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On the Ability of Withdrawing of Some Jurassic Ammonoids

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7 Text-Figures and 1 Table

Jurassic
Ammonoids
Palaeobiology
Palaeopathology

Contents

Über das Retraktionsvermögen einiger jurassischer Ammonoideen

Zusammenfassung

Hinweise über die Fähigkeit der Ammoniten, sich in ihr Gehäuse zurückzuziehen, erhalten wir von verheilten Schalenfrakturen. Verletzungen an Ammoniten sind keine Seltenheit. Nahezu alle verheilten Verletzungen sind Schalenausbrüche, die vom interimistischen Mündungsrand ausgingen. Die tiefsten der verheilten Schalenausbrüche, die für diese Untersuchung an Dactylioceraten und Hildoceraten (Unter-Toarcium) und an Perisphinctiden des Oxfordiums beobachtet wurden, betreffen mehr als ein Drittel der Wohnkammerlänge. Sie wurden sehr wahrscheinlich von dekapoden Krebsen verursacht. Dactylioceraten und Perisphinctiden auf der einen Seite und Hildoceratiden auf der anderen zeigen unterschiedliche Verheilungsmodi. Bei Hildoceratiden wurde die Skulptur der zu reparierenden Schale entsprechend der Verletzung verzerrt angelegt. Bei Dactylioceraten und Perisphincten dagegen kam es nur in seltenen Fällen zur Verzerrung der Skulptur der zu reparierenden Schale. Da die Wachstumsstreifen und Skulpturelemente auf die entsprechende Position des Mundrandepithels verweisen, bedeutet dies, dass nur bei letzteren der gesamte Weichkörper bis zur tiefsten Stelle der Verletzung zurückgezogen wurde, ohne dass das Mundrandepithel nennenswert gedehnt werden musste. Der Weichkörper konnte bei *Dactylioceras* mindestens weiter als ⅓ der Wohnkammerlänge in die Wohnkammer, bei Perisphincten weiter als bis zur Hälfte der Länge der Wohnkammer zurückgezogen werden. Die Weichkörper bei diesen Gattungen waren demnach sehr viel kleiner, als die Länge der Wohnkammer vermuten lässt.

Abstract

The evidences of the ability of withdrawing are derived from healing patterns of shell injuries. Healed injuries on ammonoid shells are common. Nearly all healed injuries are aperture-breakouts. The deepest healed aperture-breakouts observed in Lower Toarcian Dactylioceratids and Hildoceratids and in Oxfordian Perisphinctids are presented here. The slit-like injuries are affecting as much as one third of the body chamber and most probably caused by decapod crustaceans. The healing patterns of Perisphinctids/Dactylioceratids and Hildoceratids are distinctive. Hildoceratids stretched the sculptural elements of the repairing shell along the rim of the breakage. Whereas Dactylioceratids and Perisphinctids very seldom stretched the sculptural elements of the repairing shell. Normally its repairing shell is more or less regularly sculptured. Because the growth lines and ribs are almost parallel to the interimistic aperture these healing patterns show that Dactylioceratids and Perisphinctids where able to withdraw the whole soft body onto the deepest parts of the observed injuries. Consequently the soft bodies of only these animals where able to withdraw very deep into the living chamber. The soft body could have withdrawn in *Dactylioceras* deeper than ⅓ of the entire length of the living chamber, in Perisphinctids as much as ½ of the body chamber length. In these taxa the soft body is significantly smaller than would be suggested by the body chamber volume.

