon, M.A., Boczarowski, A. & Sitek, L. 2008: Taphonomy of dense ophiuroids accumulations from the Middle Triassic of Poland. *Lethaia* 41, 47–58.