

Life and death of *Saccocoma tenella* (GOLDFUSS)

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Abstract The morphology of the small stalkless *Saccocoma tenella* is unique among crinoids. It is characterized by an extremely light skeleton with dish-like lateral wings on the proximal brachials and peculiar paired vertical processes flanking the food grooves of more distal brachials. The arms are heavily branched. The lateral wings obviously were involved in vertical movement. For the vertical processes a “baffle rail” function for arm curling and “snap swimming” has been postulated, with muscles between the processes. However, there is no evidence that the processes were connected by muscles. For food collection a “pulsating funnel” model in the water column is advocated, with the processes serving to collect plankton during upward movement of the arms. The resulting mouth-up position is supported by the biostratinomy. *Saccocoma tenella* is considered to have been pelagic, a benthic lifestyle is rejected on ecologic and taphonomic grounds. Adorally-curved arms are considered a reaction to hostile environment before death, not a taphonomic artefact.

Keywords Crinoidea · *Saccocoma tenella* · Tithonian · Biostratinomy · Functional morphology

Zusammenfassung Die kleine ungestielte *Saccocoma tenella* hat eine unter Crinoiden einzigartige Morphologie.

Das Skelett ist äußerst leicht gebaut; die proximalen Armglieder tragen seitlich absteigende “Schwimmplatten” oder Flügel, die distalen gepaarte vertikale Fortsätze welche die Nahrungsfurche flankieren. Die Arme sind reich verzweigt. Die Flügel dienen offensichtlich zur vertikalen Bewegung. Die vertikalen Fortsätze wurden als Führung für das Einrollen der Arme zu einem “Schnapp-Schwimmen” gedeutet. Dabei wären sie durch Muskeln verbunden gewesen. Da Indizien für Muskeln zwischen den vertikalen Fortsätzen fehlen, wird zur Nahrungsaufnahme das Modell eines in der Wassersäule “pulsierenden Trichters” vorgeschlagen, mit Fang von Plankton zwischen den Fortsätzen während der Aufwärtsbewegung der Arme. Voraussetzung für das vorgeschlagene Modell ist der nach oben gerichtete Mund, was durch die biostratinomischen Befunde erhärtet wird. Für *Saccocoma tenella* wird eine pelagische Lebensweise angenommen, eine benthische Lebensweise kann aufgrund ökologischer und taphonomischer Befunde als widerlegt gelten. Oralwärts eingerollte Arme werden als Reaktion lebender Tiere auf verschlechterte Umweltbedingungen gedeutet, nicht als taphonomische Artefakte.

Institutional abbreviations

NMB Naturhistorisches Museum Basel

1 Introduction

Saccocoma tenella (GOLDFUSS) is the most common macrofossil of the Solnhofen Limestone, and it is the only species of the genus occurring in these sediments (Hess 2002, p. 19). The anatomy is unique among crinoids. In

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recent years several proposals for the mode of life were made, but only Seilacher and Hauff (2004) discussed swimming in some detail. In the present paper the problem of feeding of this pelagic crinoid is discussed based on recent morphological studies (Brodacki 2006; Hess 1999, 2002).

Saccocoma AGASSIZ belongs to the Order Roveacrinida SIEVERTS-DORECK, a group of small stalkless crinoids widely distributed in mostly pelagic sediments from the Middle Triassic to the Late Cretaceous. Roveacrinids are characterized by a delicate skeleton of cup and arms, and processes and flanges or wings are common. Triassic Roveacrinida are classified in the Somphocrinidae PECK, the Jurassic forms in the Saccocomidae D'ORBIGNY, which also occur in Cretaceous sediments, and the exclusively Cretaceous forms in the Roveacrinidae PECK. Hess (2011) proposed the family Axocrinidae for the Late Triassic (Carnian) *Axicrinus alexandri* KRISTAN-TOLLMANN. Common to all these forms is the development of a strongly-sloping, ligamental (cryptosynarthrial) articulation between the two primibrachials and the first and second secundibrachials. The arms bifurcate at the second primibrachial, and the 10 arms may carry side branches that are especially well developed in *Saccocoma tenella* (Fig. 5).

1.1 Occurrence and biostratigraphy

By far the densest occurrences of *Saccocoma tenella* in the Plattenkalk facies are known from the Schernfeld area near Eichstätt. In a sequence of only 7 m, Röper et al. (2000, p. 123) reported approximately 300 horizons with *Saccocoma* at densities of more than 30 individuals per square metre. In contrast, 27–30 m of the Mörsheim-Hummelberg profile contain only 60 horizons with mass concentrations of *Saccocoma*. In the Solnhofen area, *Saccocoma* mainly occurs on bedding planes of dense, thick limestone beds (“Flinz”); and in the Eichstätt area on thin, somewhat marly beds (“Fäule” or “Blätterflinz”). In comparison to the Solnhofen basin with thicker limestone beds, the Eichstätt basin contains approximately seven times more *Saccocoma* although there are differences between the very rich western part near Schernfeld and the somewhat less rich eastern part near Wintershof. The total number of individuals in the section correlates well with the number of sedimentation breaks or marly intervals between limestone formation (Röper et al. 2000, p. 50).

