

ON THE INTERACTIONS
BETWEEN SUCTORIAL ADHESION, GILL VENTILATION
AND OPERCULAR SPINE ERECTION IN
*XENOCARA OCCIDENTALIS**

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INTRODUCTION

Electrophysiological methods have recently been used to study gill ventilation mechanisms in fishes (see, for example, Hughes & Shelton, 1958; Hughes, 1960*a, b*; 1970; Ballintijn & Hughes, 1965; Ballintijn, 1969*a, b*; Osse, 1969). These investigations have facilitated studies of the unusual ventilation mechanisms of specialized fishes, such as suctorial forms that inhabit mountain streams.

Xenocara occidentalis (Regan, 1904) is a South American catfish of the family Loricariidae. In this fish modification of the gill ventilation mechanism has occurred for adhesion by means of an oral sucker, and for the erection of opercular spines. Oral suction is an important component of feeding in *Xenocara*. Therefore notes have been included on the feeding behaviour of this fish. In regard to gill ventilation and suctorial adhesion, *Xenocara* is essentially similar to another loricarid, *Plecostomus punctatus*, of which sufficient fishes were available for more detailed study (N. Gradwell, unpublished). Muscular action in oral valve closure has already been described in *P. punctatus* (Gradwell, 1971*a*).

Alexander (1965) has described the erection of opercular spines in the loricarid, *Ancistrus*. The present study compares the more pronounced opercular spines of *Xenocara* with those of *Ancistrus* and evaluates the effects of opercular spine erection on the mechanisms of gill ventilation and oral suction.

MATERIALS AND METHODS

Recordings were made on six adults of *Xenocara occidentalis* (Regan) obtained commercially. To the best of my knowledge, the fishes were collected in rivers of Guyana. Their snout-to-vent length was 5.2 ± 1 cm.

After 2-3 weeks acclimation to 21 °C in algae-laden aquaria individual fishes were anaesthetized in 1% urethane solution. As soon as the fishes became tractable, cannulae (PE 50, Clay-Adams Inc.) of 3 cm length were implanted by the method of Gradwell & Pasztor (1968). Care was taken to avoid constraint of ventilatory movements and muscle impalement during cannulation. One cannula was implanted through the mesethmoid and palatine, 1 mm posterior to the edge of the oral valve. Pressures from cannulae implanted 1 cm posterior to this site showed no appreciable

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difference from those farther forward. As there are no valves subdividing the buccopharynx, it was assumed that pressures monitored anteriorly were not significantly different from those in the buccopharynx adjacent to the gill clefts. The other cannula was implanted in the lateral wall of the opercular cavity, 3 mm above the opercular spines. At their apertures within the animals the cannulae were orientated with their axes approximately perpendicular to the ventilation current. The free ends of the cannulae were plugged and the fishes were returned to their aquaria for several hours to recover from anaesthesia and the implantations before recordings were begun. Movements of the cannulae and associated artifacts in the pressure recordings did not arise.

Hydrostatic pressures in the buccopharynx and opercular cavities were monitored by transducers (Hewlett-Packard 267BC differential and 1280 models) connected to the implanted cannulae. Pressures developed between sucker and substratum were monitored by the method of Gradwell (1971*b*). These pressures were monitored from the centre of the sucker, as recordings from the periphery were of smaller amplitude. The pressure waveforms and an electrically derived differential pressure were recorded simultaneously by a rectilinear oscillograph.

Movements of the opercular spines and opercular valves were monitored with a movement transducer (Harvard 356), and were recorded on an oscillograph simultaneously with hydrostatic pressures. The transducer lever system was delicately balanced to minimize interference with natural movements.

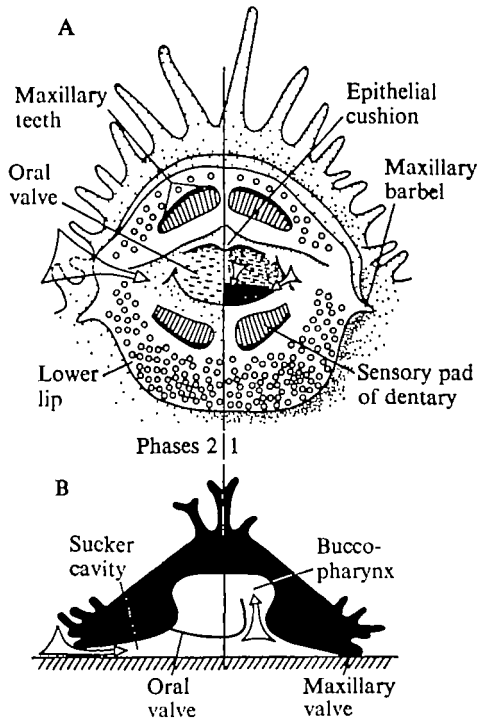
Electromyograms were recorded with bipolar electrodes of varnished and twined copper wire (80 μm diameter). Myograms and hydrostatic pressures were displayed simultaneously on an oscilloscope and recorded with an oscilloscope camera.

Laboratory behaviour

Air breathing was not seen in *Xenocara occidentalis*. The fish seems to rely largely on gill ventilation for its respiratory gas exchange. Although *Xenocara* swims well, it habitually clings to the glass of an aquarium by its oral sucker (Text-fig. 1; Plate 1). Therefore it is easy to study the functioning of the suctorial apparatus without disturbing the animals. If a stream of water is directed toward the fishes, they orientate themselves so that the water flows over them from snout to tail (Plate 1A).

In well-aerated water the most conspicuous movement in the sucker is a rhythmic opening and closing of the oral aperture by a membranous valve (at 40–50 cyc/min). Abduction of the lower jaw from the glass also occurs during cyclic oral closure, but no special upper jaw movements are apparent. Frequently, small parts of the periphery of the sucker, immediately anterior to the maxillary barbels on both sides of the fish, are also slightly abducted from the glass. Water with suspended algae was seen to enter the sucker cavity rhythmically at these peripheral regions (Text-fig. 1A, B). If the fish was clinging at an angle to the vertical axis, then often only one side was abducted, causing a unilateral flow into the sucker cavity. As the oral valve opened (Text-fig. 1A, B; Plate 1B), the periphery of the sucker became well sealed against the glass and the lower jaw's tooth-bearing areas were simultaneously pressed against the glass.

Observations of animals adhering to a glass surface showed that the movements of the oral valve were correlated with oscillations of the buccopharyngeal floor and



Text-fig. 1. Diagrams to show oral water flow during phases 1 and 2 of the breathing cycle. A, Underside of the sucker. B, Cross-section through the sucker at the level of the oral valve and maxillary inlets.

movements of the opercular valves. The opercular valves opened just after oral closure (Plate 1 C) and near the onset of elevation of the buccopharyngeal floor. Water was seen leaving through the opercular valves at this time. The oral valve then opened, the buccopharyngeal floor sank, and the opercular valves closed. The resultant increase in buccopharyngeal volume drew water into this chamber from the sucker cavity (Text-fig. 1 A), as shown by suspended algae.

