On Bipedalism in Skates and Rays

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On bipedalism in skates and rays

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SUMMARY

The anterior crurae of the pelvic fins in rajids are limb-like; this paper shows that these rays use the crurae for bipedal locomotion on the bottom at speeds around one-third of a disc length per second. It is suggested that this 'walking' pattern is employed to feed on prey within the substrate; sting rays (which feed in a different manner) do not possess such crurae. 'Walking' on a mud substrate leaves a characteristic track pattern as the crural tips dig in to propel the ray forwards; such tracks should be recognizeable in the fossil record.

1. INTRODUCTION

Skates and rays (sub-order Rajoidea) are distinguished from other batoids by several characters, including the notching or concavity of the outer margin of the pelvic fins. In some rajid genera, e.g. *Cruriraja*, this concavity is so deep 'that the anterior division of the pelvic fin forms a limb-like structure, entirely detached from the posterior part, three-jointed and (as it seems) separately movable' (Bigelow & Schroeder 1953). Similarly, von Bonde & Swart (1923) described the outer free parts of the pelvic fins of *Anacanthobatis marmoratus* as 'being leg-like'.

We show in this note that this limb-like crural part of the pelvic fin not only looks like a limb, but that it also acts like one; the rajid species we have examined use the crurae of the pectoral fins as legs to 'walk' along the bottom and to rotate the pectoral disc to bring prey to the mouth. The only references we have found to non-pectoral fin locomotion in rays are the suggestion by Bigelow & Schroeder (1953) that the pelvic limbs of *Cruriraja* 'may assist in the progress of their owners over the bottom'; the inference from dead specimens of the electric ray *Typhlonarke* by Waite (1909) that 'the anterior portion of the ventrals are modified for walking'; and the brief statement by Bratton & Ayers (1987) that the rays whose electric organ discharges they studied 'swam periodically by undulations of the pectoral fins or by gliding along the bottom substrate using the pelvic fins'.

2. MATERIALS AND METHODS

We examined newly hatched *Raia montagui* Fowler and *R. microocellata* Montagu obtained from eggs laid in the aquarium, and juveniles and adults of the same species, as well as adult *R. naevus* Müller and Henle, *R. clavata* L., and *R. brachyura* Lafont. Crural movements were observed visually, and photographed, and 16 mm ciné films at 16 frames per second were taken of the underside of small rays moving over a slightly roughened transparent plastic sheet, using a mirror mounted under the tank. The films were analysed with a Spectro HF 966A motion analysis projector. Adult rays of various species were timed visually when moving (without using the pectoral fins) over the sandy bottom of a large aquarium tank.

In other experiments, small rays were photographed when feeding on mysids, and when moving over a soft mud bottom (when they produce characteristic tracks). The skeletal structures of the pelvic fins were dissected in lightly boiled specimens.

3. OBSERVATIONS

(*a*) *Anatomical*

The cartilaginous skeleton of the pelvic fin (figure 1) reflects the marked division between the crurae anteriorly, and the remainder of the fin. The first radial is much enlarged and thicker than the four subsequent radials which together form the crura; all are linked by connective tissue and covered by skin, so forming the distinct limb-like structure obvious in intact animals (figures 2–4). Apart from the second radial (whose proximal end is free), the radials of the crura attach to the pelvic girdle directly, unlike the more posterior radials supporting the remainder of the fin, which insert on the basipterygium. The disposition of the articulations between the three major elements of the first radial suggests that particular segments are capable of movement in different planes. In freshly killed rays, the movements of the crural joints when the crurae are manipulated are: (i) the distal joint with the girdle permits antero-posterior movement of the crurae and a little dorso-ventral movement; (ii)