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1. Introduction

In recent years many new arguments were made to explain ammonoid soft body biology following rather the coleoid model than that of *Nautilus*. One of the first studies carrying out this idea was the cladistic work of Jacobs & Landman (1993). Additionally they found some functional arguments that a coleoid-like swimming could have evolved in the externally shelled ammonoids. The authors suppose a mobile coleoid-like mantle of longidome ammonoids. In 1998 Monk & Young contributed an interesting new idea on position and mobility of the soft body in the living chamber of heteromorphs following the coleoid model. They state, that the soft body of heteromorphs and ammonoids in general was much smaller than predicted from present models (as e.g. published by Lehmann [1981] and Westermann [1996]. Here it is assumed that the ammonoid soft body fills, comparable to *Nautilus*, the entire living chamber). Following Monk & Young a small soft body which did not fill the entire living chamber was able to withdraw into and push out of the shell and consequently change the position of the whole animal. This movement made sense especially in the case of heteromorph shell morphology. Kakabadzé & Sharikadzé (1993) argue for a twofold stable orientation in heteromorphs, one with aperture upward, one with a tilted aperture in direction to the sea floor. A neat solution how to change between the two stable orientations would be the shifting of the soft body in the living chamber as predicted by Monk & Young. Unfortunately the arguments of Monk & Young lack of direct evidences. This contribution will give further arguments for a mobile and small soft body in some ammonoids. “Some ammonoids” means that not all ammonoids, as will be shown, are able to withdraw into the body chamber in the same manner. Information for the ability of withdrawal is derived from the mode of repair of shell injuries caused by predators. For this purpose the author investigates more than 1000 ammonoids with healed injuries which are preserved in the collection of H. Keupp (Berlin). All named ammonoids are marked with PA-numbers.

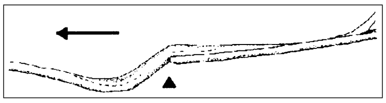
2. Material

Nearly 740 Lower Toarcian ammonoids with healed injuries from the Causses in Southern France (Tournadous), the Yorkshire Coast (Whitby) in England and the Posidonia Shale of Frankonia (Schlaifhausen, Altdorf) in Germany were observed. The Lower Toarcian ammonoids reflect a wide spectrum of species. The amount of named ammonoids with repaired injuries is dependent on the frequency in the strata. Consequently we have very different amounts of material of the different species. Most common are Dactylioceratids represented predominantly by *Dactylioceras athleticum* (Simpson) and *Dactylioceras commune* (Sowerby). Common are *Hildoceras bifrons* (Bruguieére), *Harpoceras serpentinum* (Reinecke), *Harpoceras falciferum* (Sowerby), *Cleviceras elegans* (Sowerby) and *Pseudolioceras lythense* (Young & Bird). The spectrum of species is representing a wide range of shell morphotypes: *Dactylioceras* is evolute with a long body chamber, broad whorl and a strong sculpture, *Pseudolioceras* on the other hand is involute, laterally depressed, mesodome and shows a weak sculpture. *Hildoceras* and *Harpoceras* mediate between the extremes. 283 Perisphinctids with healed injuries from the Rauracien of Sacaraha/Madagascar came additionally into account. The investigated Oxfordien ammonoids are *Lithacoceras torquatiforme* Spath, *Prososphinctes virguloides* Waagen, *Divisiosphinctes besairiei* Collignon, *Kranaosphinctes (Pachyplanulites) subevolutus* Waagen, *Kranaosphinctes (Pachyplanulites) rabei* Collignon.

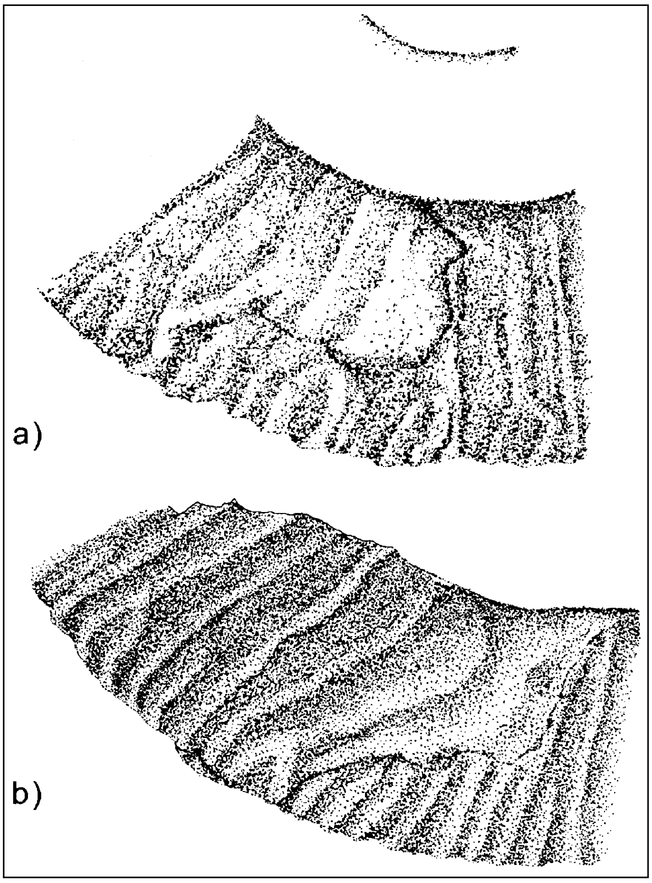
Divisiosphinctes besairiei, Prososphinctes virguloides and *Kranaosphinctes (P.) subevolutus* resembling *Dactylioceras* with its mode of ornamentation, evolute and broad whorls. *Kranaosphinctes (P.) rabei* is a cadicone, strong sculptured perisphinctid. *Lithacoceras torquatiforme* is more involute and slightly higher spired than the other perisphinctids. All observed perisphinctids have a long body chamber of about one whorl.

