EVALUATION OF PRZIBRAM'S LAW FOR OSTRACODS
BY USE OF THE ZEUTHEN CARTESIAN-DIVER
WEIGHING TECHNIQUE

BY
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VOLUME XVII

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INTRODUCTION

The Zeuthen Cartesian-diver technique offers a method of evaluating Przibram's Law as applied to ostracods. Przibram proposed (1931, p. 26) that during each ecdysis, crustaceans increase their weight to twice its former value. Hitherto no attempts have been made to test this proposal directly for ostracods because of the difficulty in weighing such small animals. The apparatus described in Part I of this paper can be used to weigh ostracods. Few micropaleontologists are familiar with the Zeuthen Cartesian-diver technique for weighing small objects; therefore, a detailed description of the apparatus and its use is offered.

If Przibram's Law, as it has been called, proves to be valid for ostracods, then weighing by this method may be useful to differentiate instars of closely related extinct species. Many living species have remarkably similar carapaces and differ conspicuously only in details of their appendages. Since appendages and other soft parts are rarely preserved, the problem of distinguishing fossil species is extremely difficult, particularly for ostracods lacking ornamentation or other distinct structures on their carapaces. If two closely related species have adult carapaces of the same weight, as well as shape, we know of no way to differentiate them. If they can be shown to differ in weight, however, there is a strong possibility that they can be separated.

Our basic concern is the validity of Przibram's Law for Ostracoda. Part II of this paper is an investigation of specimens of Welleria recovered from Middle Devonian strata encountered in a well drilled in western Saskatchewan. Studies of other ostracods, including a living species, are planned in the near future. Although our weighing of Welleria specimens indicates that they are divisible into groups, we do not know whether these groups represent different species or different populations of one species. Since this study is the first application of the weighing technique, it is exploratory. Much additional work must follow to determine the validity of Przibram's Law and to establish the limits of its practical application.

Previous work on Przibram's Law applied to ostracods.—In the past, all attempts to evaluate Przibram's Law for ostracods have avoided the basic proposal—that the weight increases to twice its former value each time the animal molts and grows. Instead, they have been based on linear dimensions. If the weight increases by a factor of 2, it has been reasoned, the volume increases by this factor also, and each dimension of the carapace increases by a factor of \( \sqrt[3]{2} \), or 1.25992 (nearly 1.26). Sohn (1950, pp. 427–34), Kesling (1952a, pp. 255–63; 1952b, pp. 773–77; 1953a, pp. 19–24; 1953b, pp. 97–109), Kesling and Copeland (1954, pp. 158,
and others have studied ontogenetic changes in carapace dimensions of fossil ostracods, comparing the observed increases with the theoretical factor of 1.26. As was pointed out (Kesling, 1952b, pp. 773, 780), however, the factor for a single dimension will be exactly 1.25992 for a species in perfect accord with Przibram’s Law only if the shape of the carapace remains the same from one instar to the next and the carapace reflects the total increase in mass of the animal during each ecdysis. By use of the Zeuthen Cartesian-diver weighing technique, it is hoped that Przibram’s original proposal can be tested.

Previous work on Cartesian-diver devices.—Although the Cartesian diver is used in this study as a balance to determine the weight of an object in water (the reduced or so-called Archimedian weight), it has been used for other purposes. In fact, the adaptation for weighing is one of the recent developments in Cartesian-diver devices.

Linderstrøm-Lang (1937) first developed a Cartesian-diver apparatus of the type used in this study, not for measuring reduced weights but for determining gas changes involved in a chemical reaction inside the diver. Specifically, he made a gasometric analysis of choline esterase activity using the Warburg technique of change in carbon dioxide tension over bicarbonate buffered reaction mixtures. Later, he and his colleagues at Carlsberg Laboratory in Copenhagen adapted the apparatus for other uses.

Since the original description of the process, several refinements have been worked out. Some apply to the use of the Cartesian diver as a microrespirometer, in which the consumption of oxygen from a bubble trapped within the diver is measured over selected intervals to determine respiration of a small organism caged in the diver. Linderstrøm-Lang and Holter (1942) investigated diffusion of gas in the Cartesian diver. Linderstrøm-Lang (1943) wrote an informative article on the theory of the microrespirometer, summarizing the knowledge of the process at that time. Holter (1943) described improved techniques of using the Cartesian diver, particularly as used for measuring oxygen consumption. Zeuthen (1943) refined the microrespirometer for very small changes in the weight of the gas, and later (1948) described a Cartesian diver balance for determining reduced weights very accurately. The latter article is especially helpful to one unacquainted with this method of microweighing, inasmuch as it explains the theory, describes the apparatus, and outlines the procedure succinctly.

The Cartesian diver apparatus has been used to measure very small changes in volume and weight, such as the oxygen used by a single cell hour by hour. Linderstrøm-Lang and Glick (1938) used it to measure the volume of gas generated by action of acetyl choline chloride on horse
serum. They illustrated their apparatus (1938, Fig. 1), in which the pressure transmitted to the diver was controlled by two syringes (one for coarse adjustment and one for fine) connected to the water column of the manometer. Zamecnik (1941) measured the respiration rate in cells grown in tissue culture. Lindahl and Holter (1941) determined respiration in eggs of the echinoderm Paracentrotus lividus during ripening. Holter and Zeuthen (1944) investigated oxygen consumption in normal eggs and embryos of the ascidian Ciona intestinalis; in the same year, Andresen, Holter, and Zeuthen studied the consumption in abnormal eggs of the same animal. Linderstrøm-Lang (1946) discussed the general phenomenon of metabolism and considered its application to frog eggs, using this technique to measure respiration. Zeuthen (1946) utilized it to find out the oxygen consumption during mitosis of a frog egg. Later (1947), he made an exhaustive study of the relation of body weight to respiration in many marine microorganisms.

More recently (1956), Daniel Mazia, of the University of California, used a device of this kind to measure periodically the growth of a single amoeba and its offspring. He reported that, with his apparatus, accuracy was attained to $1 \times 10^{-11}$ gram, or $1/100$ millimicrogram.

During the last quarter of a century, in which the Cartesian diver has been used as a scientific instrument, the theory of its operation has been extended to consideration of possible sources of error. The sequence of papers cited above is a history of continued improvements to the prototype device used by Linderstrøm-Lang in 1937. As stressed by Zeuthen (1948), one of the significant refinements in technique is maintenance of constant temperature throughout each experiment.

Our apparatus is essentially like that of Zeuthen (1948), but we have added a compensating manometer to ensure that the registering manometer will record only changes in pressure on the chamber containing the diver.

Acknowledgments.—We are very much indebted to Mr. Gunther Kessler, whose remarkable talent for glass blowing produced the delicate little Cartesian divers used in our apparatus. Mr. Herbert Wienert photographed equipment and specimens. The manuscript was critically read by Dr. G. M. Ehlers, Dr. C. A. Arnold, and Dr. L. B. Kellum. All specimens referred to by number are catalogued and deposited in the Museum of Paleontology of the University of Michigan.

PART I. ZEUTHEN CARTESIAN-DIVER WEIGHING TECHNIQUE

APPARATUS

Our apparatus used to weigh ostracods is illustrated diagrammatically in Figure 1 and photographed in Plate I, Figure 5. It consists of a
CARTESIAN-DIVER TECHNIQUE

Cartesian diver in a chamber nearly filled with water, a registering manometer, a canned atmosphere of constant pressure, and a compensating manometer.