Rhythmic movements of oral structures during suctional adhesion were further observed with a dissecting microscope. At the onset of depression of the buccopharyngeal floor the oral valve opened (Plate 1 B), apparently by its inherent elasticity. At about this time, and if ventilation was greater than *ca.* 50 cyc/min, the edge of the valve was seen to vibrate, perhaps owing to the water entering the buccopharynx from the sucker cavity. Immediately rostral to the valve an epithelial cushion protrudes from the sucker wall (Fig. 1 A; Gradwell, 1971 a). The oral valve touched this cushion during high-amplitude respiratory movements. The cushion returned to its resting position, apparently by its own elasticity during the closing (caudad) movement of the valve.

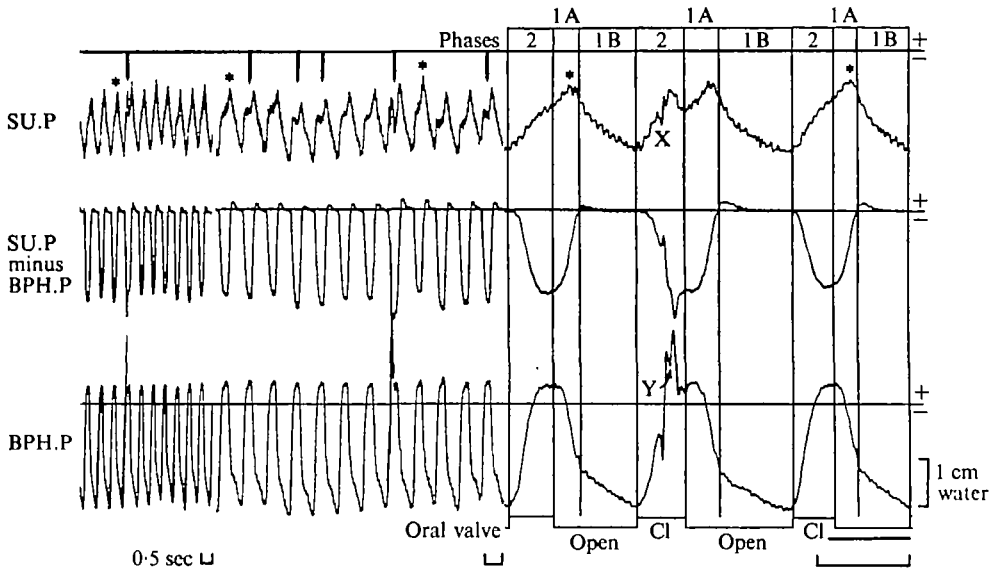
When fishes clung to the glass bottom of the aquarium, coarse particles of organic debris and sand occasionally entered the sucker cavity via the groove-like peripheral conduits (maxillary valves, Text-fig. 1 B) anterior to the barbels. Examination of the sucker from beneath the aquarium showed that fishes responded to the entry of coarse

particles into the sucker by a cough-like action, without suctorial disengagement. The response included stronger-than-usual abduction of the lower jaw from the glass and simultaneous powerful elevation of the buccopharyngeal floor. The opercular valves opened wide, and a strong exhalant flow was observed at this time. Simultaneously the sucker cavity became expanded with more inhaled water than usual, thus diluting the suspension of coarse particles. At the next buccopharyngeal inspiration these particles entered the buccopharynx. During the following ventilation cycle another similar response occurred (even when no further particles entered the sucker cavity), which flushed the material out of the respiratory system via the gill clefts and opercular valves. The soft pads at the bases of the lower jaw's dentition (Text-fig. 1A) seemed particularly sensitive to tactile stimulation, as coarse material touching this area immediately evoked the 'cough' response. The oral valve is itself also sensitive to touch. The behaviour described above occurred frequently if sand was deposited in the aquarium. All the fishes eventually preferred to cling to the sides of the aquarium under these conditions.

In undisturbed resting fishes the opercular spines were retracted into grooves of the body wall, but disturbance caused the erection of spines on one or both sides of the body (Plate 1C). Simultaneously, ventilation movements ceased and the oral and opercular valves were held closed (i.e. suctorial reinforcement occurred). When manual pressure was applied to the erected spines so as to force them back into their grooves, strong resistance was felt and the applied force eventually displaced the sucker along the glass. In response to strong stimulation, the spines remained fully erected for 15–20 min before gradual retraction occurred soon or immediately following erection, and at times a repeated stab-like erection–retraction sequence was observed on one or both sides of the fish. The animals adapted to repeated stimulation by reducing the above responses. Whereas, both instantaneous and gradual spine retraction occurred, the erection of the spines in response to tactile stimulation was always instantaneous.

Xenocara was often seen feeding on algae growing on the sides of the aquarium. This feeding was intermittent and occurred only when fishes were undisturbed. The algae were scraped off the glass by the fish's teeth during the simultaneous movement of the jaws toward each other (adduction). Immediately after this movement the jaws moved apart again (abduction). The loosened algae, suspended in water, were drawn into the buccopharynx. Cords of green algal faeces were often seen being extruded from the cloaca.

For efficient feeding, an intimate contact between the teeth and the algae would seem to be essential, at least during the adduction of the jaws. The fish's oral sucker permits this close application between teeth and substratum (Plate 1D, E) without the need for fin locomotion. There were forward or backward displacements of the entire animal during feeding. Although accompanying incidental movements of the paired fins did occur, the dorsal and caudal fins were certainly not active. Therefore the displacements (< 3 cm) of the fish during feeding could not be attributed to fin oscillations. The displacements were apparently produced by the rapid, co-ordinated movements of the jaws during their cyclic scraping action. Dorsal and caudal fin undulations were occasionally seen to shift the fishes short distances from one feeding site to another.



Text-fig. 2. Simultaneous recording of sucker (SU.P) and buccopharyngeal (BPH.P) pressures and the differential pressure between them. The detailed labelling is explained in the text. The functional condition of the oral valve, deduced from electromyograms correlated with pressure recordings, has been added.

EXPERIMENTAL RESULTS

Hydrostatic pressures and associated movements

To facilitate the description basic to this account, the gill ventilation cycle will be divided into two primary phases according to the functional condition of the oral valve (Text-fig. 2).

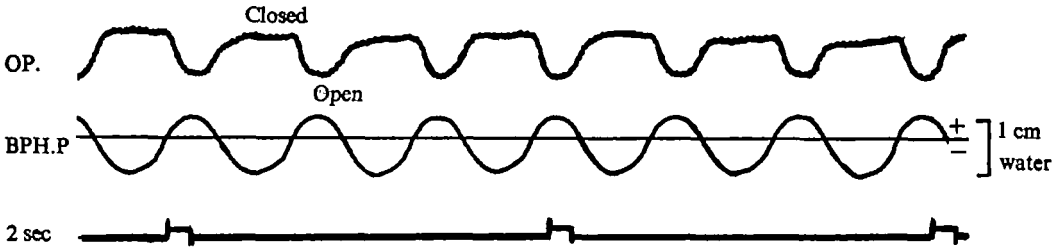
In phase 1 the oral valve is open and allows water flow between sucker and buccopharyngeal cavities. This phase is divided into two subphases dependent on the differential pressure between the two cavities. In subphase 1A a large negative differential pressure occurs briefly between the two cavities. In subphase 1B a positive differential pressure is developed which allows respiratory water to enter the buccopharynx.