The aboral side of the cup typically stands out from the surface on the underside of the beds, and the arms are distally mostly coiled or crumpled (Fig. 1). Röper et al. (2000) suggested that the animals accumulated after mass death on beds lithified by microbial mats and were later covered by sediment. The model of slow accumulation of dead animals on the bottom during long periods of non-

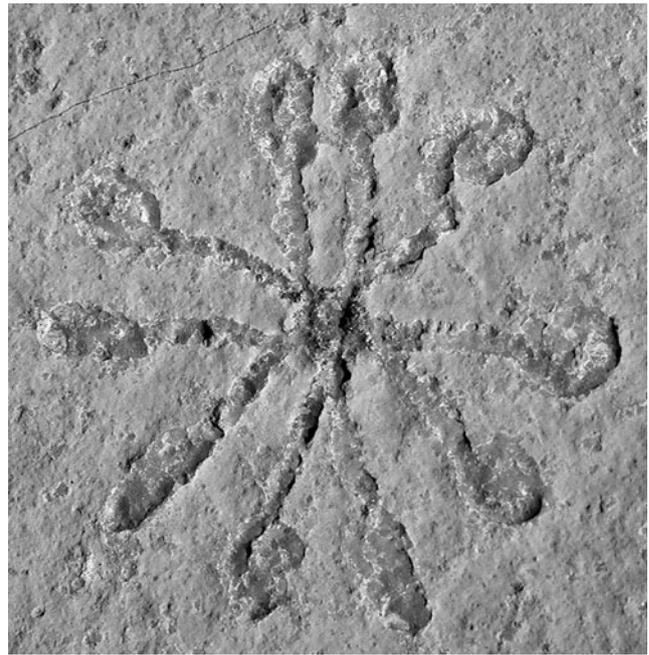


Fig. 1 Recrystallized specimen of *Saccocoma tenella* (GOLDFUSS) with curled arms, Early Tithonian, Solnhofen. NMB M6986. Magnification factor of 2×

sedimentation, followed by rapid deposition of the limestone beds that fixed the organisms at the lower surface, was proposed by Barthel (1978), p. 77. In contrast, Hess (2002) suggested that the animals were killed by an influx of fine sediment in the upper water layers and settled by virtue of size and density before the bulk of the sediment. Specimens of *Saccocoma* occasionally are preserved on the upper side of beds, exposing the oral side. Specimens with outstretched, proximally flexed arms (Hess 1999, fig. 219) and current-oriented specimens (Röper et al. 1998, fig. 35, 38) are uncommon. This is also true of specimens that combine proximally-flexed and distally-curled arms. In nearly all cases, the crinoids are preserved more or less intact, isolated cup plates and brachials are exceptional. At Nusplingen, *Saccocoma* specimens are never coiled but are slightly disarticulated though the arms are not removed far from the cup; aborally-flexed arms rarely occur (G. Schweigert, pers. comm. 2009). The available data suggest that conditions for death and preservation may have varied. The common occurrence of coprolites (*Lumbricaria*) composed entirely of remains of *Saccocoma* on the same bedding planes leaves little doubt that the crinoids lived and were preyed upon in the upper oxygen-rich water layers of the Plattenkalk basins (Hess 1999, 2002; Röper et al. 1998, 2000).

In recent years, a benthic mode of life was proposed by Milsom (1994) and Manni et al. (1997). These authors tried to explain the peculiar morphology of the arms as adaptations to life on a soupy substrate. According to Milsom

(1994) the lateral wings of the arms would prevent the animal from sinking into the substrate (“snowshoe” strategy). Manni et al. (1997) considered *Saccocoma* a “mud-sticker” with the arms pointing upward; the wings and the vertical processes served to protect the cup against invasion of mud. Such lifestyles were previously rejected and, indeed, benthic colonizers seem to be completely absent in the lithographic limestone of the Solnhofen area (e.g. Viohl 1998). Further evidence comes from an analysis of the spatial distribution of *Saccocoma* on bedding planes.

Saccocoma tenella shows, at least in the Schernfeld region, an aggregated distribution over large areas (i.e. dense accumulations cannot be traced over distances of more than a few metres). The distribution within such larger aggregates was quantitatively analyzed in two slabs using a nearest neighbour distance method (Donnelly modification of the Clark and Evans test; for details of the method see Krebs 1989; Etter 1996). One of the slabs with 41 individuals was figured by Barthel (1978; plate 29, p. 298), the other with 117 juvenile individuals is in the collections of the Naturhistorisches Museum Basel (NMB) and is reproduced here (Figs. 2, 3). On both slabs, *Saccocoma* has a slightly aggregated distribution although the pattern shows no highly significant difference from a random distribution. On both slabs, the majority of the individuals is in normal “mouth up” position (90 and 85%, respectively).

This spatial distribution pattern is in itself not conclusive for a pelagic mode of life of *Saccocoma*. Benthic suspension feeders commonly show an aggregated distribution over large areas and typically a random distribution within the aggregates (Levinton 1972). However, in dense populations of epibenthic suspension feeders competition for space leads to a regular (=uniform) distribution (Levinton 1972; Pemberton and Frey 1984). This is certainly not the case in the analyzed slabs where many closely-spaced individuals show considerable overlap (Fig. 2b).