The Cartesian diver is the most delicate and critical part of the apparatus. It is made of thin glass, and consists of a small cup at the top and a hollow tube at the base. In our first model (Pl. I, Fig. 1), the upper part of the tube is expanded to form a bulb, and the lower part is attenuated to a small opening at the bottom. To keep the diver upright in the water, small glass weights are fused to the lower part of the tube to overcompensate for the weight of the cup.

In our improved models (Pl. I, Figs. 2–4; Pl. II, Figs. 1–9), the upper part of the tube is sealed off, enclosing an air chamber to act as a counter-balance for part of the weight of glass, leaving the lower part open so that

Fig. 1. Diagram of apparatus used in this study. Photograph of actual apparatus shown in Plate I, Figure 5.
the bubble within it can react to pressure exerted on the water in which it operates. These divers require delicate adjustments between the total weight of the diver, the size of the air chamber, and the amount of glass added as weights near the base. Such adjustments can be made most readily by varying the amount of glass within the weights. Short lengths of fine platinum wire can also be used to bring about the desired balance.

The sensitivity and accuracy of the whole apparatus depends largely upon the form of the diver. The diver and the bubble trapped in its tube must displace enough water to support their combined weight, and the diver must have a tube spacious enough for the bubble to expand further to support the added weight of the ostracod. If the diver is too large, its inertia is so great that it can be brought to equilibrium in the water extremely slowly; such a diver might require many minutes to adjust finally to a standstill. If the diver is too small, its bubble cannot expand sufficiently to support the added weight of an ostracod. Furthermore, if the walls of the diver are too thick, the bubble will not be large enough to offset the weight of the glass. If the walls are too thin, the bubble required to produce equilibrium will be very small and will have to expand to many times its volume in order to support the added weight of the ostracod; to cause such expansion of the bubble, an extreme pressure change is necessary, and this introduces the attendant problem of designing a manometer long enough to register the change. For weighing most fossil ostracods (which are solid, with a steinkern filling the carapace), the Cartesian diver should be at equilibrium when it contains a bubble larger than 3 mm³ but smaller than 8 mm³. For living ostracods, the bubble should be less than 3 mm³.

In the improved divers, the sealing off of the air chamber is a critical operation. As soon as the chamber is sealed, any further heating forms a very thin-walled bulb which usually bursts. The juncture between the chamber and the open tube below must be strong, and the whole diver must be straight in order to offer low and steady resistance as it moves up and down. Mr. Kessler made the most successful divers on a small glass blower’s lathe, using the following steps: (1) drawing the glass to a thin tube; (2) blowing the cup as a small bubble, later to be cut through the middle; (3) sealing it off; (4) blowing a bulb adjacent to the seal; (5) sealing off the air chamber by drawing out the tube at the desired place until it separates, reheating the ends to seal them, and fusing them together; (6) cutting off the section containing the diver; (7) cutting the bubble to form the cup with a thin-bladed saw; and (8) adding glass weights, a small increment at a time, testing the diver after each increment to observe the size of the bubble at equilibrium. The last step is the
most time-consuming, but it must be done carefully, for it determines the characteristics of the diver.

The chamber with the Cartesian diver (Fig. 1) is connected at one end to the registering manometer and at the other end to two braking pipettes through which pressure can be changed very gradually. Valve A shuts off the chamber from air in the room and holds pressure at the desired value. Valve B shuts off the chamber from the manometer.

The registering manometer is a U-tube half-filled with water, with a millimeter scale mounted between the arms of the U. At one side, near the base, the U-tube is connected to a short blind section of rubber hose, which can be compressed by a clamp for fine adjustment of pressure. In our apparatus, the U-tube is one meter long.

To eliminate the variable of change in barometric pressure during the weighing, the registering manometer is connected to a canned atmosphere that can be kept at constant pressure. The canned atmosphere is housed in a series of large bottles connected to a compensating manometer. The compensating manometer is a duplicate of the registering manometer, except it lacks a fine adjustment. By manipulation of the compensating manometer, the pressure of the canned atmosphere is maintained at the desired value. As soon as the water level drops in the adjacent tube of the registering manometer, the level in the compensating manometer can be made to rise the same distance, thereby keeping volume of the canned atmosphere constant. The pressure in the compensating manometer is adjusted through two braking pipettes and held by valve C.

Throughout the weighing procedure, room temperature must be constant. Otherwise, certain computations are required to adjust the data to constant-temperature values. The bottles containing the canned atmosphere act as an air thermometer; expansion or contraction of the canned atmosphere registers on the manometers as pressure change. In addition, temperature affects the density of (1) water in the manometers, (2) water in which the Cartesian diver operates, and (3) air and water vapor in the bubble in the diver.

Our present apparatus is slightly modified from the initial set-up shown in Plate I, Figure 5. The bottles for canned atmosphere were packed in insulating material and sealed in a box, with only the necks protruding. The insulation greatly reduced the temperature effects recorded on the manometers. It was found that the sensitivity of the bottles and manometers in detecting small changes in room temperature was greater than that of the mercury thermometer which we used.
By adjustment of the pressure, the volume of the Cartesian diver and the bubble it contains can be made to equal exactly the volume of water having a weight equal to their combined weights. The system of diver, bubble, and water is then in equilibrium, and the diver has its weight counterbalanced by a buoying force due to the displaced water. It tends neither to sink nor to rise. The pressure on the bubble consists of the pressure on the water \( P_1 \), which can be read by means of a manometer, and the pressure caused by the depth to which the diver is submerged \( P_w \).

If an ostracod is placed on the diver, equilibrium can be restored by decreasing the pressure on the water until the combined volumes of diver, bubble, and ostracod displace exactly the volume of water equivalent to their combined weights. The new pressure on the water \( P_2 \) is read on the manometer.

In this process, pressure is the only parameter measured. To compute the weight of the ostracod in water, it is necessary to find the relationship between this weight and the pressures.

Three parts of the apparatus can be considered separately, the Cartesian diver, the air within the bubble, and the registering manometer.

**Cartesian diver.**—Archimedes' Principle states that a body wholly or partly immersed in a fluid is buoyed up by a force equal to the weight of the displaced fluid. For a body wholly immersed in water, the buoying force \( B \) is the difference between the weight of the body in air \( W \) and its weight in water \( R \):

\[
B = W - R.
\]

However, when a body is in equilibrium with the water, \( R \) is no longer a force, and

\[
B = W.
\]

Thus, when the Cartesian diver and the bubble are counterbalanced by the buoying force,

\[
B_1 = W_o + W_{a1},
\]

where \( W_o \) is the weight of the Cartesian diver in air, and \( W_{a1} \) is the weight of the air in the bubble at pressure of \( P_1 + P_w \).

When the ostracod is placed on the diver, it is buoyed up by a force \( B_o \) equal to its weight in air \( W_o \) minus its weight in water \( R_o \):

\[
B_o = W_o - R_o.
\]

This buoying force \( B_o \) is independent of the Cartesian diver and the bubble, since it results from the displacement of water by the ostracod itself.
When the system, including the ostracod, is brought to equilibrium at $P_2 + P_w$, the buoying forces equal the combined weights of diver, bubble, and ostracod:

$$B_2 + B_o = W_c + W_{a2} + W_o;$$

but $B_o = W_o - R_o$, and the equation becomes

$$B_2 = W_c + W_{a2} + R_o.$$

Subtracting the equation for $B_2$ gives

$$B_2 - B_1 = W_{a2} - W_{a1} + R_o$$

$$\Delta B = R_o + \Delta W_a.$$ 

From this it follows that

$$R_o = \Delta B - \Delta W_a = \Delta B'$$

where $\Delta B'$ is the effective increase in buoying force of the Cartesian diver and bubble.