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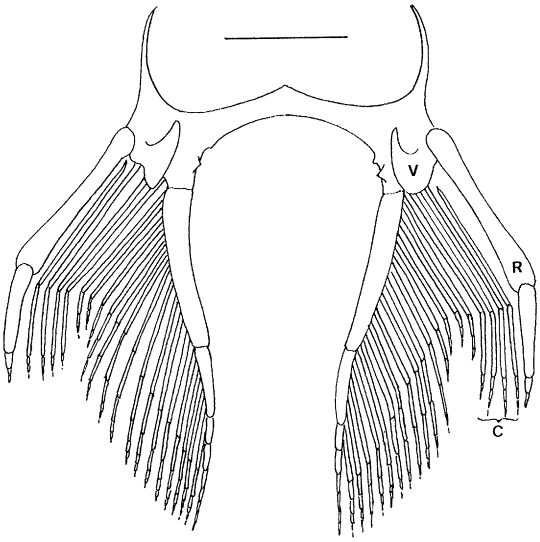


Figure 1. Ventral view of pelvic skeleton of adult *R. microocellata* showing enlarged first radial of crura (R), and the four subsequent crural radials (C). The retractor muscle of the first radial attaches to the ventral process of the pelvic girdle (V). Scale bar: 2 cm.

the next joint mainly dorso-ventral flexions; and (iii) the final joint flexion in almost any plane. In line with these movements permitted by the joints between the fin cartilages in fresh material, the actual positions adopted by different regions of the 'limb' in living rays are varied (figures 2–4), but result in a backward power stroke and forward recovery stroke. The musculature is complex and includes both red (slow) fibre bundles and white (twitch) fibre bundles, attached to tendons inserting at different points along the skeletal elements. The most conspicuous muscle inserts on the ventral horn of the pelvic girdle (figure 1, v) and is attached to the distal segment of the first radial; this evidently contracts during the backward power stroke of the crura. Backman (1913) gives a detailed description of the pelvic fins in several rajid species including figures of the musculature.