The distally-coiled arms of most specimens of *Saccocoma tenella* are in sharp contrast to the preservation of the comatulid *Comatulella* (formerly *Pterocoma*) *pennata* (see Hess 1999). This slender crinoid has ten long arms (up to 130 mm) with very long pinnules (up to 15 mm). Ligamentary articulations (syzygies) occur at intervals of four to five secundibrachials in the proximal part, where many fossils have arm breaks. The arms typically are flexed aborally and tangled in the proximal part, and the tips are straight with pinnules widely extended. *C. pennata* probably lived on soft-bottom areas in the oxygenated surface zone (Viohl 1998, pl. 1) and was transported intact into the hostile bottom zone. The arms must have flexed post-mortem, quite similar to the arching of fish skeletons and *Archaeopteryx* necks (Wellnhofer 2008). The orally-situated muscles relaxed their tension while the aboral

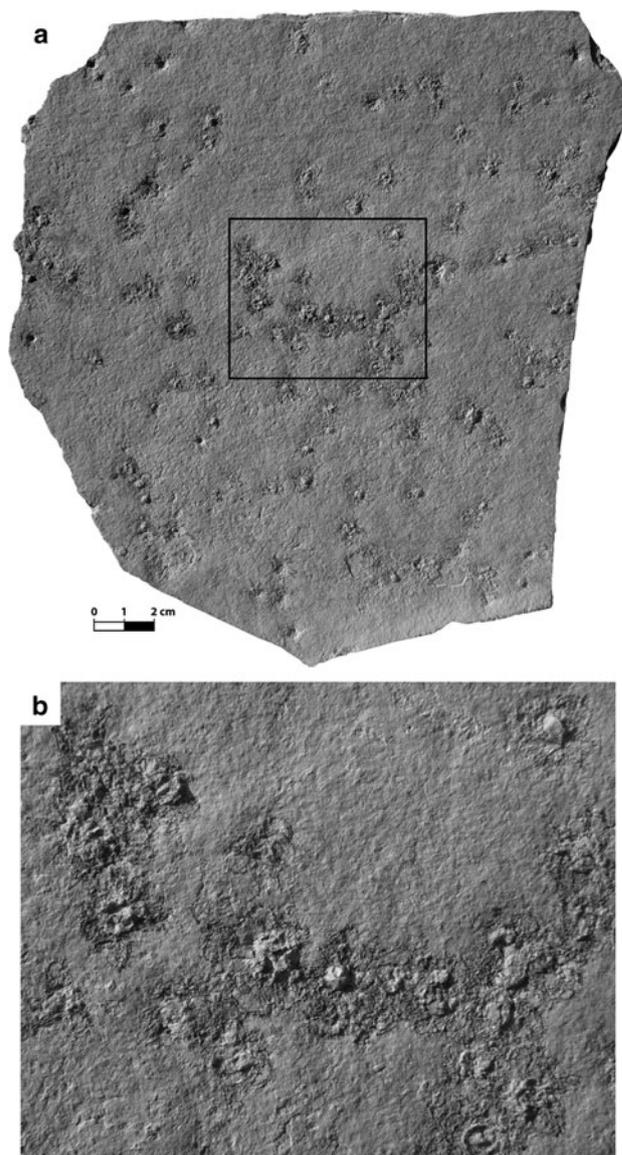
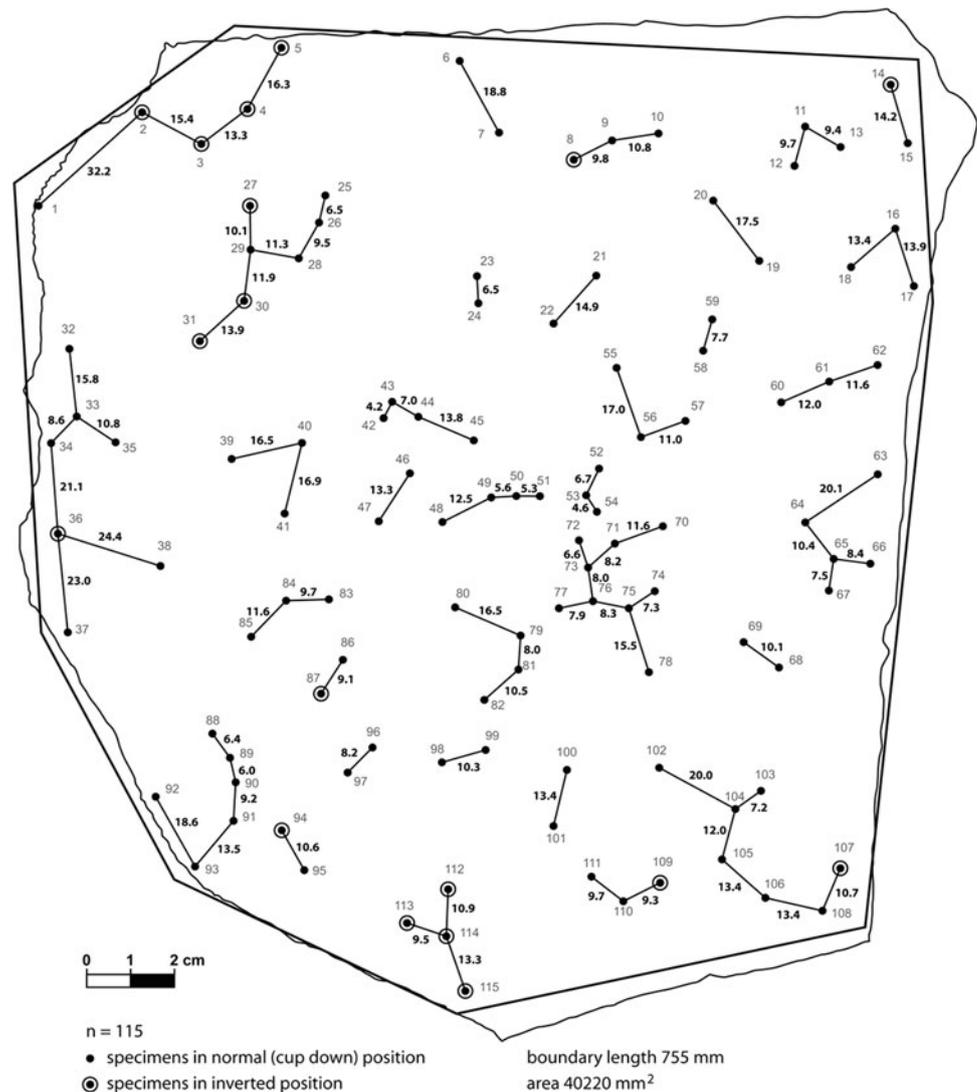