In phase 2 muscles hold the oral valve closed, thus isolating the sucker from the respiratory apparatus. Ambient water enters the sucker cavity during this phase owing to sucker expansion. The opercular valve is not directly referable to the phases described above, but opens to release exhalent water midway through phase 2 and closes near the end of subphase 1A (Text-figs. 3, 4).

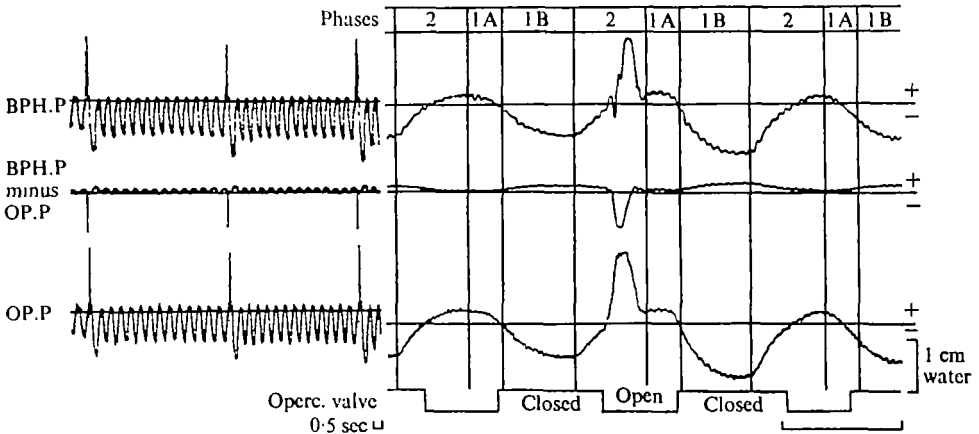
Sucker pressure waveform

Dependent on the general level of respiratory performance needed by the animal, there is variation in the shape, frequency, amplitude, and general pressure range of the sucker pressure waveform (Text-fig. 5).

While the sucker adheres to a surface, the pressure in the sucker cavity is always negative relative to ambient pressure. Rhythmic pressure fluctuations were measured in the sucker cavity and were visually correlated with relevant movements. Pressures from the sucker cavity were obtained by gently sliding the engaged sucker over a flush



Text-fig. 3. Movements of the opercular valve (OP) recorded simultaneously with bucco-pharyngeal pressures (BPH.P).

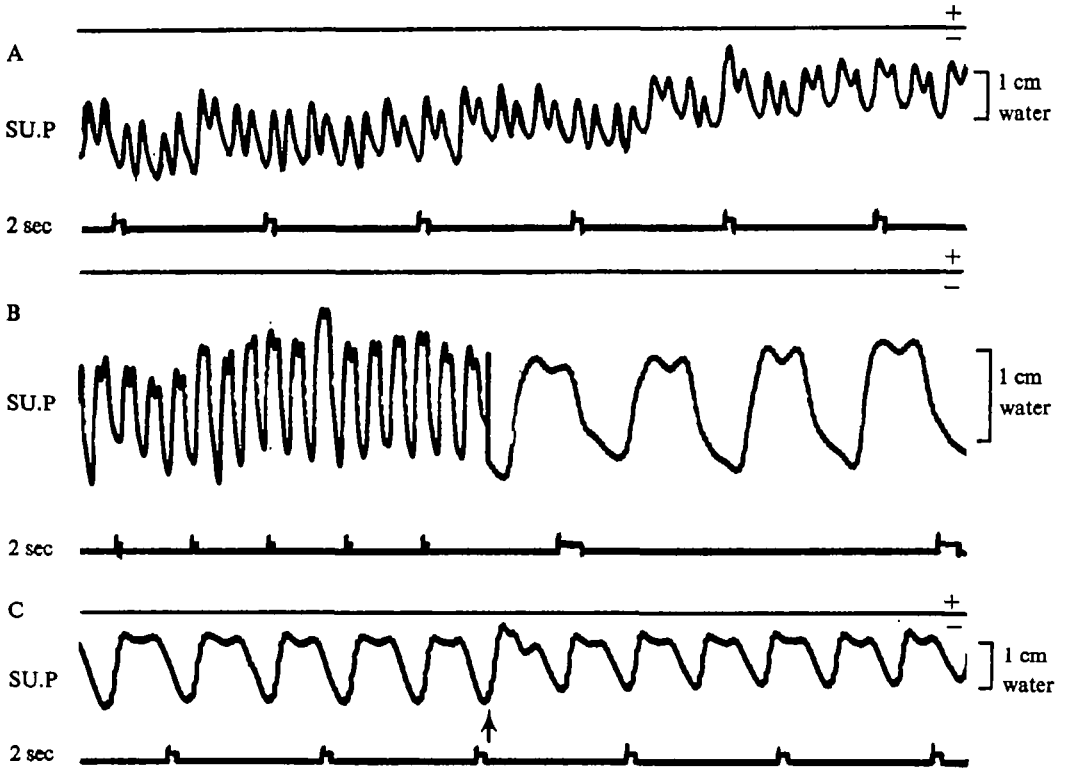


Text-fig. 4. Simultaneous recording of bucco-pharyngeal (BPH.P) and opercular (OP.P) pressures and the differential pressure between them. See text for detailed analysis. Functional positions of the opercular valves have been added (see Text-fig. 3).

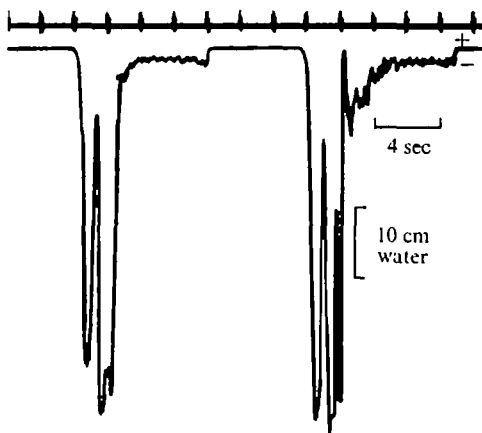
connection to a pressure transducer (Gradwell, 1971*b*). The pressure monitor registered a strong suction (Text-fig. 6) simultaneously with observed unilateral or bilateral opercular spine erection. High-amplitude fluctuation of sucker pressure was seen initially, but in the absence of further disturbance the frequency and amplitude of the fish's respiratory movements decreased and there was a concomitant fall in the amplitude of sucker pressure fluctuations.