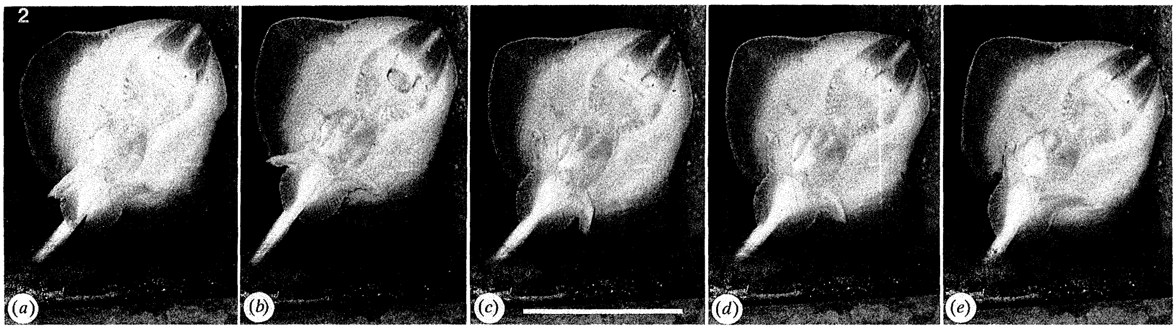
(*b*) *Behavioural*

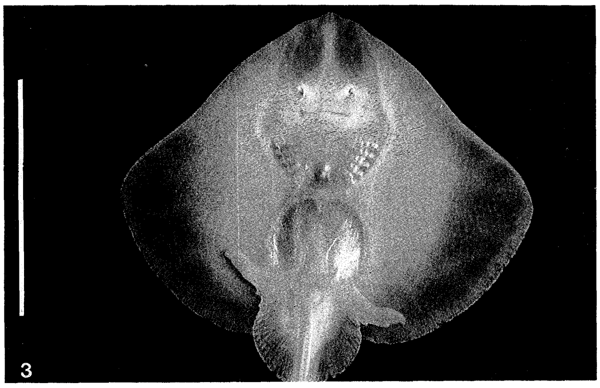
Just as other bipedal animals, rays can use the crurae of either side independently (to turn the disc), or together, or alternately (during forward progression). Simultaneous movements of both crurae (as of human legs during breast stroke swimming) were sometimes seen in newly hatched rays attempting to maintain position on the vertical walls of small aquaria (figure 4), but have not been seen during horizontal forward 'walking'. During 'walking', the crurae are used alternately, and the ray moves steadily forwards over the substrate. On sand, no obvious trace is left behind the ray as it moves forwards, but if rays 'walk' over soft mud, they leave a characteristic track clearly showing the imprints of the crural tips (figures 5 and 6). Measured speeds of newly hatched rays (disc lengths around 7 cm) 'walking' over coarse sand were 0.38 disc lengths per second ± 0.11 ($n=6$; range 0.26–0.55), i.e. around 2.7 cm per second, and up to 3.8 cm per second. The instantaneous velocities as they move forwards (figure 7) show that some accelerations and decelerations occur with the crural power strokes on either side, but these are small, and the ray glides forward smoothly. Adult rays 'walk' at similar relative speeds, around 0.3 disc lengths per second. In shallow acquaria, with a sandy bottom, rays are normally quiescent when illuminated by daylight, and often lie almost completely buried by the sand thrown up by flapping movements of the pectorals when the rays come to rest after swimming. With hatchling rays, which are more active under such conditions, gentle mechanical stimuli often provoked a short period of 'walking', and we have observed occasional 'spontaneous' 1–2 m 'walks' by adults in larger aquaria with other rays. However, we cannot say how frequent 'walking' may be under more natural conditions, or at night.

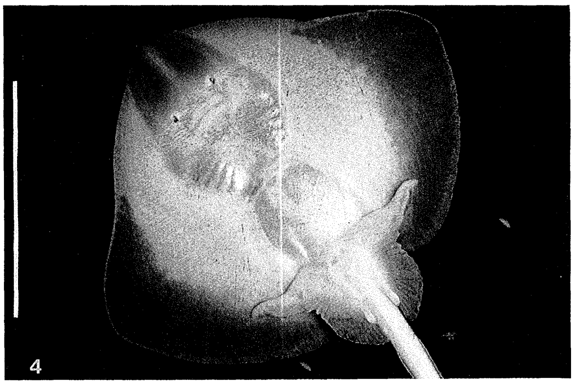
4. DISCUSSION

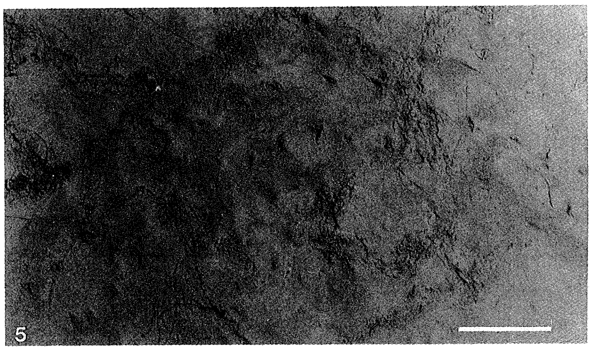
Our observations have clearly substantiated earlier suggestions that rajids can use their pelvic crurae as walking limbs, and although we have not been able to determine how important 'walking' may be in the behavioural repertoire of the ray species we observed, it seems probable that most rajids spend at least some of their time 'walking' over the substrate. The differences in crural morphology seen in different rajids (as seen, for example, in the species figures by Bigelow & Schroeder (1953)) suggest that there may be specific differences in the importance of 'walking', perhaps related to the nature of the substrate on which they live. As Bigelow & Schroeder noted, the genera *Cruriraja* and *Springeria* (an anacanthobatid) both live in relatively deep water (where the bottom is likely to be soft mud), and in both the crurae are quite separate from the remainder of the pelvic fin, and strikingly limb-like. When rays 'walk', they are moving slowly forwards with the mouth and the ventral ampullary electroreceptors in close contact with the substrate in which the invertebrates on which they feed are living. It seems therefore highly probable that 'walking' is a rajid feeding technique whereby prey can be located and captured with minimum disturbance as the ray moves forwards. Dasyatid and myliobatid stingrays, which lack the crurae, and feed on molluscs, do so in a different manner, jetting water out of the gill openings to excavate pits which remain conspicuous features of the seabed where stingrays are abundant (Bigelow & Schroeder 1953; Gregory *et al.* 1979). Electric rays, with the sole exception of *Typhlonarke*, also lack the crurae. The habits of *Typhlonarke* are unknown, but other electric rays capture fish using their electric discharges to stun them.