Fig. 2 Underside of slab with curled-up specimens of *Saccocoma tenella* (GOLDFUSS) from Schernfeld, NMB M10813. **a** Overview showing 117 individuals. **b** Detail (marked with square in **a**) showing crowding and partial overlap of individuals

ligaments retained their stored elastic energy and exerted a pull, leading to arching. In contrast, adoral curling of the distal arms of *Saccocoma tenella* must have resulted from muscle contraction between brachials of animals still alive, as already suggested by Jaekel (1892, p. 679). The reason for muscle contraction of *Saccocoma* specimens can only be speculated about. Hess (1999, 2002) proposed that it was a reflex of the animals against invasion of mud to protect the food grooves. In contrast, aboral bending of the proximal arms observed in specimens of *S. tenella* (Hess 1999, fig. 219; Seilacher and Hauff 2004, fig. 12A-E) appears to have been a taphonomic event after the animal died, as suggested by Seilacher and Hauff (2004) and

Fig. 3 Nearest neighbour distances for *Saccocoma* individuals on slab of Fig. 2. $R = 0.064$ indicates aggregated distribution, $z = -1.87$ confirms aggregated distribution at the 90% confidence level



similar to the preservation of *C. pennata*. Preservation with arm bases completely detached from the cup and with the arm tips near the cup (such specimens were described as *Saccocoma schwertschlagerei* WALTHER, 1904) is due to autotomy of the ligamental articulation between the primibrachials (Manni and Nicosia 1986), presumably the result of unfavourable environment when animals reached the bottom still alive.

1.2 Constructional morphology

Morphology of *Saccocoma tenella* (GOLDFUSS) is well documented though the articular facets in middle and distal arm regions are poorly known because of their small size and modification by the common recrystallization. Jaekel's (1892) seminal paper remains the base for the subsequent descriptions. Jaekel (1892, 1918) reconstructed the animal in aboral view, as if compressed in a herbarium. 3D views

based on the characters of the individual brachials were attempted only recently (Hess 1999, fig. 220; Brodacki 2006, fig. 2). The articular facets of the brachials are crucial to a reconstruction of the mode of life of *Saccocoma*.

The cup of *Saccocoma tenella* is a hemispherical or slightly conical open bowl with a diameter reaching 5 mm, composed of five very thin radials. The surface of the radials is covered with a network of anastomizing ribs, and a median ridge is thickened on top to reinforce the area beneath the radial articular facet. This facet has a small aboral part and elongate muscle fossae articulating with V-shaped muscle fossae on the first primibrachial. The exposed aboral surface of the first primibrachial is low, the distal surface is a sloping cryptosynarthry that is hidden by the aboral surface of the axillary second primibrachial (Fig. 4). Thus, the two primibrachials are connected by rather large, tight ligamentary articulation that allowed for very little movement. The same type of articulation is

Fig. 4 Reconstruction of *Saccocoma tenella*, sculpturing omitted (modified from Brodacki 2006). *R* Radial, *IBr* primibrachial, *IIBr* secundibrachial. Magnification factor of approximately 8×