The events which occur in the sucker during a typical cycle of gill ventilation will now be described. The cycle begins with closure of the maxillary inlet valves and opening of the oral valve (subphase 1A, Text-fig. 2). During subphase 1B there is adduction of the lower jaw against the substratum and simultaneous depression of the bucco-pharyngeal floor. As the events of subphase 1B occur relatively slowly, the pressure record (Text-fig. 2) shows a slow fall until the end of this subphase.

Phase 2 begins with closure of the oral valve. During this phase the sucker pressure waveform is primarily influenced by a rise in bucco-pharyngeal pressure which is transmitted to the sucker via the closed but flexible oral valve. This basic waveform is secondarily influenced by abduction of the lower jaw from the substratum, within the sucker, which increases the suction by increasing the volume of the sucker cavity. The superposition of this secondary increase in suction upon the basic waveform causes a cyclic notch in the record (Text-fig. 5A, B, C). The notch divides the primary sucker pressure curve into two peaks, which may be equal or unequal in size (Text-fig. 5A, B).



Text-fig. 5. Recordings of sucker pressures (SU.P) from a fish during different states of respiratory performance. (A) Immediately after opercular spine erection. (B) Two minutes after opercular spine erection. (C) Spines retracted; prolonged resting in the dark without disturbance (left of arrow). The record to the right of the arrow shows the effect on breathing of a 30 W light beam shone suddenly on the fish (30 cm range).



Text-fig. 6. Pressures recorded during manual sliding of the fish's sucker over a pressure monitor. The initial large pressures were associated with jab-like movements of the opercular spines. The horizontal base-line indicates ambient pressure when the sucker is off the pressure monitor.

depending on the co-ordination between the movements of lower jaw abduction and elevation of the buccopharyngeal floor. The size of the notch depends on the extent of lower jaw abduction, as observed large-amplitude abductions of the lower jaw were always associated with large notches in the pressure waveform (Text-fig. 5A) (also seen in the 'cough' response, Text-fig. 2). In addition, when lower jaw abduction was negligible or absent, no secondary deflexion of the pressure waveform occurred (Text-fig. 2).

Observation with a dissecting microscope of algae in the ambient inflow through the maxillary inlets showed that little water entered the sucker cavity when lower jaw abduction was slight. Occasionally in quiet animals the maxillary inlets remained closed for short periods. As no respiratory inflow or outflow occurs at this time, these periods may be termed suspended ventilation. Throughout the ventilation cycle the sucker pressure is negative relative to ambient pressure. Therefore the opening of the maxillary valves cannot occur by hydrostatic pressure. They are probably opened by muscular abduction of the maxillae from the substratum.

There is variation in the level of suction applied to the substratum. In well-rested fishes visual and tactile stimuli caused immediate irregularities in the sucker pressure (Text-fig. 5A, B), and although the range of sucker pressure fluctuations soon stabilized, the shape of individual cycles took longer to become uniform (Text-figs. 5A, B). If the fish was left undisturbed, the fluctuations of sucker pressure eventually became stable in all respects (Text-figs. 2, 5C).

Buccopharyngeal pressure waveform

The pressure waveforms recorded from cannulae in the buccopharynx (Text-figs. 2, 4) show a fall (phase 1) followed by a more rapid rise (phase 2) within each cycle. A large negative differential pressure develops between sucker and buccopharynx during phase 2, but no backflow of water from the buccopharynx into the sucker can occur in this phase, as the oral valve is closed. This negative differential persists into subphase 1A and here, as the oral valve opens, slight reflux may occur. This reflux may contribute to the rapid decline of buccopharyngeal pressure at this time and may also assist the opening (elastic recoil) of the oral valve. In subphase 1B a positive differential pressure is seen (Text-fig. 2) and water flows from the sucker into the buccopharynx. Toward the end of this subphase the oral valve starts to close, the differential pressure approaches zero (ambient pressure), and water flow between the two cavities ceases.

Opercular pressure waveform

The opercular pressure waveform is similar to that of the buccopharynx (Text-fig. 4). A positive differential pressure develops between the buccopharynx and opercular cavities in subphase 1B and continues, although decreasing, during phase 2. This indicates that, if unobstructed, buccopharyngeal water could flow over the gills into the opercular cavities at this time. In Text-fig. 4 differential pressure is absent during the positive peaks of the waveforms, indicating that perhaps in *Xenocara* the opercular suction pump is dominant over buccopharyngeal compression. The opercular valves open at or immediately after the opercular pressure rises above ambient pressure near the middle of phase 2 (Text-fig. 3). The use of India ink as a flow marker demonstrated water gushing from the opercular valves at this time. During

The latter part of subphase 1 A, when the opercular pressure falls below the ambient level, the opercular valves close. Therefore, although these valves have adductor and abductor muscles, their action during quiet breathing seems possible by hydrostatic pressure alone.

The ventilation cycle

The salient points of gill ventilation and suctorial adhesion are summarized in the following account of the sequence of events during a typical cycle.

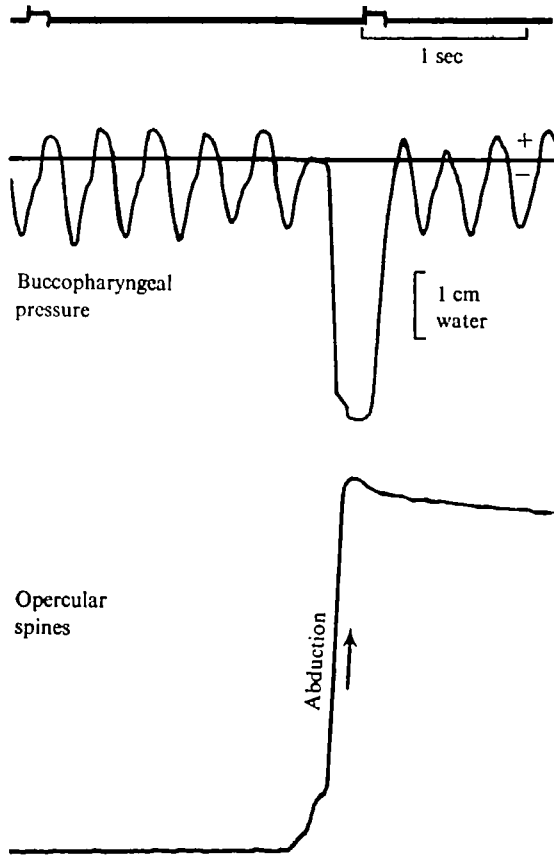
The oral valve opens by its own elasticity at the onset of subphase 1 A. As the valve opens, the large negative differential pressure (Text-fig. 2) between sucker and buccopharynx, caused by rapid buccopharyngeal expansion, is soon lost. Reflux (as shown by India ink) past the oral valve into the sucker cavity may be partly responsible for the loss of negative differential pressure and may also itself facilitate movement of the valve. A rapid reduction of pressure develops in the buccopharynx during subphase 1 A and continues into subphase 1 B. This causes a positive differential pressure between sucker and buccopharynx which draws water into the buccopharynx from the sucker. Buccopharyngeal and opercular pressures are very similar in subphase 1 A when little or no water may flow over the gills. However, in subphase 1 B increased suction in the opercular cavities produces a positive differential pressure which may drive water over the gills, but as the opercular valves are closed, no exhalation occurs at this time.