Th characteristic tracks produced by rays 'walking' on soft mud, seen in figures 5 and 6, have not been observed on the seabed as far as we are aware, but naturally raise the possibility that some of the fossil marine trackways attributed to other animals may in fact be those of rays. Rajids first appear in the fossil









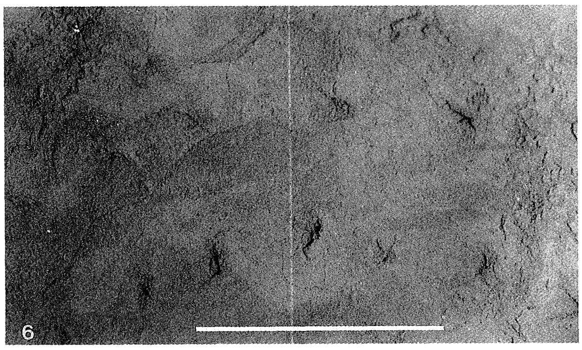


Figure 2. (*a–e*) Successive photographs at 1 s intervals of position of crurae in hatchling *R. microocellata* maintaining its position against side of aquarium tank. Scale bar: 5 cm.

Figure 3. Hatchling *R. montagui* against vertical wall of tank. Scale bar: 5 cm.

Figure 4. Similar view of hatchling *R. microocellata* showing symmetrical crural position. Scale bar: 5 cm.

Figures 5 and 6. Tracks left by hatchling *R. microocellata* after 'walking' on soft mud. Figure 6 is an enlargement of the central portion of the track shown in figure 5. Scale bars: 4 cm.

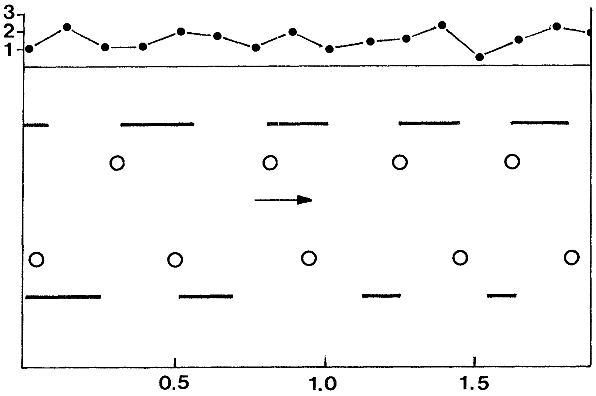


Figure 7. Schematic diagram of 'walking' (from ciné-film of hatchling *R. microocellata* 'walking' along a slightly roughened glass surface). The ray is moving to the right of the page. Bars represent the backward power stroke of the crurae on either side, and the most anterior positions of the crural tips are shown at large open circles. The points above are instantaneous velocities (in centimetres per second) during the progress of the ray along the substrate.

record in the Upper Cretaceous, and we would urge geologists examining marine sediments from that or later ages to bear in mind the possibility of rays as causal agents of any trackways found. Other fossil traces of ray activities have been found, for plug-shaped structures from shallow-water Miocene beds in New Zealand near Auckland are apparently the analogues of the foraging pits of modern stingrays (Gregory *et al.* 1990).