*Air within the bubble.*—At the moment the Cartesian diver is dropped into the water and the bubble is trapped within it, the air in the bubble is at atmospheric pressure and contains the same proportion of water vapor as the outside air. When, very soon, the air in the bubble becomes saturated with water vapor, the volume of the bubble is increased by the addition of this gas. Pressure within the bubble, however, does not increase as the vapor pressure rises to the saturation value. Inasmuch as the bubble is free to react, the pressure always adjusts to equal the pressure caused by the depth to which it is submerged in water ($P_w$) and the air pressure on the surface of the water.

For dry air, the bubble is a closed system for practical purposes; the diffusion of air into the water is very slow, so slow that loss of air can only be detected after an interval of 24 hours. For water vapor, however, the surface of the bubble is an interface of exchange between the gas in the bubble and the surrounding medium, with condensation when pressure is increased and the bubble is compressed, and with additional evaporation when pressure is decreased and the bubble is expanded.

After the diver has been introduced into the water, pressure inside the bubble is the sum of atmospheric and water pressure, $P_a + P_w$. Before the Cartesian diver can be used, however, part of the air must be extracted from the bubble. This is accomplished by decreasing pressure in the chamber containing the diver until some of the air escapes from the diver as small bubbles. When the pressure on the water is restored to that of the air outside, the air in the bubble is again at $P_a + P_w$.

Only rarely will $P_a + P_w$ be the exact pressure to bring the diver to equilibrium. Usually, the volume of the bubble must be increased or decreased by a slight change in pressure. The amount of this pressure change
($\zeta P_1$) is measured by the registering manometer. The pressure at equilibrium is

$$P_1 + P_w = P_a + \zeta P_1 + P_w.$$  

When a weight of any kind is added to the diver, equilibrium can be established at

$$P_2 + P_w = P_a + \zeta P_2 + P_w.$$  

Note that $P_2 + P_w$ will always be less than $P_1 + P_w$, since the bubble in the diver must expand to support the additional weight. Thus, the pressure is lowered, and the pressure change ($\Delta P$) is negative:

$$\Delta P = P_2 - P_1 = \zeta P_2 - \zeta P_1,$$

or

$$-\Delta P = \zeta P_1 - \zeta P_2.$$  

Because the bubble reacts according to Boyle's Law, the product of pressure ($P$) and volume ($V$) is a constant at any given temperature ($T = k$); that is,

$$PV = K_1 |_{T = k}$$

Inasmuch as this relationship holds for all isothermal states of the system:

$$(P_1 + P_w)V_1 = (P_2 + P_w)V_2$$

and

$$V_2 = \frac{P_2 + P_w}{P_2 + P_w} V_1.$$  

As shown above, when pressure on the water containing the diver decreases from $P_1$ to $P_2$, the change in pressure ($-\Delta P$) produces an increase in volume of the bubble ($\Delta V$). An additional effective force ($\Delta B'$) is created, equal to the weight of water displaced by expansion ($\Delta B$ or $\Delta W_w$) minus the weight of air added to the bubble ($\Delta W_a$):

$$\Delta B' = \Delta W_w - \Delta W_a.$$  

Computation of $\Delta B'$ would be greatly simplified if the air in the bubble had constant density, because $\Delta W_a$ would then be a function of $\Delta V$. However, the density of the air depends upon pressure. Within the bubble, the dry air and the water vapor may be considered separately. According to Dalton's Law, the total pressure exerted by a mixture of perfect gases is equal to the sum of the partial pressures of each of the components when each component occupies by itself the volume of the mixture at the temperature of the mixture. The total pressure of the air in the bubble ($P + P_w$ or $P'$) is the sum of the partial pressures of dry air and water vapor, thus

$$P + P_w = P' = P_d + e$$

where $e$ is the partial pressure exerted by water vapor and $P_d$ is the partial pressure of the dry air.
The density of air in the bubble ($\rho_a$) is the sum of the density of dry air ($\rho_d$) and density of water vapor ($\rho_v$),

$$\rho_a = \rho_d + \rho_v.$$ 

The density equations may be written

$$\rho_d = \frac{P_d}{RT} = \frac{P' - e}{RT} \quad \text{and} \quad \rho_v = \frac{.622 \ e}{RT}$$

where $R$ is the gas constant of dry air and $T$ is the temperature in °A.

The weight of air in the bubble ($W_a$) is the combined weights of the dry air ($W_d$) and water vapor ($W_v$):

$$W_a = W_d + W_v$$

and the increase in the weight of air as the pressure changes from $P_1 + P_w$ to $P_2 + P_w$ is

$$\Delta W_a = W_{a2} - W_{a1} = (W_{d2} + W_{v2}) - (W_{d1} + W_{v1})$$

$$= (W_{d2} - W_{d1}) + (W_{v2} - W_{v1}).$$

Since the process is isothermal, the vapor pressure remains the same at all pressures; it is conservative only with respect to temperature. Thus, when pressure is reduced under nonadiabatic conditions, additional water vapor is added to the bubble by evaporation, so as to maintain constant density, and

$$\rho_v = K_2 = \rho_{v1}.$$ 

The dry air, on the other hand, does not maintain constant density with reduced pressure. Instead, it decreases in density as the bubble expands. Obviously, since no dry air is added or taken away, its weight remains constant. Because weight is the product of density and volume,

$$W_{d2} = \rho_{d2}V_2 = \frac{P_{d2}}{RT}V_2 \quad \text{and} \quad W_{d1} = \rho_{d1}V_1 = \frac{P_{d1}}{RT}V_1.$$ 

However,

$$P_{d2}V_2 = K_3 = P_{d1}V_1;$$

hence,

$$W_{d2} = \frac{K_3}{RT} = W_{d1} \quad \text{and} \quad W_{d2} - W_{d1} = 0.$$ 

Therefore,

$$\Delta W_a = W_{v2} - W_{v1} = \rho_{v2}V_2 - \rho_{v1}V_1,$$

and, since $\rho_v$ is constant,

$$\Delta W_a = \rho_v (V_2 - V_1) = \rho_v \Delta V = \Delta V \frac{.622 \ e}{RT}$$

If temperature is maintained at 22°C, $e = 19.844$ mm of mercury = 26.456 millibars = 26456 dynes/cm², and

$$\rho_v = \frac{.622 \times 26.456 \times 10^3}{2.87 \times 10^6 \times 295} = .0000194 \ \text{g/cm}^3.$$
Substituting in the previous equation,
\[ \Delta W_a = 0.0000194 \Delta V. \]

The density of water at \( T = 22^\circ C \) is 0.997770 g/cm\(^3\) and the weight of water is displaced by expansion is
\[ \Delta W_w = 0.997770 \Delta V. \]

The additional effective buoying force created by the expansion \( \Delta V \) becomes
\[ \Delta B' = \Delta W_w - \Delta W_a = (0.997770 - 0.000019) \Delta V = 0.997751 \Delta V. \]