At the onset of phase 2 the oral valve closes by the action of its own muscles. Buccopharyngeal pressure may be transmitted to the sucker by distortion of the flexible oral valve. This movement may contribute to the general lessening of negativity in the sucker during this phase. However, toward the end of phase 2, suction is usually increased by lower jaw abduction from the substratum. At about the same time, the maxillary inlets permit ambient water to flow into the sucker cavity. Water flow over the gills may also continue into phase 2, as a positive differential pressure still exists briefly between the buccopharynx and opercular cavities in this phase (Text-fig. 4). As the differential pressure declines, both buccopharyngeal and opercular pressures become positive relative to ambient pressure and the opercular valves open suddenly, allowing exhalation to occur. This exhalation continues into and throughout the next subphase, 1 A, toward the end of which the opercular valves close.

Opercular spine movements

In addition to opercular spine erection during manual displacement of the sucker, the erection response was also evoked by other tactile stimulation. Text-fig. 7 shows simultaneous opercular spine erection associated with an increased negative pressure in the buccopharynx. Gradual retraction of the spines began immediately following erection, but the buccopharyngeal pressure returned to its usual range of fluctuations much sooner.

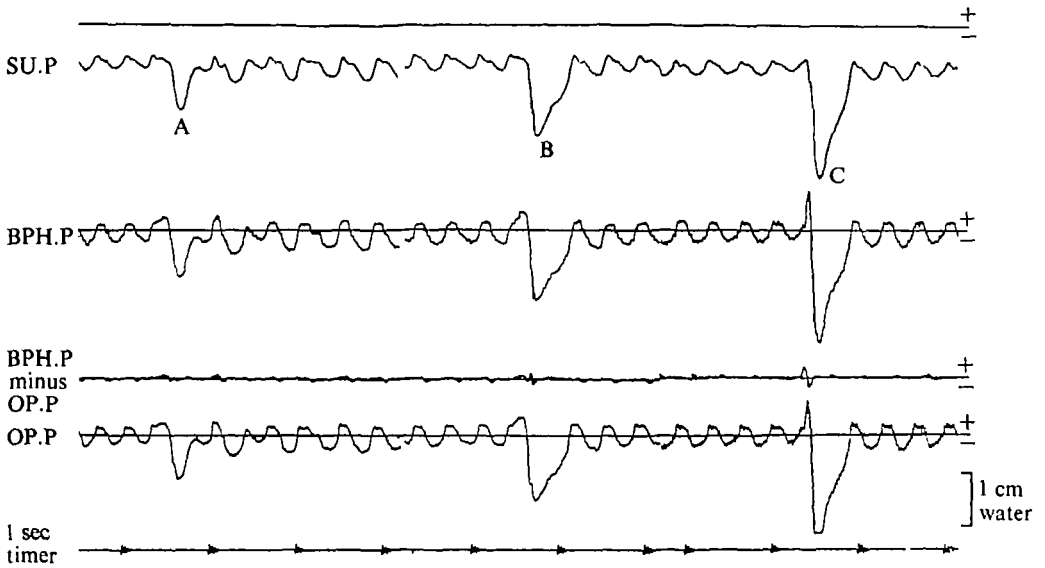
Rhythmic gill ventilation continued during the variable periods of maintained spine erection and the normal operation of the opercular valves did not appear to be altered by the functional condition of the opercular spines. However, throughout the ventilation system stronger negative pressures were correlated with unilateral spine erection (Text-fig. 8A, B). When simultaneous bilateral spine erection occurred (Text-fig. 8C), the negative pressures were approximately double this magnitude.



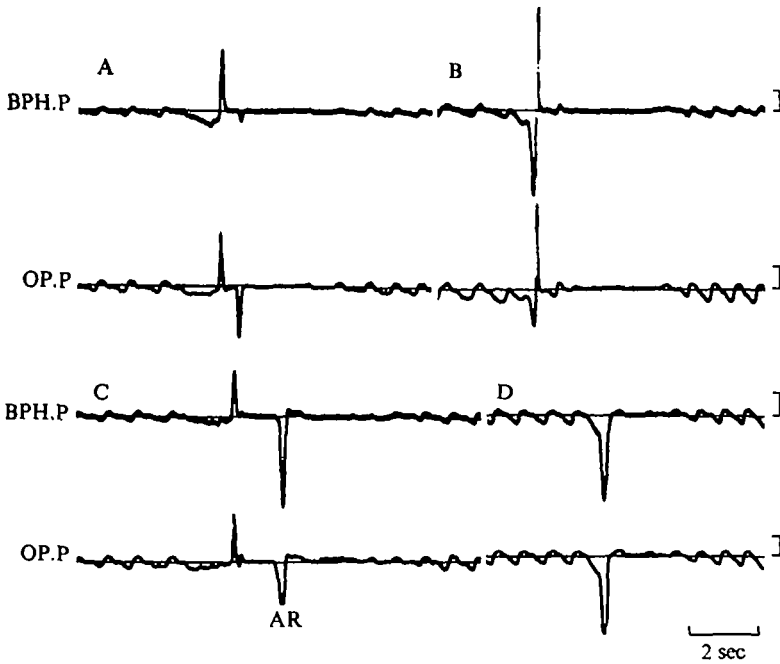
Text-fig. 7. Simultaneous recording of pressures and movements during opercular spine erection. Due to mechanical constraint of the recording pen the complete fall of the pressure waveform is not shown.

Also in response to tactile stimulation, fishes sometimes erected and then immediately retracted their opercular spines. At the same time, the buccopharyngeal and opercular pressures showed large fluctuations (Text-fig. 9A, B). Occasionally, tactile stimulation of the snout's tentacles first elicited a large positive rise in buccopharyngeal and opercular pressures without opercular spine movement, and then a fall in the pressure records from both cavities, associated with opercular spine erection (Text-fig. 9C). Sometimes the increase in negative pressures associated with spine erection was about equal throughout the ventilation system (Text-fig. 8A, B, C; Text-fig. 9). At other times, perhaps depending on the participation of the opercular valves, the pressures associated with opercular spine erection were unequal at least in the buccopharynx and opercular cavities (Text-fig. 9A, B).

Curtailement or suspension of gill ventilation for short periods sometimes occurred immediately after the large pressure fluctuations associated with tactile stimulation (Text-fig. 9). If not further disturbed, the fishes gradually resumed rhythmic ventilation.



Text-fig. 8. Simultaneous recordings of sucker (SU.P), buccopharyngeal (BPH.P) and opercular (OP.P) pressures during opercular spine erection. The differential pressure (BPH.P-OP.P) is also shown. (A) Slight erection of left spines only. (B) Full erection of right spines only. (C) Full erection bilaterally.