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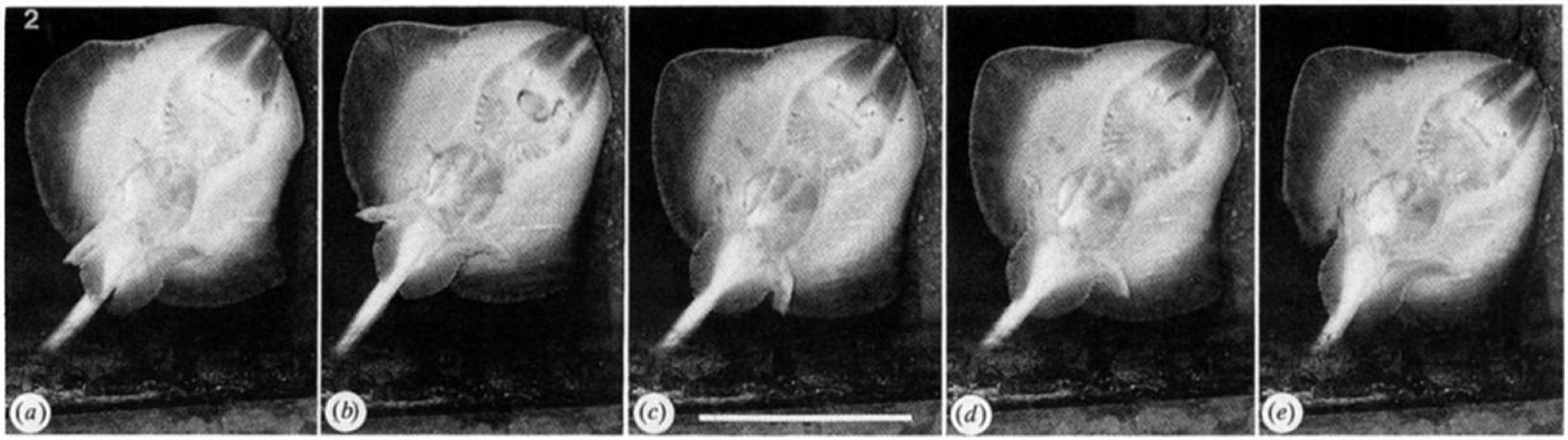