The weight of the ostracod in water (\( R_o \)), the so-called **reduced weight**, is counterbalanced by the additional buoying force, and therefore equals it:
\[ R_o = \Delta B' = 0.997751 \Delta V \bigg|_{T = 22^\circ C} \]

The relationship between \( R_o \) and \( \Delta V \) has now been established at temperature of 22°C. Next, the relationship between \( \Delta V \) and pressure must be found. From Boyle's Law,
\[
\begin{align*}
V_2 &= \frac{P_1 + P_w}{P_2 + P_w} V_1 \\
V_2 - V_1 &= \frac{P_1 - P_2}{P_2 + P_w} V_1 \\
\Delta V &= \frac{\Delta P}{P_2 + P_w} V_1.
\end{align*}
\]

Hence, the reduced weight of the ostracod is a function of the pressure change, the final pressure, the depth of water above the diver, and the initial volume of the bubble:
\[ R_o = 0.997751 V_1 \frac{\Delta P}{P_2 + P_w}. \]

**Registering manometer.**—The liquid used in the registering manometer (Fig. 1) determines the vertical displacement which will result from a particular reduction in pressure.

Arbitrarily, a pressure of one normal atmosphere \( (A) \) is defined as that pressure balanced by a column 760 mm long of mercury with a density of 13.5955 g/cm\(^3\), at a temperature of 0°C and gravity of 980 cm/sec\(^2\). If mercury is used in the manometer tube, the displacement \( (h_A) \) for the normal atmosphere is
\[ h_A = 760 \text{ mm} \bigg|_{T = 0^\circ C} = 760.55 \text{ mm} \bigg|_{T = 4^\circ C} = 763.08 \text{ mm} \bigg|_{T = 22^\circ C}. \]

However, if water is used in the tube,
\[ h_A = 10334.2 \text{ mm} \bigg|_{T = 0^\circ C} = 10332.9 \text{ mm} \bigg|_{T = 4^\circ C} = 10355.7 \text{ mm} \bigg|_{T = 22^\circ C}. \]

Thus, if the reduction in pressure is .01 \( A \), the displacement in a tube using mercury at 22°C is only
\[ h_{.01A} = 7.63 \text{ mm}, \]
whereas the displacement in a tube of water at the same temperature is

\[ h_{0.014} = 103.56 \text{ mm}. \]

For a given reduction of pressure \((-\Delta P)\), therefore, the lower the density of the liquid in the manometer tube, the longer the displacement \((h)\) and the greater the accuracy with which it can be read.

Selection of a liquid for the manometer must be related to the change in volume of the bubble necessary to restore equilibrium in the weighing process, and this, in turn, is related to the size of the bubble. For example, suppose the bubble must expand to twice its initial size \((V_1)\) to support the reduced weight of the ostracod, and assume that \(P_1 = A\). Then, neglecting the small factor of \(P_w\),

\[
2 V_1 P_2 = V_1 P_1 \\
2 P_2 = P_1 \\
-\Delta P = P_1 - P_2 = P_1/2
\]

and the necessary displacement of liquid in a water manometer would be 5178 mm at 22°C. Thus, for such conditions the two arms of the manometer would have to be over 5 meters long. This would be inconvenient to build or to use. If mercury were substituted, the two arms of the manometer would have to be only .382 meter long.

The apparatus can be designed, therefore, to suit one or the other of two sets of conditions: (1) a small bubble in the Cartesian diver \((V_1 \text{ small})\) and mercury in the manometer to measure the necessarily large \(-\Delta P\), or (2) a large bubble in the diver \((V_1 \text{ large})\) and water in the manometer to measure the small \(-\Delta P\) more accurately.

In the present experiments, we have used a relatively large bubble in the diver and water in the manometer.

Atmospheric pressure \((P)\) as measured by a mercurial barometer has the following value:

\[
P = \rho G (1 - \beta T) H
\]

where \(P = \text{pressure in dynes/cm}\)
\(
\rho = \text{density of mercury at 0°C}
\)
\(
G = \text{acceleration of gravity at 45° latitude and sea level = 980.621 cm/sec}^2
\)
\(
\beta = \text{coefficient of thermal expansion of mercury = .0001818}
\)
\(
T = \text{temperature of mercury in °C}
\)
\(
H = \text{height of column of mercury}
\)

Similarly, for a change in pressure

\[
-\Delta P = -\rho G (1 - \beta T) \Delta H.
\]

In the use of these quantities, however, they form a ratio, so that

\[
\frac{-\Delta P}{P} = \frac{-\rho G (1 - \beta T) \Delta H}{\rho G (1 - \beta T) H} = \frac{-\Delta H}{H},
\]
and
\[ \frac{-\Delta P}{P + P_w} = \frac{-\Delta H}{H + P_w}. \]

If atmospheric pressure, therefore, can be determined by barometer as millimeters of mercury at 22°C, it will not be necessary to correct the value of \(-\Delta P\) as read on the manometer for temperature and gravity, because both \(P\) and \(-\Delta P\) are measured at the same temperature and gravity. By the same reasoning, when \(P\) is computed in equivalent millimeters of water at 22°C, \(-\Delta P\) read by water manometer at that temperature needs no correction.

In computing the volume of the bubble for the diver alone at equilibrium \((V_1)\) or the reduced weight of the ostracod \((R_o)\), it is necessary to find the change in pressure \((-\Delta P)\) from that producing equilibrium for the diver alone to that producing equilibrium for the diver plus the weight. This change is
\[ -\Delta P = (P_1 + P_w) - (P_2 + P_w) = (\bar{P} + \bar{P}_1 + P_w) - (\bar{P} + \bar{P}_2 + P_w), \]
or
\[ -\Delta P = \bar{P}_1 - \bar{P}_2. \]

If the registering manometer were connected only to the chamber containing the Cartesian diver, it would record not only the decrease in pressure in the chamber, but also the changes in atmospheric pressure. In other words, the open end of the registering manometer would cause it to act in part as a barometer. To measure accurately the pressure decrease affecting the Cartesian diver \((-\Delta P)\), the other end of the manometer must be connected to atmosphere of the same pressure as that at which the bubble was trapped in the diver \((P_a)\). An easy way to ensure that the atmospheric pressure affecting the manometer will remain constant is to connect the manometer with containers in which a sample of the air is trapped at pressure of \(P_a\). This canned atmosphere (Fig. 1) prevents rises and falls in exterior atmospheric pressure during the experiment from registering on the manometer.

When pressure is decreased in the chamber containing the diver, however, the water in the manometer is sucked up in the tube connected to the chamber and falls in the tube connected to the canned atmosphere. In the latter tube, the fall in water level decreases the pressure, since it increases the volume. This produces only a very small error in measurement of \(-\Delta P\), because the increase in volume within the manometer tube is only a very small fraction of the total volume of canned atmosphere. Nevertheless, this error can be eliminated by connecting the containers of canned atmosphere to a second manometer, which compensates for the decrease in
CARTESIAN-DIVER TECHNIQUE

pressure by decreasing the volume. If the two manometers have tubes of the same diameter, the pressure of the canned atmosphere can be corrected by regulating the compensating manometer to the same reading as that of the registering manometer. Thus, if the water level drops 53.5 mm in the tube of the registering manometer, the water level can be made to rise 53.5 mm in the tube of the compensating manometer.