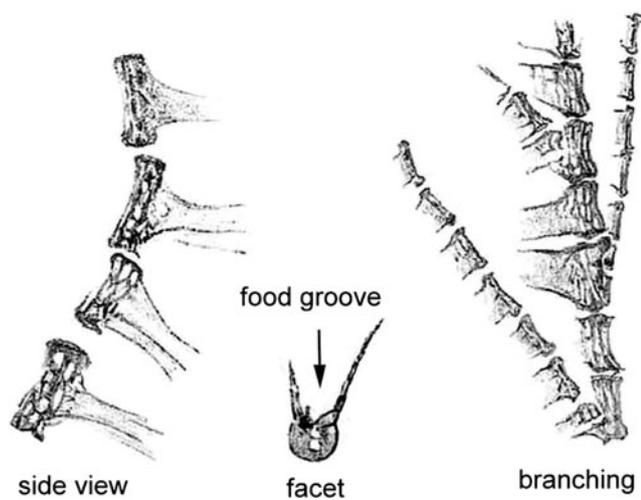
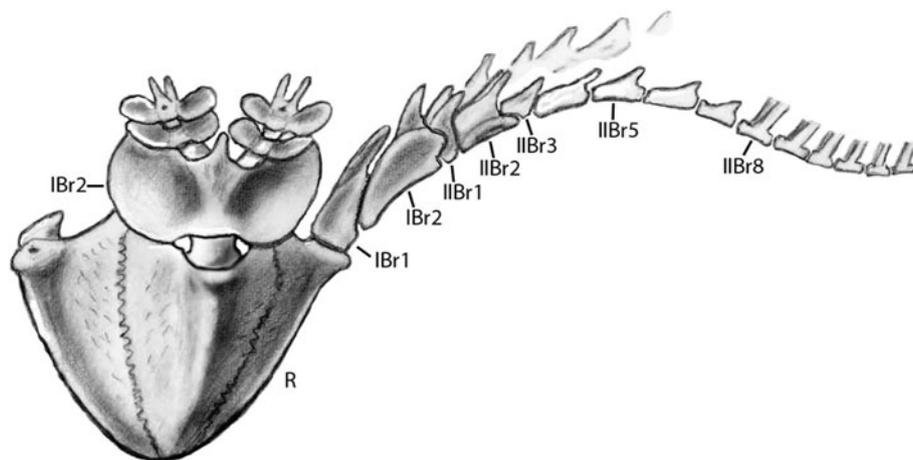


Fig. 5 Brachials of *Saccocoma tenella* with oral processes. Magnification factor of 15× for the side and branching views and of 20× for the facet (Jaekel 1892)

developed between the first and second secundibrachials. In contrast, the wingless third and the winged fourth secundibrachials are connected by a synostosal articulation perpendicular to the axis of the arm. All subsequent articulations are muscular, with a pronounced aboral ligament fossa (Brodacki 2006; Fig. 6). The ten main arms rising from the second primibrachials (primaxils) bear a number of side arms or armlets. These originate in some sort of pinnule socket but their elements are essentially comparable to the elements of the main arms and, thus, cannot be classified as true pinnules (Fig. 5).

The axillary second primibrachial as well as some of the more distal brachials bear conspicuous, symmetric, dish-like lateral wings with dense, porcelain-like structure (Jaekel's "Schwimmlatten") and weak oral processes. Interleaved between the winged brachials are the wingless first and third secundibrachials (Jaekel 1892; Hess 1999; Brodacki 2006), the absence of wings likely avoided

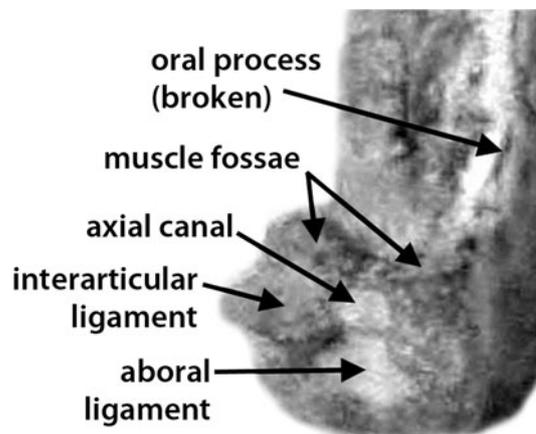


Fig. 6 Facet of brachial from middle part of arm on lower side of slab, Early Tithonian, Wintershof near Eichstätt; axial canal and aboral ligament fossa are filled by fine sediment. NMB M10812. Magnification factor of 100×

interference of the winged brachials during arm movement. Away from the cup the lateral wings are progressively reduced and, in contrast, paired vertical processes or baffles are present to the very tips of the arms. On the proximal (oldest) brachials the height of the processes exceeds the length of the corresponding arm ossicle (Jaekel 1892 fig. 9; Fig. 5). The processes flanked the food grooves during life, so that food was transported through a deep gutter. Jaekel (1892, p. 671) suggested that the processes were connected by a soft membrane and, thus, a continuous gutter protected tube feet and reproductive organs, an opinion that cannot be corroborated. In any case, the processes would have impeded lateral spreading of tube feet for particle capture. This is in contrast to the filtration fan of living crinoids where the tube feet are extended between the pinnules (Baumiller 1997, fig. 5).