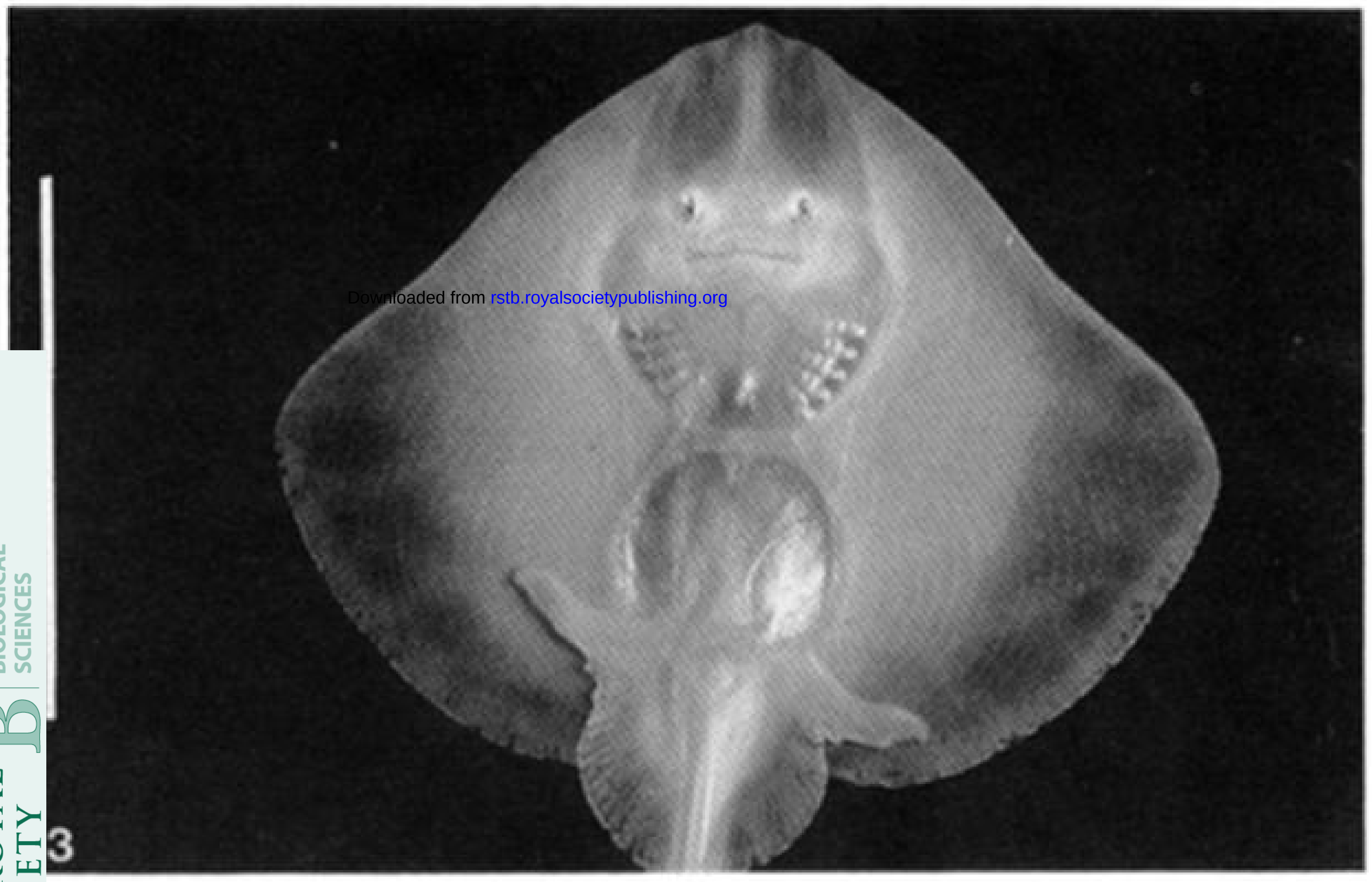

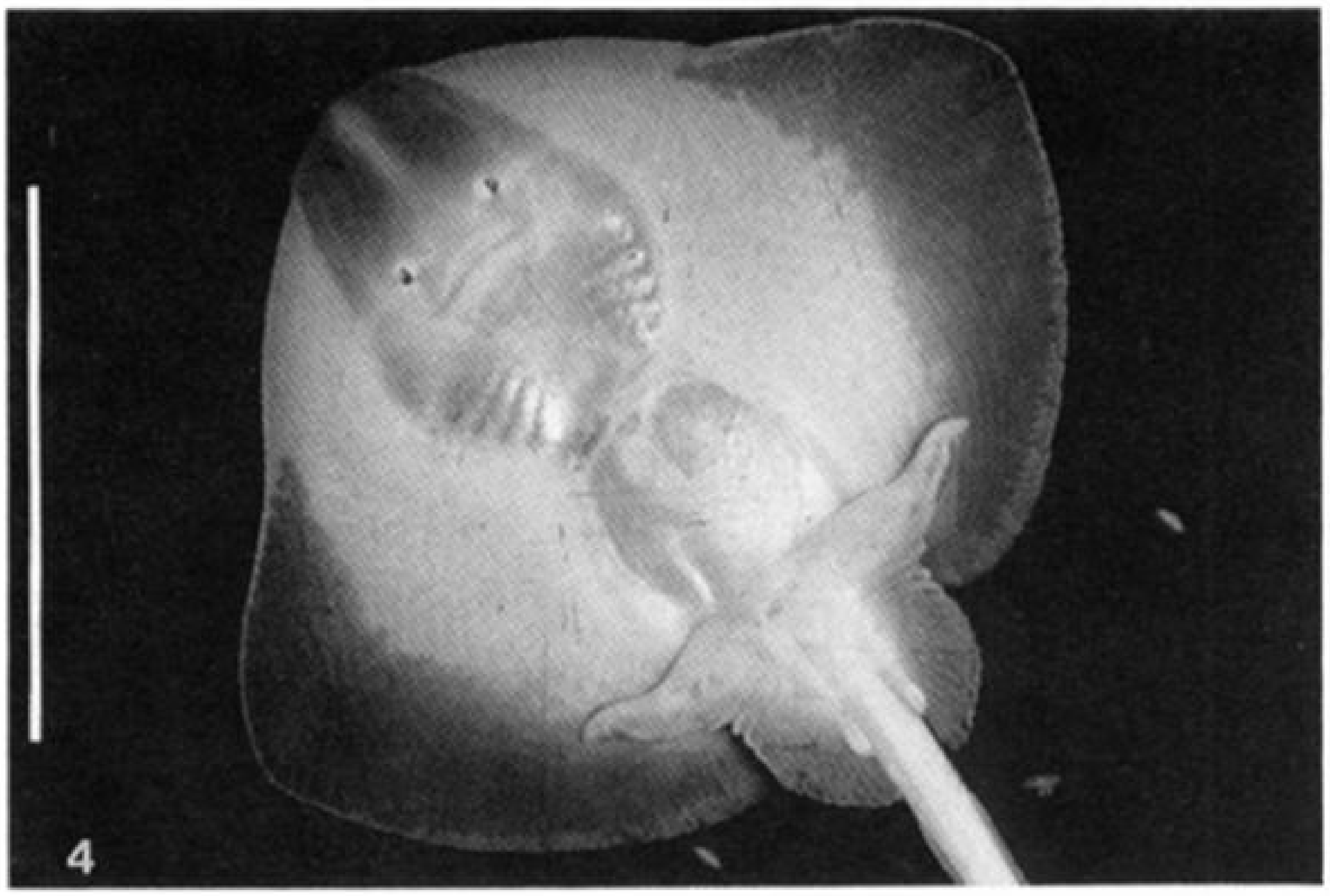