PROCEDURE

Weighing with the Zeuthen Cartesian-diver apparatus involves two operations: (1) determining equilibrium conditions for the diver and an object of known weight, from which the volume of the bubble at equilibrium is calculated; and (2) determining conditions for the diver and the ostracod, from which the weight of the ostracod is found.

The first operation reveals the sensitivity of the diver. The smaller the bubble that will support the diver alone, the more sensitive the diver. It also indirectly establishes the limits of objects that can be weighed with the diver, since the expansion of the bubble cannot proceed beyond the pressure changes registered by the manometer. Fortunately, this operation need be carried out only once for each diver, and thereafter the same value for \( V \) can be used, inasmuch as the mass of the diver does not change from one experiment to another.

In this part of the procedure, an object of known weight is used as a standard, from which the \(-\Delta P\) can be found. In our experiments, a standard of 282 micrograms was made by cutting a short strip (0.1 x 1.0 cm) from a sheet of aluminum foil (with an area of 10,000 cm\(^2\)) for which the reduced weight had been found by using an analytical balance. The same standard was used for all divers.

The first operation, the “calibration” of the diver, is accomplished in the following steps:

1. Open the outside valve of the bottles for canned atmosphere (shown in Pl. I, Fig. 5, but not in Fig. 1), open all other valves, remove the chamber with the Cartesian diver, take out the diver and dry it, and bring all apparatus to room temperature (including water in the manometers and chamber). A temperature of 22°C will enable computations to be made from the formula given in the following section on computations, and for that reason is preferred. Whatever temperature is used, it should be kept constant throughout the weighing.

2. Lower the Cartesian diver into the water in the chamber, attach the chamber, close valve \( B \), and apply suction on the adjacent braking pipette. Small bubbles will be drawn out at the bottom end of the diver and will
escape to the surface of the water. Test whether the diver will sink. If it does not sink, open valve $B$ and see if it will sink with an increase of pressure that can be registered by the manometer. If it does sink, open valve $B$ and determine whether it will come to equilibrium with only a slight decrease of pressure. If the diver cannot be made to sink, close valve $B$, slowly apply suction to extract more air, and test the diver again. Cautiously repeat until the diver is near equilibrium, slowly rising or sinking with small changes in pressure. If too much air is withdrawn and the bubble is too small, remove the diver from the chamber, extract the water from it, and repeat this step.

3. Record atmospheric pressure from a mercurial barometer at $22^\circ C$ or from an aneroid barometer. Record room temperature.

4. Close the outside valve of the bottles for canned atmosphere, trapping air at existing atmospheric pressure.

5. Record readings of the manometers.

6. Remove the chamber containing the diver, place the weight in the small cup, and replace the chamber.

7. Open valve $B$, bring the diver and weight to equilibrium at a particular level, close valve $A$, adjust the compensating manometer, and close valve $C$. If they do not remain at that level, open valve $A$, bring them to equilibrium, close valve $A$, open valve $C$, adjust the compensating manometer, and close valve $C$. Repeat if necessary to produce equilibrium.

8. Record readings of the registering manometer and room temperature.

9. Remove weight from the diver.

10. Bring diver alone to equilibrium, with registering and compensating manometers set at the same reading, following the same sequence of manipulations as those described above.

11. Record readings of the registering manometer and room temperature.

12. Compute $-\Delta P$, $P_2 + P_w$, and finally $V_1$, the volume of the bubble when the diver alone is at equilibrium.

The second operation, finding the weight of the ostracod, follows the same general pattern as the first operation, except the ostracod is substituted for the standard weight. Fossil ostracods should be cleaned of all dust and matrix. If they have a film of hydrocarbon, they should be washed in carbon tetrachloride, soap solution, and water. Living ostracods can be anesthetized in 15 per cent sodium nembutol solution; after they become inactive, they must be washed repeatedly in water so that no sodium nembutol is added to the water in the chamber containing the diver. In the last step of this operation, compute $-\Delta P$, $P_2 + P_w$, and finally $R_o$, the reduced weight of the ostracod.
Several weighings can be made before the air in the bubble and the canned atmosphere need to be replaced. Their initial conditions still prevail as long as the Cartesian diver returns to equilibrium at, or nearly at, the first equilibrium pressure for the diver alone.

**COMPUTATIONS**

If the experiments are carried out at 22°C, the formula for computing $V_1$, the volume of the bubble when the diver is at equilibrium, is

$$V_1 = -\frac{K_4}{0.997751} \left[ \frac{P_2 + P_w}{\Delta P} \right] V_1,$$

where $K_4$ is the standard weight used to "calibrate" the diver and includes values observed in this operation. The formula for computing $R_o$, the weight of the ostracod, is

$$R_o = -0.997751 V_1 \left[ \frac{\Delta P}{P_2 + P_w} \right] R_o,$$

where $\left[ \frac{\Delta P}{P_2 + P_w} \right] R_o$ includes pressure values observed in the second operation. By combining the two equations, we have

$$R_o = K_4 \left[ \frac{P_2 + P_w}{\Delta P} \right] V_1 \left[ \frac{\Delta P}{P_2 + P_w} \right] R_o.$$

It is not possible, however, to use the formula for $R_o$ in the second form unless both operations (see Procedure, p. 15ff.) are performed at 22°C, since all factors of pressure must be expressed as values at the same temperature. Otherwise, the factors of pressure found in determination of $V_1$, are not comparable to those found in $R_o$.

Since $P_w$ and $-\Delta P$ are observed in centimeters of water, it is convenient to convert values of $P_2$ to their equivalents in the same units. $P_2$ is composed of atmospheric pressure ($P_a$) and a small addition or reduction ($\delta P_2$); $\delta P_2$ is measured by the registering manometer in terms of centimeters of water, but $P_a$ is measured by a barometer in millimeters of mercury or in millibars. Computations for conversion of pressure depend on the type of barometer used. Those for readings from a mercurial barometer differ from those of an aneroid barometer.

If the barometer is the mercurial type, the observed reading is higher than actual pressure, since pressure is defined as the value at 0°C and mercury expands with temperature increase. A convenient temperature to which values observed with both mercurial and water instruments can be converted can be selected in the range of room temperatures; we chose
22° C as the standard temperature for our computations. The coefficient of expansion of a mercury column is 0.000181/°C or 0.0001010/°F. Atmospheric pressure reading from a mercurial barometer ($P_m$) in determination of either $V_1$ or $R_0$, observed at room temperature ($T_m$), can be converted to the equivalent value at 22° C ($P_a$) by the formula

$$P_a = P_m \left[1 - 0.000181 \left(T_m - 22\right)\right].$$

### TABLE I

**CONVERSION OF MILLIMETERS OF MERCURY TO CENTIMETERS OF WATER AT 22°C**

<table>
<thead>
<tr>
<th>Mercury (mm)</th>
<th>Water (cm)</th>
<th>Mercury (cm)</th>
<th>Water (cm)</th>
<th>Mercury (mm)</th>
<th>Water (cm)</th>
<th>Mercury (mm)</th>
<th>Water (cm)</th>
</tr>
</thead>
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</table>

The resulting value of $P_a$ is in terms of millimeters of mercury, and can be changed to the equivalent in centimeters of water at 22° C by using Table I.