Text-fig. 9. Simultaneous recordings of buccopharyngeal (BPH.P) and opercular (OP.P) pressures during single, jab-like, erection and retraction of the opercular spines. AR, Artifact of arrested pen movement. Calibrations: + 1 cm water above horizontal base-lines of ambient pressure.

Cough-like responses

A convulsive action was occasionally recorded from all specimens of *Xenocara*. Several authors have given the name 'cough' to apparently similar phenomena in other fishes. A cough (Text-figs. 2, 4) is associated with a large positive pressure increase in both buccopharyngeal and opercular pressures during phase 2 and with enhanced oral suction. The differential pressure records in Text-fig. 2 show that during coughs the sucker is more negative than usual, relative to the buccopharynx. However, oral valve closure during coughs prevents buccopharyngeal water from entering the sucker cavity.

A cough begins about midway through phase 2. This response is always seen superposed on the rise of the buccopharyngeal and sucker pressure records in phase 2. Initially, a slight fall occurs in the pressure (*X*, Text-fig. 2), after which both records rise steeply during strong elevation of the buccopharyngeal floor. As the oral valve is closed during a cough, the steep rise of sucker pressure (after *X*, Text-fig. 2) may be due to buccopharyngeal pressure transmitted across the flexible oral valve. A notch (*Y*, Text-fig. 2) usually occurs in the buccopharyngeal pressure records, but it is not clearly evident in the sucker pressure waveform. Steep falls of the pressure records occur from their highest peaks in the sucker and buccopharynx. Lower jaw abduction may contribute at least partly to this sudden increase in suction (also transmitted to the buccopharynx via flexible oral valve). Phase 2 ends, as usual, with the opening of the oral valve.

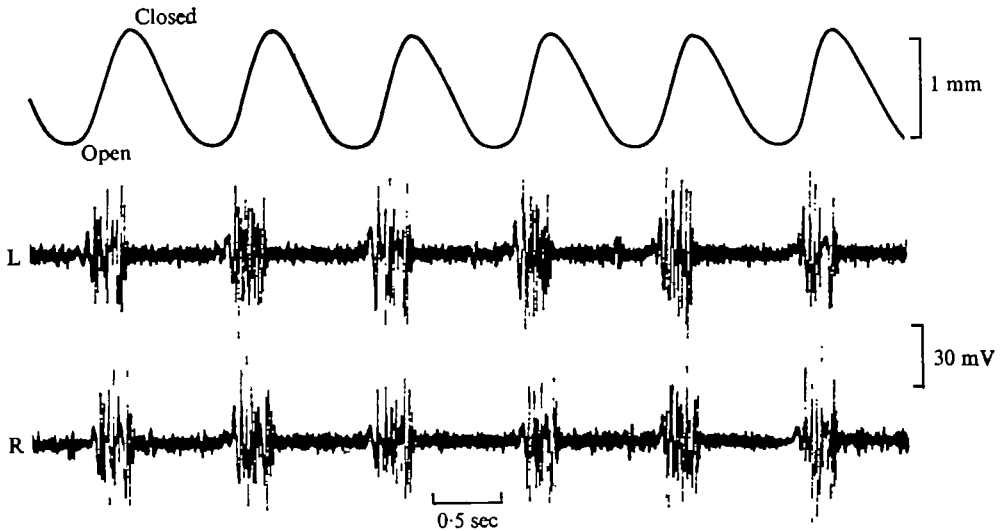
The hemibranchs of individual gills are invariably adducted against each other during coughs (direct observations through opercular valves). Therefore, except perhaps by constriction at the gill rakers, the gill clefts do not occlude the buccopharynx from the opercular cavities during coughs. As coughs are associated with large negativity in the differential pressure between the buccopharynx and opercular cavities (Text-fig. 4), a reflux of opercular water into the buccopharynx may occur. However, if the opercular valves open at this time, a strong flow leaves the opercular cavities through them. The differential pressure between the buccopharynx and opercular cavities is slightly positive during the latter part of phase 2 and during the following subphase 1A (Text-fig. 4). After the large negative differential pressure in phase 2, the rapid reversal of the pressure gradient may help to loosen and discharge irritants from the respiratory system.

Electromyography

The oral valve of *Xenocara* is rhythmically closed by a pair of striated muscles which are inserted on the extreme lateroposterior edges of the valve. The muscles originate dorsally on the pterygoids, lateral and anterior to the external nares. Near their insertions they are almost circular in cross-section, and they flatten dorsoventrally near their origins.

Bipolar electrodes were inserted bilaterally into the oral valve muscles of two unanaesthetized fishes whose buccopharynges had previously been cannulated. Electromyograms and simultaneous hydrostatic pressures were recorded during heavy breathing (Text-fig. 10).

At the onset of phase 2 the oral valve muscles contract (adduction) simultaneously



Text-fig. 10. Simultaneous recording of oral valve movements (RCA 5374 transducer) and electromyograms from its left and right muscles.

on both sides of the fish. The muscles relax throughout phase 1 while the oral valve is open. The adductors of the oral valve have no functionally antagonistic muscles. Opening of the valve is apparently caused by elastic recoil, perhaps assisted by hydrostatic pressure (see earlier results).

DISCUSSION

Mechanical interactions and structural modification enable *Xenocara occidentalis* to use its sucker simultaneously as a respiratory inflow and for adhesion to the substratum. Suctorial adhesion is not restricted to perfectly flat surfaces; strands and sheets of connective tissue bind the bones of the sucker together so that it is strong and also flexible enough to conform to slight irregularities of the substratum.

The oral valve is the most striking feature of the sucker. While many teleosts have two oral valves (upper and lower), *Xenocara* and some other fishes (Gudger, 1946) have only the upper oral valve. In adult lampreys the denticulated tongue is provided with muscles and may function as an oral valve (N. Gradwell, in preparation). However, *Xenocara* (and some other loricarids) so far appear to be unique in having a membranous oral valve which is closed by direct muscular action (Gradwell, 1971a). In addition to this valve, *Xenocara*, *Ancistrus* and *Plecostomus* have bilateral suctorial inlet valves which are operated by movements of the maxillae (N. Gradwell, unpublished).