3. Shell Injuries and Techniques of Reparation

Repaired shell injuries of ammonoids are common. The populations given here show rates of healed injuries between 1,6 % (*Hildoceras* from Tournadous, after Keupp, pers. comm.) and more than 10 % (Perisphinctids of Madagascar, after Keupp, pers. comm.). The injuries are mainly caused by durophagous fishes (see Martill, 1990), coleoids and crustaceans (for a discussion see Roll [1935], Mehl [1978], Keupp [1991] and Kröger [1999]). Almost all healed shell injuries are breakouts from the aperture. Although most of these injuries are only minor, reaching not deeper as 20° from the aperture into the living chamber, some of them are very deep. The deepest observed repaired injuries are slit-like ones that occur mainly in serpenticone ammonoids like Dactylioceras and Perisphinctids. Most probably these injuries were caused by peeling of crustaceans. Hollmann (1969), Zipser & Vermeij (1978) and others described the peeling of gastropodes as a common behaviour of recent crustaceans. The typical technique of reparation of shell injuries in ammonoids following Hölder (1973) is called “forma aegra substructa”. Hölder (1956) founded a nomenclature of pathological phenomena organized in so called forma-types, best understood as symptoms in a medical sense (see Hengsbach, 1996). Forma substructa is the consequence of taking new shell material under the undamaged rim of the shell injury (see Text-Fig. 1). For that purpose the apertural margin (peristome) more ore less had to mimic the rim of the breakage and excrete new shell material to repair at least the whole injury (see Keupp [1998] for detailed description of the process of undertaking). Consequently the epithelium of the peristome had to stretch. Stretching of the peristomal mantle is indicated by a temporary lateral shifting of elements of the sculpture (see Text-Fig. 2). Checa & Westermann (1989) and Bucher et al. (1996) showed that ribbing and constriction patterns of ammonoids are in almost all cases parallel to the orientation of the peristome. Consequently stretched and shifted sculpture elements of the repaired shell are a measure disposition of the peristome caused by shell injury. But the ability of stretching is limited and deep injuries demand withdrawing of the whole soft body. Otherwise there is no necessity for stretching of the peristome if the entire soft body is able to withdraw onto the deepest point of injury and start to secret new shell material under the injured area.



Text-Fig. 1.
Shell injury regenerated by substructed shell in Recent *Nautilus* (redrawn after Keupp [1998]).
Arrow = 1 cm in growth direction; triangle = rim of the breakage.



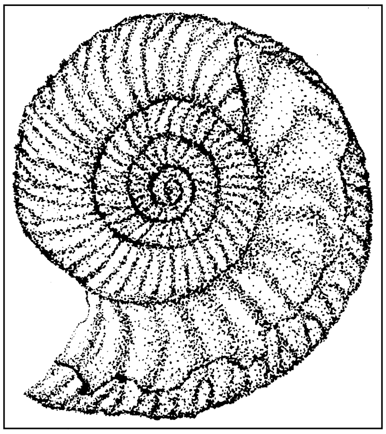
Text-Fig. 2.
Dactylioceras commune.
a) *Dactylioceras commune* (Sowerby) (PA 627) from Whitby (England) with a healed injury without stretched sculpture.
b) *Dactylioceras commune* (PA 1073) from Whitby (England) with a healed injury with stretched sculpture.
× 2.