The sloping ligamentary articulation between the two primibrachials and the first two secundibrachials made the

arm bases relatively stiff. In contrast, the non-sloping synostosis between the third and fourth secundibrachials may have been a preformed breaking point, as in other crinoids. As noted above, autotomy of the ligamentary articulation between the primibrachials led to the preservational state described as “*Saccocoma schwertschlageri*”. *Saccocoma tenella* shares with other roveacrinids well-developed elongate muscle fossae between radials and first primibrachials (Brodacki 2006, fig. 3E4; Hess 2002, pl. 1), indicating powerful movement between cup and arms. The two distal muscular facets of the second primibrachial form an angle of approximately 45° with the axis. The arms were nearly horizontal at the fourth to fifth secundibrachials (Brodacki 2006). The aboral ligament fossa is well-developed in all brachials. The muscle fossae are very rarely exposed in the fossils; they form a narrow band bordering the rather large interarticular ligament area (Fig. 6). Thus, the muscle fossae are restricted to the main body of the brachials and do not extend onto the paired processes. Sieverts (1932, figs. 9b, 12, 15b, 19) figured secundibrachials of *Drepanocrinus sessilis* JAEKEL (= *Roveacrinus communis* DOUGLAS) with oral processes that do not appear to have served for muscle attachment; the muscle fossae are narrow bands on the adoral side of flat, broad interarticular ligaments, similar to *S. tenella*. In contrast, Jagt (2005, fig. 3C) described a secundibrachial of the roveacrinid *Birgenelocrinus degraafi* JAGT with muscle fossae extending to the base of the processes that rise from the articular facet. The processes or flanges of this form were considered by Jagt an indication of a pelagic lifestyle.

1.3 Feeding

Living crinoids are passive suspension feeders. They deploy filtration fans into the current whereby the plankton

is caught by mucus of the tube feet (podia) extended between the pinnules (Baumiller 1997). Fixed fossil forms also were passive suspension feeders even though some cases of active feeding have been postulated (Meyer and Lane 1976; Jefferies 1989; Seilacher and Hauff 2004). How pelagic roveacrinids could have fed has not been discussed in detail. In any case, they must have caught food moving actively through the water. According to the “snap swimming” model (Seilacher and Hauff 2004; Fig. 7) the inter-baffle muscles would have loaded the aboral collagen spring during coiling of the arms. The energy thus stored could be released instantaneously in a fast active stroke. The authors did not discuss whether food was captured during the slow recovery stroke of arm coiling or during the fast active stroke of ligament recoil. Seilacher (pers. comm. 2009) thought that food was collected during the fast downward movement. However, food particles would mostly have streamed past the vertical processes without reaching the protected food groove. Extension of tube feet between the armlets would have been impeded by the processes. Even more important, there is no evidence that the processes were connected by muscles. Similar to living forms, the arms of *S. tenella* displayed a filtration fan to increase the food-collecting surface. Position of the oral processes flanking the food groove suggests involvement in food collection. For this purpose, a “pulsating funnel” model is advocated (Fig. 8). Muscle contraction between cup and arms and proximal brachials flexed the arms inward and upward so that a funnel was formed. During upward movement the middle and especially the distal, branched region scooped plankton between the vertical processes. Baumiller (pers. comm. 2010) argued that in this model fluid and particles would either move past the arms, or they would be “squeezed” out as the arms closed orally. However, this may not have been much of a problem if the

Fig. 7 “Snap swimming” of *Saccocoma tenella* (after Seilacher and Hauff 2004)