In most fishes it is the action of the oral valves that actually seals the mouth before buccopharyngeal compression, and it is difficult to predict the exact functional condition of the oral valves from recordings of jaw movements alone. Fortunately, in *Xenocara* it is possible to study oral valve action both by direct observation through a glass substratum and by electromyograms (Text-fig. 10) of the oral valve muscles. With these two techniques accurate interrelation between oral valve closure and other respiratory events was possible. Oral valve closure was seen to occur simultaneously with buccopharyngeal compression; on the other hand, buccopharyngeal pressure

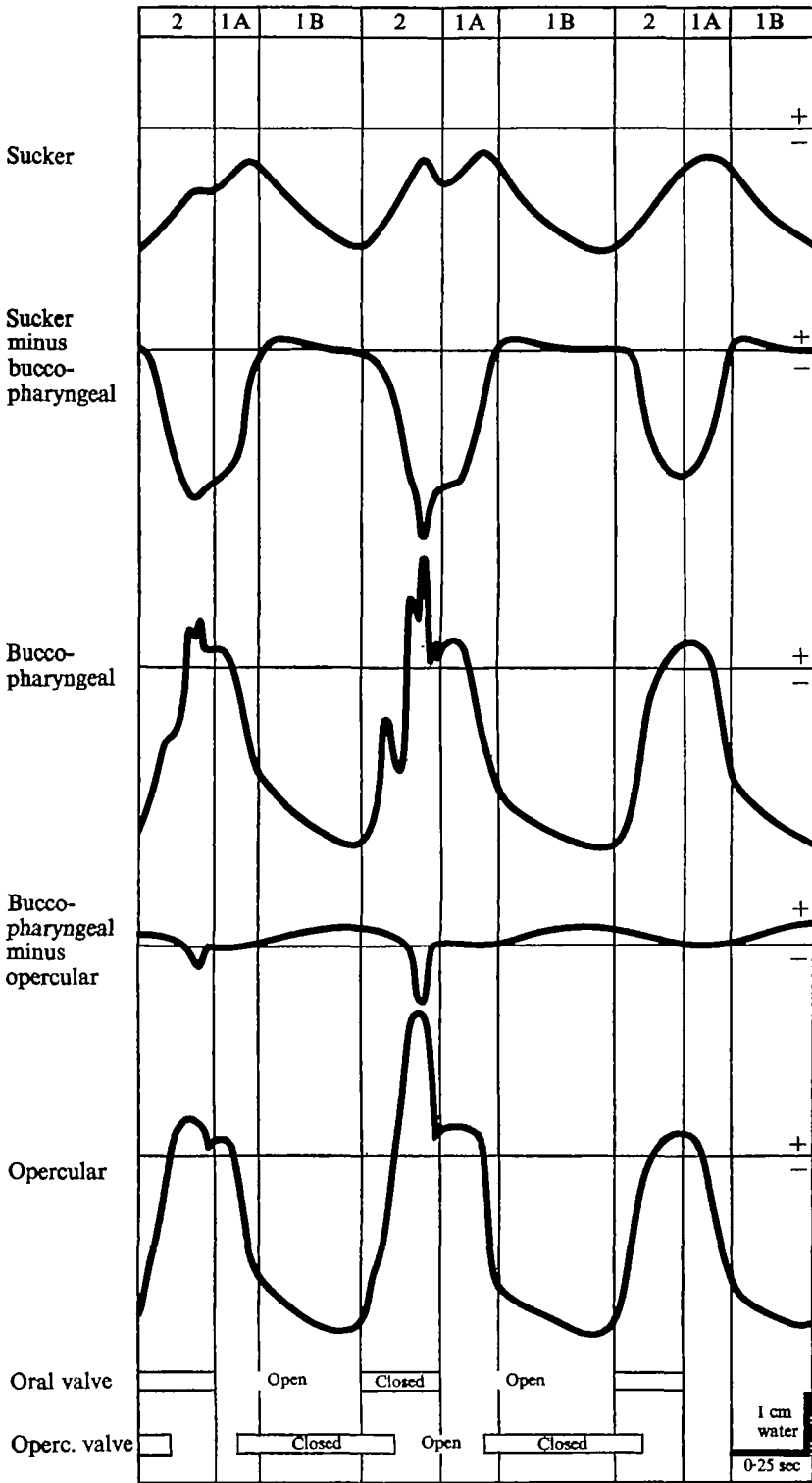
diminished immediately on opening of the oral valve. Video recording (N. Gradwell, unpublished) has shown that this timing is identical in *Plecostomus punctatus*, but it differs from that described for the non-suctorial trout (Hughes & Shelton, 1958) in which the oral valves close and open out of phase with the positive (compression) peak in the buccopharyngeal pressure. Data on the action of the oral valve in other fishes have not been published, perhaps because these valves are somewhat concealed, except for the muscular tongue of lampreys.

Aspects of the relevant hydrostatic pressure waveforms and electromyograms have been used by previous authors as markers to divide the gill ventilation cycle into functional phases. These internal phenomena are directly associated with externally visible valvular actions (e.g. oral and opercular valve movements) which are of primary importance in determining water flow into or out of the respiratory pumping chambers. Surprisingly, these valvular actions have been little used in the determination of the phases of the respiratory cycle. In the present study a ventilation cycle is divided into two main phases, phase 1 (oral valve open) and phase 2 (oral valve closed). Phase 1 is further divided into subphases 1 A and 1 B, according to the differential pressure across the oral valve. In animals where the oral valves are not easily visible opercular valve action could be used to allow similar analysis based on externally visible functional states.

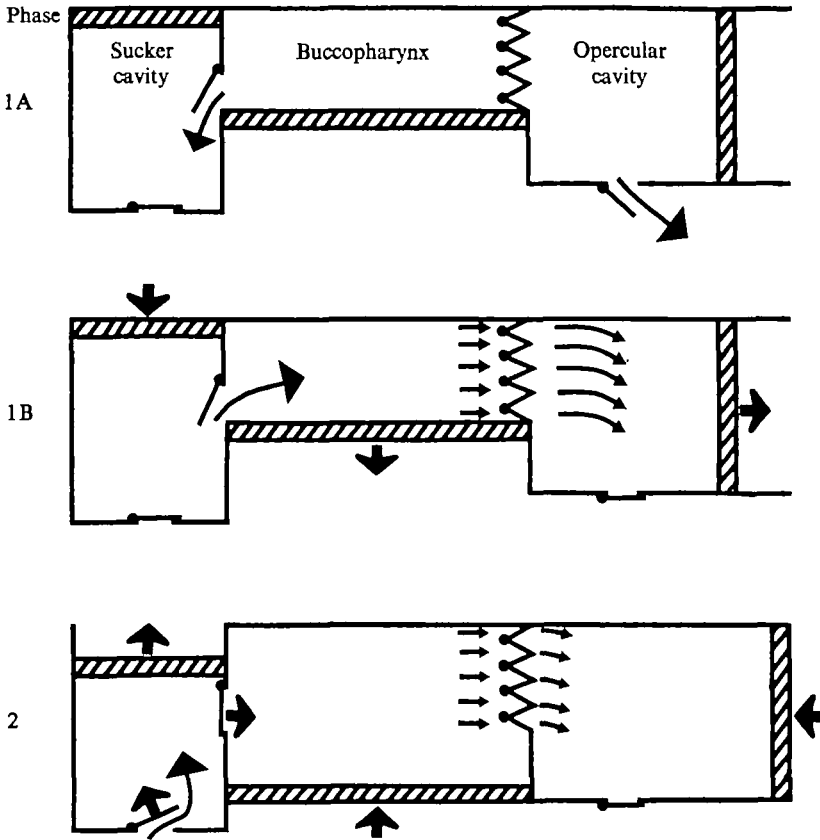
In *Xenocara* water flow across the oral valve is not unidirectional. In addition, sucker inspiration may coincide with opercular expiration. Therefore the terms 'inspiration' and 'expiration' have been avoided in the present study wherever such usage may be misleading. Incidentally, oral opening and opercular closure occur at about the same time in *Xenocara*, although the oral and opercular apparatus are not mechanically coupled as they are in certain other fishes (see Hughes, 1970).