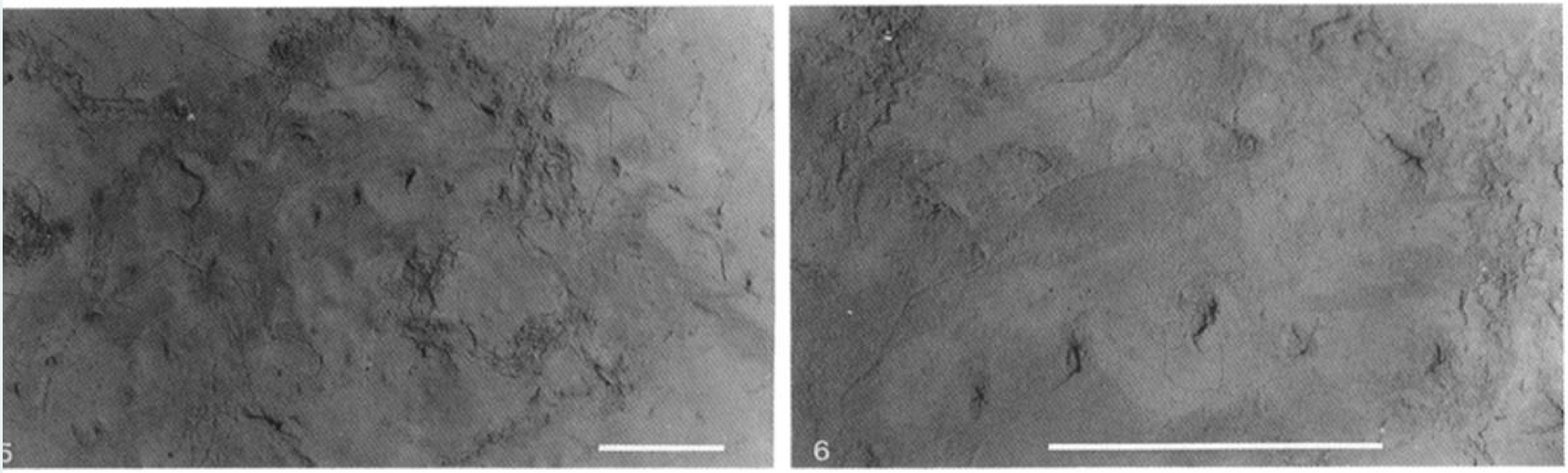

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