If the barometer is the aneroid type, the observed reading is actual pressure, inasmuch as the instrument automatically compensates for expansion or contraction of its parts with temperature changes. The formula for $R_0$ may be rewritten as

$$R_0 = K_4 \left[\frac{P_a + \delta P_2 + P_w}{\Delta P}\right]_{V_1} \left[\frac{\Delta P}{P_a + \delta P_2 + P_w}\right]_{R_0},$$

from which it is apparent that the ratio

$$\left[\frac{P_a + \delta P_2 + P_w}{P_a + \delta P_2 + P_w}\right]_{V_1} \left[\frac{P_a + \delta P_2 + P_w}{P_a + \delta P_2 + P_w}\right]_{R_0}$$
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is nearly the same as the ratio involving true atmospheric pressure \((P_o)\), which is based on the value at 0°C:

\[
\frac{[P_o + \delta P_2 + P_w]}{[P_o + \delta P_2 + P_w]_R_o}
\]

This is true because the value of atmospheric pressure is about the same in the operation for finding \(V_1\) as for that for finding \(R_o\). The difference between the two ratios, in most weighing experiments, is less than the inaccuracy in reading the aneroid barometer. Therefore, the readings may be utilized directly in computations of \(V_1\) and \(R_o\). If greater accuracy is desired, atmospheric pressure can be expressed (for both \(V_1\) and \(R_o\) computations) in equivalent values at 22°C \((P_a)\) by the following formula:

\[
P_a = P_o [1 + 0.0001818 (22)] = 12.39996 P_o.
\]

Table II converts millibars to centimeters of water.

**TABLE II**

**CONVERSION OF MILLIBARS TO CENTIMETERS OF WATER AT 22°C**

<table>
<thead>
<tr>
<th>Millibars</th>
<th>Water (cm)</th>
<th>Millibars</th>
<th>Water (cm)</th>
<th>Millibars</th>
<th>Water (cm)</th>
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</thead>
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**TABLE III**

**ABSOLUTE DENSITY OF WATER**

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<thead>
<tr>
<th>Temperature (°F)</th>
<th>Absolute Density (g/cm³)</th>
<th>Logarithm of Abs. Density</th>
<th>Temperature (°F)</th>
<th>Absolute Density (g/cm³)</th>
<th>Logarithm of Abs. Density</th>
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Regardless of the instrument used to measure atmospheric pressure, certain corrections must be included for the density of water in the chamber containing the Cartesian diver, for density of water vapor within the bubble, and for conversion of $P_w$ and monometer readings to equivalent values at 22°C. These correction factors are listed in Tables IV, V, and VI, which are based on the values of absolute density given in Table III. The correction of $P_w$ readings is insignificant, but the correction for density of water in the chamber and density of water vapor in the bubble ($C_v$) and that for manometer readings to determine $-\Delta P$ ($C_{v_r}$) are

**TABLE IV**

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Absolute Density of Water (g/cm³)</th>
<th>Density of Water Vapor (g/cm³)</th>
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<th>Logarithm of Corr. Factor</th>
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<td>.000 0338</td>
<td>.994 989</td>
<td>.997 8184</td>
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</table>

**TABLE V**

<table>
<thead>
<tr>
<th></th>
<th></th>
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</tr>
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<tbody>
<tr>
<td>72</td>
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<td>.998 9998</td>
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<td>.996 426</td>
<td>.998 4451</td>
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<tr>
<td>73</td>
<td>.997 569</td>
<td>.998 9430</td>
<td>82</td>
<td>.996 270</td>
<td>.998 3770</td>
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<td>74</td>
<td>.997 436</td>
<td>.998 8851</td>
<td>83</td>
<td>.996 111</td>
<td>.998 3076</td>
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<td>75</td>
<td>.997 301</td>
<td>.998 8260</td>
<td>84</td>
<td>.995 949</td>
<td>.998 2370</td>
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<td>76</td>
<td>.997 162</td>
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<td>85</td>
<td>.995 784</td>
<td>.998 1651</td>
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<td>.998 0170</td>
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<td>79</td>
<td>.996 729</td>
<td>.998 5772</td>
<td>88</td>
<td>.995 270</td>
<td>.997 9409</td>
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<tr>
<td>80</td>
<td>.996 579</td>
<td>.998 5118</td>
<td>89</td>
<td>.995 092</td>
<td>.997 8634</td>
</tr>
</tbody>
</table>
large. If these two factors are included, the formulas for $V_1$ and $R_o$ become

$$V_1 = K_4 \frac{P_o + C_{VI} (\delta P_o) + P_w}{C_V C_{VI} (-\Delta P)}$$

and

$$R_o = \frac{C_V C_{VI} V_1 (-\Delta P)}{P_o + C_{VI} (\delta P_o) + P_w}.$$ 

Computations for the data in Table VII are given in Table VIII. Logarithms were used, but a slide rule would yield accuracy commensurate with the measurements of pressure.

If constant temperature is maintained throughout the weighing procedures, a simple slide rule (Fig. 2) can be constructed from double logarithm paper to solve for $V_1$ and $R_o$. It is accurate enough for low values of $-\Delta P$ and offers a quick check on the magnitude of $R_o$ for high values of $-\Delta P$. The expressions for $V_1$ and $R_o$ may be expressed as

$$V_1 = \frac{K_4 (P_o + P_w)}{C_V (-\Delta P)}$$

and

$$R_o = \frac{V_1 C_V (-\Delta P)}{P_o + P_w}.$$ 

In these forms, $C_V$ is the same for all operations, since the temperature is constant.

The upper part of the slide rule is double logarithm paper with 45° lines drawn at intervals parallel to the line through points (1,1) and (10,10). It should contain at least one cycle along each co-ordinate. The bottom of the rule is a fixed logarithmic cycle aligned with that of the upper part. The movable slide has a cycle like that of the bottom, with arrows opposite the 1 and 10 marks.
In use, the value of $P_z + P_w$ on the slide is aligned with that of $-\Delta P$ on the bottom of the rule. One or the other of the two arrows will point to an abscissa on the upper part of the slide rule. For an object of known reduced weight, used to calibrate the diver, the value of reduced weight can be located on the $R$ scale at the left. This scale is offset slightly from the ordinates on the right by a constant computed for the temperature at which the weighings are made; as illustrated (Fig. 2), 0.997751 on the $R$ scale is aligned with 1 on the double logarithm ordinates to represent the relationship at $T = 22^\circ C$. A horizontal line (ordinate) extended through the value of $R$ will intersect the abscissa aligned with the arrow of the slide. The $45^\circ$ line through this point of intersection has the value of the initial volume of the bubble ($V_1$) and is read on the scale at the right, either at its intersection with the abscissa of 10 or directly opposite to its intersection with the abscissa of 1. Note that the units used to measure $-\Delta P$ and $P_z + P_w$ do not affect their ratio; if all readings are in the same