During gill ventilation water enters the sucker via the bilateral maxillary inlets, and sufficient suction is maintained by the muscular closure of the oral valve and the simultaneous expansion of the sucker cavity. The cusp of the oral valve closes outside the mandible (Gradwell, 1971*a*). Therefore, as hydrostatic pressures across the valve have shown, were it not for muscular closure of the oral valve, reflux of water from the buccopharynx would flood the sucker cavity during phase 2 and abolish suction. Instead, the oral valve is held closed by muscles and a slight abduction of the maxillary inlets allows water to enter the sucker cavity. This water is later pumped through the mouth, buccopharynx and opercular cavities by the interaction between the buccopharyngeal and opercular pumps. Thus, maintenance of suctorial adhesion normally depends on both the specialized structure of the sucker and a precise co-ordination between the movements of the paired inlet valves, lower jaw, oral valve, and buccopharyngeal and opercular complex.

For comparison with other fishes, the movement and pressure data of *Xenocara* are summarized in Text-figs. 11 and 12. In contrast to the dual water pumps of certain fishes (Hughes & Shelton, 1958; Hughes & Ballintijn, 1965), *Xenocara* has three rhythmic water pumps: the sucker, buccopharynx and opercular cavities. The differential pressure measured between the buccopharynx and opercular cavities (Text-fig. 4) indicates that a balance occurs between buccopharyngeal compression and opercular suction pumps. In this respect *Xenocara* is similar to the several fishes in which dual water pumps have been described. *Xenocara* normally applies itself closely



Text-fig. 11. Summary prepared from tracings of the pressure waveforms of *Xenocara occidentalis* during gill ventilation. Valvular actions, based on Text-fig. 3 and electromyograms of the oral valve muscles, have been included.



Text-fig. 12. A model of the gill ventilation mechanism of *Xenocara occidentalis*. The bilateral opercular cavities are represented by a single chamber in the diagram.

to the substratum and is similar to benthic teleosts like the blenny and plaice (Hughes, 1960a) and to rays among the elasmobranchs (Hughes, 1960b), in which the differential (buccopharyngeal minus opercular) pressures are seldom or never negative (relative to ambient pressure) during the typical ventilation cycle. Therefore the danger of contamination or injury to the gills by reflux of sand or debris through the opercular valves is reduced.

In *Xenocara* a positive pressure gradient occurs across the gills in subphase 1B before the compression stroke of the buccopharyngeal pump. When buccopharyngeal compression occurs in phase 2, it helps to maintain the pressure gradient until both opercular and buccopharyngeal pressures reach their positive maxima. At this time the differential (buccopharyngeal minus opercular) pressure falls and a positive pressure in the opercular cavities expels water through the open opercular valves. The occurrence of the greatest differential pressure across the gills during the opercular suction phase suggests that, at least in quiet suctional adhesion, the opercular pump may be the primary factor causing water flow over the gills. This situation may be similar to that observed in the blenny and plaice studied by Hughes (1960a).

The opercular spines of *Xenocara* are erected by a lever system similar to that in *Ancistrus* (see Alexander, 1965). However, for fishes of identical size, the opercular

Table 1. *Salient differences and similarities between two suctorial, stream-dwelling vertebrates, adult Xenocara (Pisces, Loricariidae) and Ascaphus tadpole (Amphibia, Leiopelmidae)*

	<i>Xenocara</i>	<i>Ascaphus</i>
Oral valve	Muscular	Non-muscular
Inflow	Rhythmic; mouth only; suctorial leak	Rhythmic; mouth and nares; watertight sucker
Outflow	Rhythmic; bilateral ventral opercular valves	Continuous; single, midventral outlet
Water pumps	Lower jaw, buccopharynx, opercular cavities	Buccal cavity, pharynx
Gills	Five pairs; 4 ventral clefts	Four pairs; 3 ventral clefts
Feeding	Algae eater during suctorial crawling; numerous small denticles; somewhat rugulose pharynx	Same
Air breathing	Absent	Absent
Habitat	Mountain streams of South America	Mountain streams of N.W. U.S.A. and British Columbia
Integument	Rough skin over dorsal bony plates; soft smooth skin on underside; erectile opercular and fin spines	Entire body covered by soft smooth skin; poison glands
Body shape	Streamlined, dorsoventrally flattened	Same

spines of *Xenocara* are larger than those of *Ancistrus*. Defence against predators (by complementing the sharp pectoral spines) and competitive jostling among individuals for suitable clinging surfaces may be the survival value in nature of opercular spines. The suctorial and gill ventilation mechanisms interact with opercular spine erection by developing very large negative pressures. The increased suctorial adhesion anchors the fish more firmly, and it is thus better able to use its spines for offence or defence. The above-described interaction may have a neurological basis because large suction were sometimes recorded without spine erection, and there are no mechanical couplings between the opercular spine complex and the water pumps.

The above-described suctorial and respiratory adaptations of *Xenocara* to mountain streams are not necessarily essential for aquatic vertebrates to live in such a habitat. For example, the sucker-bearing tadpole *Ascaphus* has evolved several different adaptations to permit its survival in a habitat similar to that of *Xenocara* (Table 1; see also Gradwell, 1971 *b*). Moreover, the stream-dwelling Asian cyprinids *Gyrinocheilus* and *Pseudogastromyzon*, as well as parasitic adult lampreys, utilize suctorial adhesion and have also evolved interesting interactions between their suctorial and gill-ventilation mechanisms (N. Gradwell, in preparation).

SUMMARY

1. Except for brief swimming from one site of adhesion to another, the oral sucker of *Xenocara* is constantly used to anchor the fish to the substratum.
2. During adhesion oral inhalation is by rhythmic water flow through special grooves in the sucker wall. Coarse particles entering with the respiratory water elicit a cough-like response which is associated with large positive pressures in the buccopharynx and opercular cavities, and with enhancement of suctorial adhesion.

3. Stronger adhesion occurs when the fish responds to tactile stimulation, during which large negative pressures are developed throughout the respiratory system and the opercular spines are thrust outward.

4. In all responses separation of suctorial and respiratory function is facilitated by the action of a muscular oral valve. Precise co-ordination between the inlet valves of the maxillary barbels and the oral and opercular valves is important for efficiency of the suction and force pumps before the gills and the opercular suction pump behind them.

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EXPLANATION OF PLATE

Photographs of *Xenocara occidentalis*. (A) Profile view of the anterior part of the fish, orientated against a gentle current (arrow). (B) Oral valve open. (C) Right opercular spines erected; upper jaw slightly adducted. (D) Oral valve closed. (E) Further adduction of upper jaw. The premaxillary teeth and the median gap between them are apparent.

