Evidence of Additional Functions of the Pericardial Sacs in the Bronchial Ventilation in the Grapsid Crab *Grapsus tenuicrustatus*

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**Abstract.** The pericardial sacs play an important role in branchial ventilation mechanisms in the semi-terrestrial grapsid crab *Grapsus tenuicrustatus*. The pressure change in these sacs leads to open or close the posterior branchial apertures. Air flow inside the branchial chamber causes pressure changes in the pericardial sac which enable the crab to absorb water from damp substratum. Examination of scaphognathite beat patterns indicated a number of distinct ventilation strategies, depending on whether the crabs were emersed or were immersed in sea water. In former case, the pattern employed depends on the crabs activity state. The volume of air ventilated by rested crabs was determined.

**Introduction**

The studies on functions and anatomy of the pericardial sacs for terrestrial, semi-terrestrial, and aquatic crabs has been reviewed by Bliss (1963). Milne-Edwards (1834) thought that he could detect a canal running from each sac to the exterior and wondered if these organs could be the site of an excretory product, analogous to urine. Cuenot (1891) suggested that the pericardial sacs may play a mechanical role of unknown sort. Pearson (1908), Borradiale et al. (1935) and Loach Head (1950) have stated that the function of these sacs is unknown. Drach (1939) studied the pericardial sacs in relation to molting. Bliss (1956) suggested that the pericardial sacs of the terrestrial crab *Gecarcinus lateralis* play an important role in the premolt uptake and in retention of water. Bliss (1963) studied the morphology, surface area, histology
holes drilled through the ventral carapace lateral to the 3rd maxillipeds, and were cemented in place using cyanoacrylate adhesive. The electrodes were connected to impedance pneumograph couplers (Starthkelvin instruments, Glasgow) and impedance changes were amplified and recorded using Washington MD2 or MD4 oscillographies (Searle Bioscience, Sheerness, Kent). Changes in the air pressure in the branchial chambers and the pericardial sacs were determined using a PT400 blood pressure transducer connected via an FC 137 coupler to a Washington oscillograph (all Searle Bioscience). A catheter, constructed from the nozzle of a disposable syringe, was cemented into the roof of the epibranchial chamber and connected to polythene catheter tubing (2 mm internal diameter). The catheter turnb was filled with sea water but none was introduced into the branchial chamber. Another was inserted in the posterior epibranchial just above the pericardial sac to detect any expansion or contraction in these sacs, and cemented in place. In either case the catheter tubing was connected to the PT400 pressure transducer. No attempt was made to quantify air pressure, but pressure changes were used to indicate the direction of the ventilatory current. In the pressure traces illustrated in the figures, an upward deflection of the pen indicates a positive pulse coincident with reversal of the respiratory current. Forward pumping generates negative pressure within the branchial chamber. Current direction was confirmed in immersed crabs by using ink to trace the water current or by using detergent (to observe bubble production) in partially emerged crabs and by using smoke in totally emerged crabs.

Further recordings of the direction of the respiratory current were carried out by means of a respiratory mask constructed from a balloon sealed with a cyanoacrylate adhesive around the interior of the crab. The balloon was connected via polythene tubing to a gas flow meter. Observations of the movement of a soap bubble within the flow meter burette enabled not only the direction of the ventilatory current to be established but also allowed some measurements of the ventilation volume of the crabs to be obtained. Recordings of ventilation volume were made only on quiescent emerged crabs which exhibited the characteristic burst pattern of reversed ventilation. All measurements were made at 25°C. Thermocouples (RS components) were used to monitor temperature changes in various micro-habitats occupied by the crabs and were also used to record crab body temperature.

Results

The pericardial sacs of Grapsus tenuicrustatus are similar to pericardial sacs of Cardisoma guanhumi described by Bliss (1963). Each pericardial sac has an outward extension, with a pointed tip which overlaps the gills. Also each pericardial sac has posterior pointed tip extension, inserted into small lacuna and fringed with hydrophilic setae. When a crab is obliquely oriented all the water drains posteriorly from the abdomen. The drained water is then absorbed by the expansion of the pericardial sacs through the setal tufts. This can be seen clearly from the reduction of pressure inside the branchial chamber in consistence with the increase in pressure in the pericardial sac (Fig. 1). Such a response was consistently seen in crabs that have been kept in dry conditions for several hours and were then transferred to damp sub-
FIG. 2. Recordings of the pressure in the Right Pericardial Sac. (a) and right branchial chamber (b) of a *Grapsus tenuicrustatus* engaged in lung flushing pattern, (E) and (C) Expansion and contraction of the pericardial sac respectively, (F) Forward pumping (FF) Fast reversed pumping result in large positive pressure in the branchial chamber.

curred, sometimes synchronously with increasing pressure in the pericardial sacs (Fig. 3), which open the posterior branchial apertures. In this situation, the water exits from the posterior branchial apertures, whereas in the absence of pressure build up, the circulating water enters from prebranchial apertures and leaves through the Milne-Edward's openings instead of the posterior branchial apertures. These were
case of forward pumping), the posterior branchial apertures were kept open. This was confirmed from the building up of pressure in the pericardial sac which lead to the entrance of air from the posterior branchial aperture and exit of air through the prebranchial aperture and Milne-Edward’s openings. The current direction was also confirmed by the stream of bubbles around Milne-Edward’s openings and the prebranchial apertures adjacent to the mouth. During bursts of reversed pumping, which occur at low pressure in the pericardial sacs with the posterior aperture kept closed, the bubble around the Milne-Edward’s openings were seen clearly (Fig. 6). After a period of time ranging from minutes to hours, a different pattern of pumping