<table>
<thead>
<tr>
<th>Object</th>
<th>Diver</th>
<th>Registering manometer</th>
<th>Atmos. Pressure (mbs)</th>
<th>Temp. ($^\circ F$)</th>
<th>Pressures (cm water)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Left Tube</td>
<td>Right Tube</td>
<td>$P_\beta$</td>
<td>$P_w$</td>
</tr>
<tr>
<td>Standard weight 282μg</td>
<td>B</td>
<td>With object</td>
<td>50.06</td>
<td>50.06</td>
<td>988.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>With object</td>
<td>58.29</td>
<td>41.94</td>
<td>$P_w = 8.55$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>With object</td>
<td>50.17</td>
<td>49.79</td>
<td>$P_\beta = 3.00$</td>
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<tr>
<td></td>
<td></td>
<td>With object</td>
<td>49.90</td>
<td>49.90</td>
<td>976.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>With object</td>
<td>87.84</td>
<td>12.97</td>
<td>$P_w = 8.30$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>With object</td>
<td>49.93</td>
<td>49.86</td>
<td>$P_\beta = 3.00$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>With object</td>
<td>14.38</td>
<td>85.08</td>
<td>$P_w = 8.30$</td>
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<tr>
<td></td>
<td></td>
<td>With object</td>
<td>50.03</td>
<td>49.80</td>
<td>975.8</td>
</tr>
<tr>
<td>Standard weight 282μg</td>
<td>C</td>
<td>With object</td>
<td>50.04</td>
<td>50.04</td>
<td>986.2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>With object</td>
<td>52.69</td>
<td>47.41</td>
<td>$P_w = 9.92$</td>
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<td></td>
<td></td>
<td>With object</td>
<td>50.16</td>
<td>49.89</td>
<td>$P_\beta = 3.00$</td>
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<td></td>
<td></td>
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<td>68.07</td>
<td>$P_w = 8.30$</td>
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<tr>
<td></td>
<td></td>
<td>With object</td>
<td>50.58</td>
<td>49.38</td>
<td>986.1</td>
</tr>
<tr>
<td>Ostracod 3</td>
<td>C</td>
<td>With object</td>
<td>50.02</td>
<td>50.02</td>
<td>985.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>With object</td>
<td>76.14</td>
<td>24.40</td>
<td>$P_w = 9.92$</td>
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<td></td>
<td></td>
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<td>49.64</td>
<td>$P_\beta = 3.00$</td>
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<td></td>
<td></td>
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<td>37.00</td>
<td>62.91</td>
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<td></td>
<td></td>
<td>With object</td>
<td>50.72</td>
<td>49.24</td>
<td>985.2</td>
</tr>
</tbody>
</table>
CARTESIAN-DIVER TECHNIQUE

units, pressures may be read as inches of mercury, millimeters of water, or inches of water. As illustrated, each scale of the slide rule is labeled from 1 to 10 and the magnitude of each variable must be recognized.

When the line representing $V_1$ is found, computations for objects of unknown reduced weight can be made readily. The upper part of the slide rule has two lines for each value of $V_1$, one sloping down from the abscissa and another sloping up from the abscissa of 1. Mark these lines clearly on the rule. Each possible abscissa will intersect one or the other of these two lines. Set the slide with $P_z + P_w$ opposite $-\Delta P$, follow the abscissa aligned with the arrow upward to the intersection with the sloping line for $V_1$, and follow the horizontal line (ordinate) through this point to the $R$ scale. The reading will be the value of $R_o$.

For example, Figure 2 illustrates the determination of $V_1$. The slide is set for $P_z + P_w = 429$ mm of mercury and $-\Delta P = 310$ mm of mercury.

| TABLE VIII |
| COMPUTATIONS FOR DATA IN TABLE VII* |

To Determine $V_1$ of Cartesian Diver

<table>
<thead>
<tr>
<th>Factor</th>
<th>Logarithm</th>
<th>Factor</th>
<th>Logarithm</th>
</tr>
</thead>
<tbody>
<tr>
<td>$-\Delta P = 79.70$</td>
<td>901 4583</td>
<td>$-\Delta P = 41.49$</td>
<td>617 9434</td>
</tr>
<tr>
<td>Corr. (Table V)</td>
<td>998 2011</td>
<td>Corr. (Table V)</td>
<td>998 9140</td>
</tr>
<tr>
<td>Corr. (Table VI)</td>
<td>999 1824</td>
<td>Corr. (Table VI)</td>
<td>999 8940</td>
</tr>
<tr>
<td></td>
<td>898 8418</td>
<td></td>
<td>616 7514</td>
</tr>
<tr>
<td>$V_1 = 3.585 \text{ mm}^3$</td>
<td>554 4670</td>
<td>$V_1 = 6.934 \text{ mm}^3$</td>
<td>840 9596</td>
</tr>
</tbody>
</table>

To Determine $R_o$ of Ostracod

<table>
<thead>
<tr>
<th>Factor</th>
<th>Logarithm</th>
<th>Factor</th>
<th>Logarithm</th>
</tr>
</thead>
<tbody>
<tr>
<td>$-\Delta P = 145.57$</td>
<td>163 0719</td>
<td>$-\Delta P = 77.65$</td>
<td>890 1415</td>
</tr>
<tr>
<td>$V_1 = 3.585 \text{ mm}^3$</td>
<td>554 4670</td>
<td>$V_1 = 6.934 \text{ mm}^3$</td>
<td>840 9596</td>
</tr>
<tr>
<td>Corr. (Table V)</td>
<td>998 1430</td>
<td>Corr. (Table V)</td>
<td>998 6093</td>
</tr>
<tr>
<td>Corr. (Table VI)</td>
<td>999 1251</td>
<td>Corr. (Table VI)</td>
<td>999 5888</td>
</tr>
<tr>
<td></td>
<td>714 8070</td>
<td></td>
<td>729 2992</td>
</tr>
<tr>
<td>$P_z + P_w = 935.80$</td>
<td>971 1830</td>
<td>$P_z + P_w = 970.00$</td>
<td>986 7717</td>
</tr>
<tr>
<td>$R_o = 554.2\mu g$</td>
<td>743 6240</td>
<td>$R_o = 552.8\mu g$</td>
<td>742 5275</td>
</tr>
</tbody>
</table>

* All values of $-\Delta P$ and $P_z + P_w$ are in cm of water at 22°C.
Fig. 2. Special slide rule for use in computing volume of bubble when diver is at equilibrium and reduced weight of a small object. The part labeled \( P_2 + P_w \) is a movable slide. The rule illustrated is for weighings made at 22°C, but slight changes in the position of the \( R_0 \) scale will adapt it for weighings at other temperatures. The following abbreviations are used: \( P_2 \) — total pressure on water when diver and object are in equilibrium; \( P_w \) — pressure of water above diver at equilibrium position in chamber; \( -\Delta P \) — change in pressure between equilibrium conditions of diver alone and diver plus object; \( V_1 \) — volume of bubble when diver is in equilibrium; and \( R_0 \) — reduced weight of object when weighing procedure is accomplished at 22°C.
At the top of the slide rule, the ratio of \(-\Delta P/P_2 + P_w\) is shown as an abscissa, 0.7226. The value of this ratio, however, need not be noted to determine \(V_1\). Suppose the test object has a known reduced weight of 0.00274 g (the encircled dot on the \(R\) scale in the figure). The ordinate through this point intersects the abscissa of \(-\Delta P/P_2 + P_w\) (the encircled cross). The sloping line through the intersection has a value of 0.0038 cm\(^3\) or 3.8 mm\(^3\) and represents \(V_1\). Another line, sloping upward from the left side of the rule, also has this value. With the two lines distinctly marked, the slide rule is ready for determinations of \(R_o\).