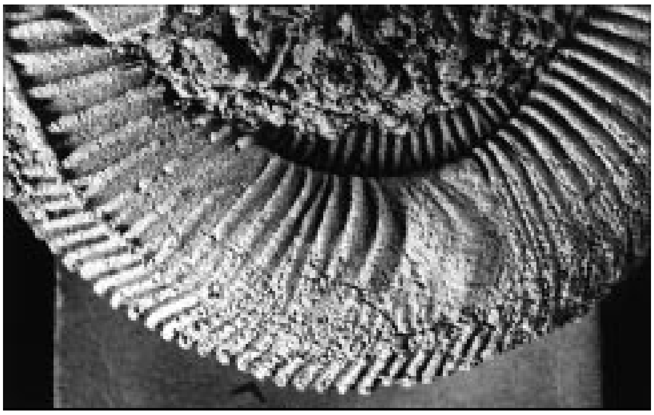
Only the peristome is able to build a periostracum which serves as a matrix for the underlaying carbonate shell and to build a regular sculpture (Clark, 1976; Bandel, 1981). As in gastropods, the shell which is spontaneously secreted by the mantle epithelium (as occurred after shell damage behind the aperture), shows an unspecific or no sculpture. This is due to the inability of the mantle epithelium to build a periostracum (Saleuddin, 1971; Blackwelder & Watabe, 1977). Consequently the maximal withdrawing of the peristome is indicated by the starting point of sculpture in repaired injuries.

4. Results

It is apparent that species with longer body chambers tolerate much deeper injuries than ammonoids with short body chambers. Table 1 gives the values for deepest repaired injuries observed in comparison to the approx. body chamber length. As expected the deepest healed injuries observed occur in the ammonoids with very long body chambers. By taking a more detailed view on the mode of regeneration it can be shown that the ammonoids with long body chambers show only very slight or seldom stretched or shifted sculpture caused by injuries. In the 283 observed perisphinctids all 37 repaired injuries that reached deeper than 45° behind the aperture show normal sculptures of repaired shell up to the deepest ends of injuries. The deepest repaired injury was found in *Kranaosphinctes (P.) rabei* with a measure of more than 180° (see Text-Fig. 3) back into the living chamber.

Text-Fig. 3.
Kranaosphinctes (P.) rabei Waagen (PA 11525) from Sacaraha (Madagascar) with a slit-like repaired injury of 180° aboral range. The sculpture of the repaired shell is only slightly streched or shifted.
×1.5.

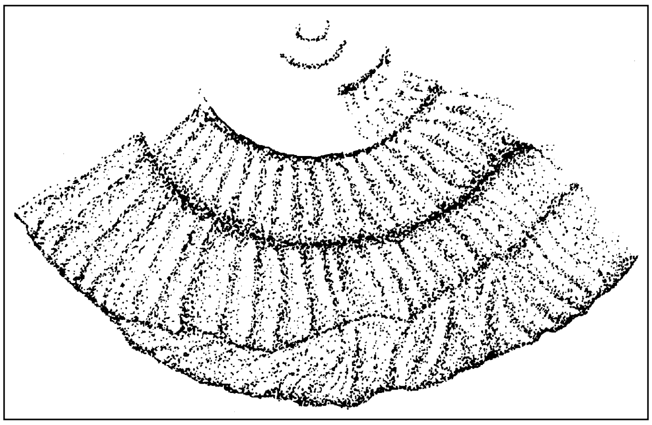




Text-Fig. 4.
Dactylioceras athleticum (Simpson)(PA 7697) from Schlaifhausen/Frankonia (Germany), forma substructa.
The sculpture of the repairing shell of the slit-like injury is starting in the most aboral part of breakage.
×2.5.

Out of 415 investigated *Dactylioceras* with repaired injuries 38 reached deeper than 45° behind the aperture. Most of them show a regular developed sculpture only until approx. 35°–45°. Behind that level the sculpture abruptly changes to irregular, simplified patterns or is missing totally (Text-Fig. 4). Only two of the deep injuries (PA 2808, PA 2182) show a normal sculpture of repaired shell until the deepest point of injury at max. 155° (Text-Fig. 5).