**FIG. 6**. Recordings of the pressure in the Right Pericardial Sac. (a) right scaphognathite activity (b) and right branchial pressure (c) of a *Grapsus tenuicrustatus* engaged in forward and reverse pumping (E), and (C) Expansion and contraction of the pericardial sac (F) slow forward pumping, (FF) Fast reverse pumping, (R) Reversal.

was established. Bursts of reversed pumping by the scaphognathite were concomitant with the alternating low and high pressure in the pericardial sac. This alternation in the pericardial sac pressured occurred during an interval of 3-4 seconds duration. This alternation of pressure in the pericardial sacs results in a sudden change in the direction of air and according in trapping some of the circulating fresh air inside the branchial chamber (Fig. 7).

**FIG. 7**. Recordings of the Right Pericardial Sac pressure (a) Right scaphognathite activity (b) and right branchial pressure (c) from a *Grapsus tenuicrustatus* engaged in changing air direction in the branchial chamber E and C = Expansion and Contraction of the pericardial sac respectively, (F) slow forward pumping (FF) fast reverse pumping.
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Fig. 9. The relationship between ventilation volume and body weight for *Grapsus tenuicrustatus* maintained in air at 25°C. The data are for quiescent crabs which exhibited the characteristic pattern of bursts of reverse ventilation.

**Recordings in situ**

Experiments were carried out in simulated natural environment of the large outdoor aquarium tank to assess the relationship between ventilation rate, crab body temperature and environmental temperature. Crabs were able to move freely (through trailing fine wires). Fig. 10 illustrates the results of experiment in which the temperature differential between the crab body and the air was assessed in the sun and in the shade. It is evident that the differential is greatest at high temperature in sunlight ($3.4 + 0.3^\circ C$ $n = 10$) and least at comparatively low temperature ($1.3 +$
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Drach (1939) suggested that the sacs may regulate and limit hydrostatic pressure during molting, by storing water while it is being absorbed. There is agreement to some extent between the present work on *Grapsus tenuicrustatus* and that of Drach (1958) on *Gecarcinus lateralis* regarding regulating the hydrostatic pressure during molting. The present study indicates that the changing in the pressure in the pericardial sacs of *Grapsus tenuicrustatus* play an important mechanical role in the respiration mechanism in such a way that the pericardial sacs control the posterior apertures of the branchial chambers, where the increase of pressure inside the pericardial sacs opens these two apertures during forward pumping in air, whereas decreasing pressure in these two sacs closes these two apertures during reversed pumping admitting fresh air to flush the branchial lungs. Bliss (1963) indicated that the pericardial sacs take up water from damp substratum. The present work seems to agree with Bliss (1963), but the mechanisms in *Grapsus tenuicrustatus* is completely different from that of *Gecarcinus lateralis* described by Bliss (1963). It has been observed that the dip of the posterior extension of the pericardial sacs is fringed with hydrophilic setae and each inserted in small lacuna which lead to the abdomen. When the crab is oriented obliquely, all the water in the abdomen is drain towards the hydrophilic tuftitis. Changing the pressure in the pericardial sacs, transfers the water to these acts through the hydrophilic setae.

*Grapsus tenuicrustatus* exhibits a number of ventilation strategies similar to that of *Ocypode saratan* (Eshky et al. 1990) which are clearly adapted to its semi-terrestrial mode of life. When *Grapsus tenuicrustatus* enters the water, it behaves like an aquatic crab. Its pattern of pumping is a forward pattern where water enters through the Milne-Edward’s openings and is expelled from the prebranchial chambers aperture near the mouth. This occurs along with periodic reversals of the respiratory current. When in air, however, *Grapsus tenuicrustatus* displays a distinctive pattern of pumping, which consists of bursts of reverse pumping separated by periods of apnoea. The functional significance of the fact that air flow in reversed direction is very important since the forward pumping is relatively slower than that of reverse pumping. This allows the crabs to renew the air inside the branchial chambers with more oxygenated air. In the case of quiescent crab which consists of bursts of reverse pumping separated by long periods of apnoea providing the average weight crab with an amount of 13 ml min⁻¹ of air, which contains 2.6 ml O₂. *Ocypode saratan* of comparable weight (Eshky et al. 1988) consumes 0.39 ml of oxygen per minute, which means that the reversal pumping provides the crabs with enough oxygenated air and enables the crab to save its own energy. During the present study of *Grapsus tenuicrustatus*, it appeared that during the contraction of the pericardial sacs, the posterior apertures of the branchial chambers remained closed to prevent drainage of branchial water. Air circulation during reversal pumping took place almost entirely between the prebranchial apertures and the Milne-Edward’s openings. In gecarcinids, when wholly in air, ventilation flow through the branchial chambers is predominantly in a forward direction, and may be continuous or intermittent depending on the species and activity state (Cameron and Mecklenberg 1973; Taylor and Davis 1981; McMahon and Burggren 1988). When partly immersed, however, the gecarcinid *Cardisom gunnhumi*, engages in alternating periods of forward and reversed scaphognathite
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