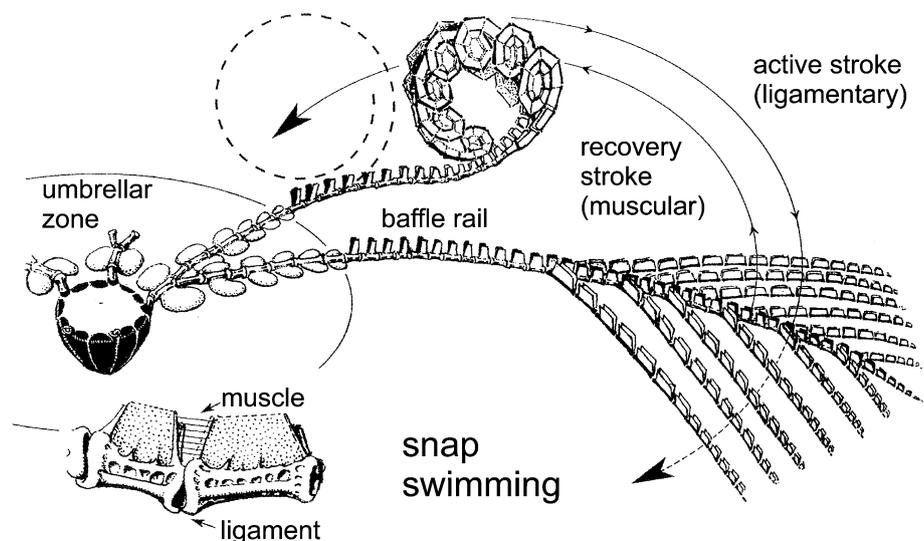
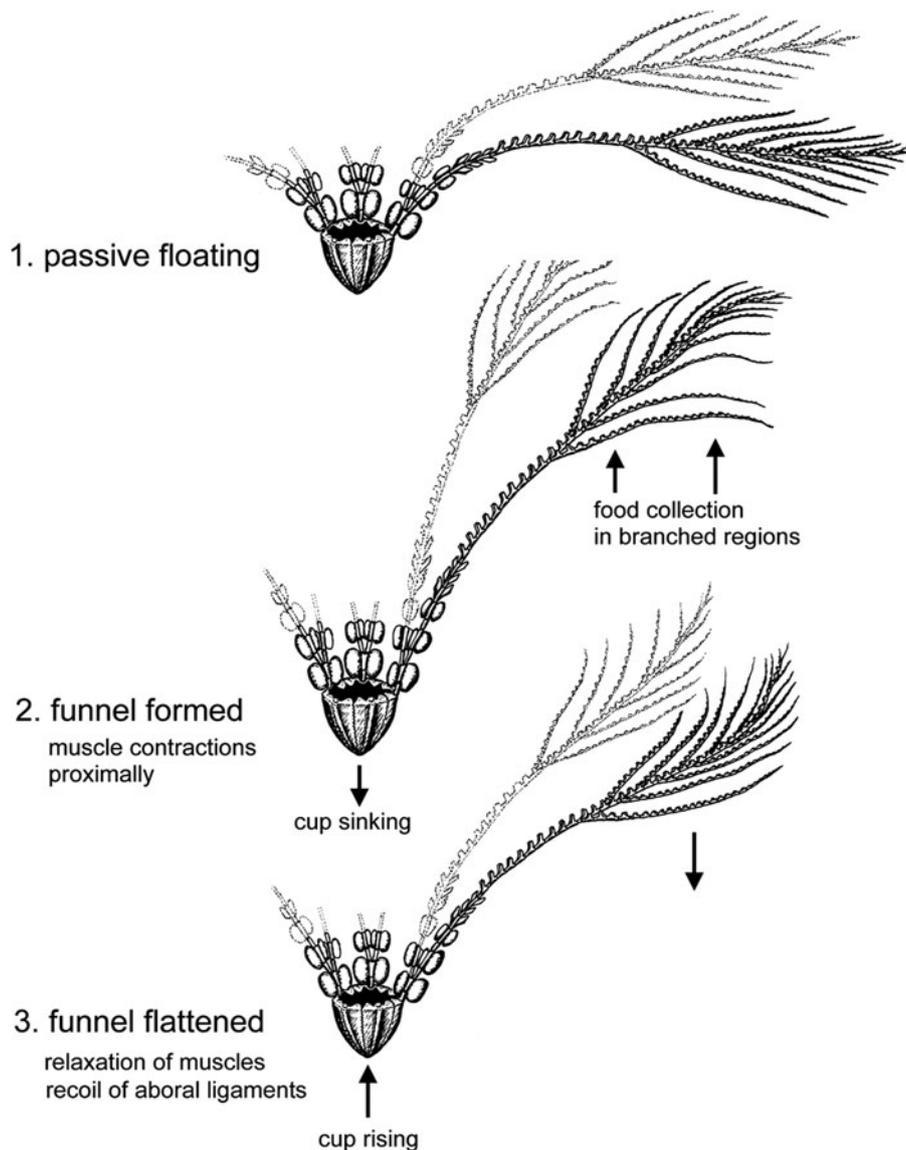


Fig. 8 “Pulsating funnel”
model of *Saccocoma tenella*
(drawing by W. Etter)



arms flexed rather slowly and the funnel remained wide in the distal part. How the particles were actually captured is conjectural, but it may be assumed that tube feet with an adhesive surface were present along the food grooves. Muscle relaxation caused elastic recoil of the antagonistic aboral ligaments, and the downward-concave wings at the base of the widened funnel acted as paddles, pushing the cup upward. In this model the animals floated mouth-up, a position supported by the biostratinomy.

2 Conclusions

Understanding the feeding mode of fossil crinoids relies on comparison with living representatives or analogues. The roveacrinids died out by the Late Cretaceous so that their

mode of feeding is conjectural. This is especially true of *Saccocoma tenella*, a large form by roveacrinid standards. Some characters, such as the very thin delicate skeleton and the lateral wings on proximal brachials to push the animal upward, are adaptations consistent with a pelagic lifestyle. In contrast, the paired oral processes along the food grooves are not seen in other roveacrinids. An explanation of their function as baffle rails connected by muscles and serving for arm curling (Seilacher and Hauff 2004) is not supported by the morphology of the brachial facets. The position of the processes flanking the food grooves suggests that they served to scoop plankton into the gutters of the arms. They did this during upward movement of the arms in the proposed “pulsating funnel” model. Food collection during sinking seems improbable because particles would have streamed past the processes

without reaching the food grooves. In common with living crinoids, *S. tenella* deployed a filtration fan but food was not collected downstream by tube feet extended between the armllets but by active upward movement of the arms. This would represent the only instance of crinoid feeding on particles captured on the oral side of the arms. In such “upstream feeding” *Saccocoma tenella* may have differed from other, diminutive roveacrinids feeding downstream while sinking. More data on brachial facets of other roveacrinids are needed to understand how these fascinating crinoids moved and fed.