The mesodome species *Hildoceras* and *Harpoceras* on the other hand show in almost every case some kind of



Text-Fig. 5.
Dactylioceras commune (Sowerby) (PA 2182) from Whitby (England) with a slit like repaired injury of 90°.
The sculpture of the repaired shell is only slightly stretched or shifted.
×1.

Table. 1.
greatest observed aboral range of regenerated injuries compared with average body chamber length.

genus	max. aborale range of injury		max. length of the living chamber
	in°	in % of the length of the living chamber	
Perisphinctids (Oxfordium)	180	49	370°
Dactylioceras	155	40	390°
Hildoceras	94	36	260°
Harpoceras	88	34	260°
Pseudolioceras	51	23	220°

Text-Fig. 6.
Hildoceras (Hildaites) cf. *serpentinum* (Reinecke) (PA 7487) from Altdorf/Frankonia (Germany).
After two succeeding shell breakages the repairing shell is secreted with abnormal wide standing growth lines.
× 1.5.

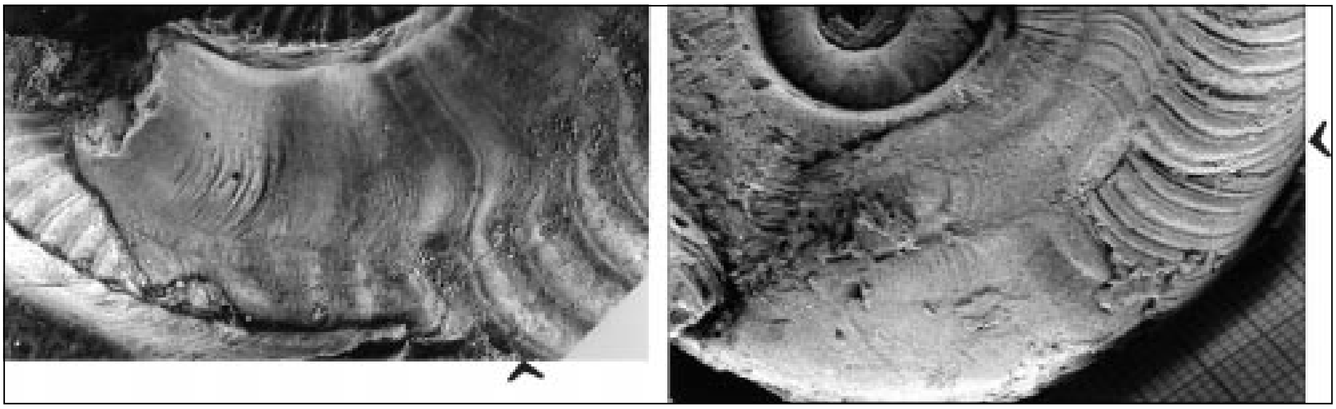
stretched sculpture or growth lines (Text-Fig. 6). If the injury is very deep the peristome failed to stretch along the rim of the breakage. Text-Fig. 7 shows two examples: In these cases the deeper parts of the lost shell where probably repaired by the mantle epithelia. The repaired shell is almost smooth, partially with very fine ribs or grooves. The regular sculptured shell, subdivided by growth lines, is restricted to the very apertural part of the regenerated injury.

5. Discussion

When Trueman (1941) measured the body chamber length of almost 81 species of ammonoids he found a twofold frequency peak: one peak at nearly 260°, a second at 380°. The numbers of Trueman demonstrate the long known existence of longidome and brevidome ammonoid morphotypes. Westermann (1996) completed the classification by a third type, the mesodome type. According to this classification the brevidome ammonoids show a body chamber length of 160°–180°, the mesodome of about 260° and the longidome of more than 360°. The specific length of the living chamber is recently interpreted as a function of the static stability and of the position of the aperture (see Saunders & Shapiro, 1986; Westermann, 1996). The morphotypes are represented here by *Dactylioceras*/Perisphinctids for the longidome type and *Hildoceratides* for the mesodome type. Bearing this in mind we come back to the idea of Monks & Young (1998).

Monks & Young (1998) state that a presumed small soft body of heteromorphs is mobile and able to shift the center of gravity and consequently the position of the aperture of these ammonoids. The idea of Monks & Young (1998) applies not only for heteromorphs but for longidome ammonoids as well. The centre of gravity in longidome animals is very close to the centre of buoyancy. Consequently its orientation in the water column is very unstable (Trueman, 1941; Saunders & Shapiro, 1986). With a mobile soft body as stated in Monks & Young the animal would be able to maintain the position of aperture. Following this point of view the unstable orientation of aperture could make sense: If the soft body reaches out of the aperture, the aperture is oriented more or less horizontally (comp. Keupp, 1997). If, presumably caused by predatory attack, the soft body withdraws into the living chamber, the entire animal will rotate upward. If the animal remains in its resting phase by withdrawing into the living chamber, the aperture is orientated upward, away from most predators (comp. Keupp, 1997).

The data represented here strongly suggest that longidome ammonoids were able to withdraw deep into the body chamber and therefore confirm these ideas. The nor-



Text-Fig. 7.
Hildoceras (Hildaites) cf. *serpentinum* (Reinecke)
a) *Hildoceras (Hildaites)* cf. *serpentinum* (Reinecke)(PA 10717).
b) *Hildoceras (Hildaites)* cf. *serpentinum* (Reinecke) (PA 10492).
In the deeper parts of both injuries the repairing shell shows fine grooves without growth lines. The first growth line starts in both cases near the interimistic peristome.
×1.6.

mal sculptures of repaired shell after deep injuries reach as much as one third of the entire length into the body chamber, indicating the maximum back-shifting of peristome. However, the withdrawing of soft body in Dactylioceratids is not a necessity. It seems that a withdrawal of more than 35° into the body chamber is only a strategy of emergency. Dactyliocatids possibly had a normal (active/resting rhythmic?) variability of soft body position between aperture and 35° behind of it.

The Perisphinctids do not show any preference comparable to Dactylioceratids. Their normal sculpture reaches back into the deepest injuries indicating a retraction of peristome of more than 180°. Such a strong withdrawal required a relative great mantle cave resp. a small soft body. With a small mobile soft body it seems impossible to manage a *Nautilus*-like jet propulsion (which is driven by the back shifting of the muscular soft body into the body chamber, see Chamberlain [1987]). If the observed longidome ammonoid could have swam by jet propulsion, a coeloid-like function as suggested by Jacobs & Landman (1993) or alternatively a hyponomic propulsion as suggested by Saunders & Ward (1994) is conceivable. In recent Coeloids the jet propulsion is produced by contraction of the mantle as a whole. The hyponomic propulsion model argues with an expanded, mobile muscular hyponome. Both constructions would have increased the mantle-cavity volume and improved swimming efficiency compared with that of *Nautilus* (Chamberlain 1991). This is necessary for the locomotion of an ammonoid with a very small soft body and a relatively big shell such as Dactylioceratids and Perisphinctids. In both models is no need for an opposing restorative moment of a stable static position of the shell which is required in the locomotion of *Nautilus*.

Hildoceratids on the other hand show no evidence for withdrawal. All injuries healed by a stretching of the peristome, indicated by the stretching of ornamentation and growth lines, or through regeneration of new shell by the mantle epithelium. Although the ability of stretching is high, the potential for withdrawal in mesodome ammonoids is very limited. There is no significant withdrawal recognised in Hildoceratids.

6. Conclusion

The mode of repair in observed longidome ammonoids is different from mesodome ammonoids. Longidome ammonoids undertake new shell material by back-shifting of the entire soft body, mesodome ammonoids in contrast mimic the rim of shell injury by stretching the peristome. The techniques of regeneration of deep shell injuries in ammonoids give us evidence for the organisation of the soft body. As Monk & Young propose, it seems that the soft body was relatively small in longidome ammonoids and filled only a part of the living chamber. These ammonoids were able to move the soft body deep into the living chamber. If the soft body moves into the living chamber consequently the centre of gravity shifts. In the case of withdrawal, the shifting centre of gravity causes a rotation of the entire animal into a position where the aperture is turned upside – possibly an emergency strategy. A small soft body as suggested by the healing pattern would have permitted the longidome ammonoids to swim in a *Nautilus*-fashion. Alternative models are the coeloid model of Jacobs & Landman (1993) or the hyponomic propulsion model of Saunders & Ward (1994).

Mesodome ammonoids on the other hand were not able to withdraw deep into the living chamber. The healing pattern of shell breakages suggests that the body chamber in these ammonoids were fulfilled by the soft body.

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