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References

- Barthel, K. W. (1978). *Solnhofen: Ein Blick in die Erdgeschichte* (p. 393). Thun: Ott Verlag.
- Baumiller, T. K. (1997). Crinoid functional morphology. In: J. A. Waters & C. G. Maples (Eds.), *Geobiology of Echinoderms, The Paleontological Society Papers vol. 3*, (pp. 45–68).
- Brodacki, M. (2006). Functional anatomy and mode of life of the latest Jurassic crinoid *Saccocoma*. *Acta Palaeontologica Polonica*, 51, 261–270.
- Etter, W. (1996). Pseudoplanktonic and benthic invertebrates in the Middle Jurassic Opalinum Clay, northern Switzerland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 126, 325–341.
- Hess, H. (1999). Upper Jurassic Solnhofen Plattenkalk of Bavaria, Germany. In: H. Hess, W. I. Ausich, C. E. Brett & M. J. Simms (Eds.), *Fossil Crinoids* (pp. 216–224). Cambridge: Cambridge University Press.
- Hess, H. (2002). Remains of Saccocomids (Crinoidea: Echinodermata) from the Upper Jurassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde, Ser. B., Nr. 329*, 57 pp.
- Hess, H. (2011). Subclass Articulata. In: W. I. Ausich (Ed.) *Treatise on Invertebrate Paleontology Revised, Pt. T, Echinodermata 2: Crinoidea, vol. 3*. University of Kansas Press (in press).
- Jaekel, O. (1892). Ueber Plicatocriniden, Hyocrinus und *Saccocoma*. *Zeitschrift der Deutschen geologischen Gesellschaft*, 44, 619–696.
- Jaekel, O. (1918). Phylogenie und System der Pelmatozoen. *Paläontologische Zeitschrift*, 3, 1–128.
- Jagt, J. W. M. (2005). The youngest pelagic crinoids (latest Maastrichtian, the Netherlands). *Bulletin of the Geological Society of Denmark*, 52, 133–139.
- Jefferies, R. (1989). The arms structure and mode of feeding of the Triassic crinoid *Encrinurus liliiformis*. *Palaeontology*, 3, 483–497.
- Krebs, C. J. (1989). *Ecological methodology* (p. 654). New York: Harper and Row.
- Levinton, J. S. (1972). Stability and trophic structure in deposit-feeding and suspension-feeding communities. *American Naturalist*, 106, 472–486.
- Manni, R., & Nicosia, U. (1986). *Saccocoma schwertschlagerei* WALTHER, 1904 junior synonym of *Saccocoma tenellum* (GOLDFUSS), 1829: Evidence of autotomy in fossil crinoids. *Bolletino della Società Paleontologica Italiana*, 24, 181–183.
- Manni, R., Nicosia, U., & Tagliacozzo, L. (1997). *Saccocoma*, a normal benthonic stemless crinoid: an opportunistic reply within mud-dominated facies. *Palaeopelagos*, 7, 121–132.
- Meyer, D. L., & Lane, N. G. (1976). The feeding behavior of some Paleozoic crinoids and basketstars. *Journal of Paleontology*, 50, 472–480.
- Milsom, C. V. (1994). *Saccocoma*: a benthic crinoid from the Jurassic Solnhofen Limestone, Germany. *Palaeontology*, 37, 121–129.
- Pemberton, S. G., & Frey, R. W. (1984). Quantitative methods in ichnology: spatial distribution among populations. *Lethaia*, 17, 33–49.
- Röper, M., Rothgaenger, M., & Rothgaenger, K. (1998). *Die Plattenkalke von Hienheim (Landkreis Kelheim). Echinodermen-Biotope im Südfränkischen Jura* (p. 110). Eichendorf: Eichendorf Verlag.
- Röper, M., Rothgaenger, M., & Rothgaenger, K. (2000). *Die Plattenkalke von Schernfeld. Museum Bergér am Blumenberg* (p. 128). Eichendorf: Eichendorf Verlag.
- Seilacher, A., & Hauff, R. B. (2004). Constructional morphology of pelagic crinoids. *Palaios*, 19, 3–16.
- Sieverts, H. (1932). Über die Crinoidengattung *Drepanocrinus* Jaekel. *Jahrbuch der Preussischen geologischen Landesanstalt*, 53, 559–610.
- Viohl, G. (1998). Die Solnhofener Plattenkalke–Entstehung und Lebensräume. *Archaeopteryx*, 16, 37–68.
- Walther, J. (1904). Die Fauna der Solnhofener Plattenkalke, bionomisch betrachtet. *Festschrift der Medizinisch-naturwissenschaftlichen Gesellschaft zu Jena*, 11, 133–214.
- Wellnhofer, P. (2008). *Archaeopteryx. Der Urvogel von Solnhofen* (p. 256). München: Verlag Dr. Friedrich Pfeil.