Figure 2 also serves to show the use of the slide rule to determine the reduced weight of an ostracod. In the evaluation of \(V_1\) above, the initial equilibrium pressure on the bubble was \(P_1 + P_w = P_2 + P_w - \Delta P = 429 + 310 = 739\) mm of mercury. This remains unchanged during use of the diver, unless air is added or taken from the bubble. Suppose the test object is removed and an ostracod substituted for it. Let equilibrium be re-established at \(P_2 + P_w = 733.7\) mm of mercury. Then \(-\Delta P = 5.3\) mm of mercury. In Figure 2, the slide is shown with 733.7 set opposite to 5.3 on the bottom scale (by coincidence, the same setting that had 429 opposite 310 in the evaluation of \(V_1\)). By following the abscissa up from the arrow to its intersection with \(V_1 = 0.0038\), and the ordinate to the left of this intersection, one finds the reduced weight of the ostracod on the \(R\) scale as \(R_o = 0.0000274\) g = 0.0274 mg = 27.4 \(\mu\)g. If the manometer can be read only to tenths of a millimeter, the measurement of \(R_o\) is accurate, for most divers, only to the nearest microgram. If this is true, the weight is reported as 27 \(\mu\)g.

**Sources of Error**

During the course of our experimenting with the Zeuthen technique, we discovered several sources of error. Others probably exist. As the technique is used to weigh ostracods, these sources may be divided into those having to do with (1) apparatus, (2) calibration, and (3) specimens. Of these, some errors arising from the nature of the apparatus are the most difficult to solve because of the scale of parts of the diver.

*Apparatus.*—Three parts of the apparatus do not always function ideally. They are the canned atmosphere, the registering manometer, and, in particular, the Cartesian diver.

Despite packing in insulation, the canned atmosphere apparently acts, to a small degree, as an air thermometer. If the containers for the canned atmosphere are large, the errors from pressure changes on the registering manometer during the weighing procedure are practically eliminated, but
the larger the container the greater the thermometer effect from expansion or contraction of the air contained therein. In rendering one source of error impotent, we foster another that is just as large and troublesome. There seems to be no better solution than to maintain temperature as nearly constant as possible during each weighing procedure. Even with these precautions, when the opposite end of the manometer is left open, certain small changes in the registering manometer appear which cannot be explained as response to barometric changes in pressure. With insulation of the containers and operation in a closed room, the temperature effect can be kept so low that it probably does not affect manometer readings by more than a few tenths of a millimeter.

In recording continual readings of the manometer as the diver approaches equilibrium, we sometimes find anomalies. The level around which “rises” and “falls” of the diver have centered suddenly shifts, in some cases by more than a millimeter. This does not, in our opinion, reflect a change in conditions of the manometer. We used water in the manometer tubes because tables on density have been worked out with greater precision for water than for other liquids of about the same specific gravity. Pure water, without a wetting agent, tends to adhere to the sides of the manometer tube. From time to time, these small drops run down the tube to raise the level in both arms of the manometer. If the manometer readings are made as soon as possible after equilibrium is established for the diver, the pressure change, determined as the difference in level between the left and right arms, is measured correctly. Some drops inside the tube also form as condensation from water vapor that evaporates from the water of the manometer. As pressure is changed, water rising in one arm or the other incorporates some of these small drops into the liquid, raising, slightly, the levels in both manometers. An ideal fluid for the manometer would be one for which density tables had been set up, which did not adhere to glass, and which did not evaporate.

Certain difficulties in establishing equilibrium arise from the characteristics of the bubble in the Cartesian diver. Our observations indicate that the surface of the bubble at times adheres to the sides of the tube. With pressure conditions constant, the bubble may suddenly expand or contract, very slightly, it is true, but sufficient to impart a “slow-motion bounce” to the diver. According to our interpretation, a “bounce” of this nature results when the adhesion of bubble to glass is broken. The bubble is not perfectly free to respond to pressure changes. To add to the difficulty, the equilibrium of the diver is an unstable equilibrium. If the diver rises above the selected level, the pressure of the overlying water is less, the bubble expands, and the diver continues to rise; conversely, if the diver
sinks below the level, the pressure of the water increases, the bubble is compressed, and the diver continues to sink. Thus, the position of equilibrium must be approached slowly, so that the momentum of the diver does not carry it beyond the selected level.

*Calibration.*—The selection of a standard weight to calibrate the Cartesian diver is beset with problems. The reduced weight of a sheet of foil or a length of fine wire can be measured accurately with an analytical balance, but the small piece cut off for the standard cannot be checked directly. The accuracy of the weight depends upon the precision with which the small standard is cut. This affects the actual weight of each object compared against the standard, but, of course, has no influence on the relative weights of all objects weighed.

*Specimens.*—Difficulties arise in trying to arrive at true reduced weights of living or fossil ostracods from the nature of the specimens. Living ostracods may have small bubbles on the carapace. If they are passed through water that is highly charged with dissolved air, the ostracods pick up a coating of microscopic bubbles. In addition, many ostracods have foreign matter clinging to their valves or appendages, which does not represent part of the weight of the animal. When some specimens are placed in the anesthetic, they void, thus reducing their normal body weight.

In selecting fossil specimens for weighing, we found only a small percentage that satisfied our requirements. All specimens must have the same parts and be preserved in the same manner. The study must include either all isolated valves or all carapaces. If valves are chosen, each must be complete and free of adhering matrix. If carapaces are used, each must have the valves completely closed. All ostracods in each study must have the same composition, and, in the carapaces, the steinkerns must also be alike. Except for ostracods having both carapaces and steinkerns of clear calcite, it is difficult to tell whether composition is uniform or differs from one specimen to another.

As a check on the accuracy of the weighing procedure, one specimen was weighed with two different divers under different conditions of pressure. As reported in Tables VII and VIII, the difference was 1.4µg in a weight of 554.2µg. This is a total difference of less than 0.3 per cent.

**PART II. STUDY OF WELLERIA MEADOWLAKENSIS, A NEW MIDDLE DEVONIAN OSTRACOD FROM WESTERN SASKATCHEWAN**

The first ostracods investigated by the weighing technique belong to a new species of *Welleria*, presumably to three distinct populations. The
specimens are from the core of one well in western Saskatchewan, although
the species is known from numerous wells drilled in Alberta and Saskatche-
wan. Indeed, it is a guide fossil in this region, and the strata in which it
occurs have been called the "Ostracod limestone."

Complete specimens were separated from the matrix with ease. Much
of the matrix was salt, which readily dissolved in hot water. Many of the
specimens fell free to the bottom of the beaker; others retained only frag-
ments of limestone, which were dislodged with a small needle.

Only specimens with well-preserved carapaces and steinkerns of calcite
were selected for weighing. They are translucent. From the uniformity of
their composition, it seems reasonable to assume that the weights of the
fossils are proportional to the weights of the ostracods when they were alive.

The species may, in the future, have stratigraphic significance. Al-
though ostracods are the only fossils that have been found in the subsurface
Meadow Lake beds, myriads of carapaces, all of the new species described
here, are present in certain layers. If Welleria meadowlakensis, the new
species, can be discovered in other formations which have been definitely
dated, then the exact age of the Meadow Lake beds, in the lower part of
the Elk Point group, can be established. Because the species closely re-
sembles Welleria aftenonensis from the Gravel Point formation of Michigan,
and, we believe, the two are closely related, W. meadowlakensis is dated
as Devonian. Its occurrence in ancient inlets to an evaporite basin indicates
an unusual ecology. The division into three populations may be related to
seasonal or climatic variations during Meadow Lake time.

The specimens were given to the senior author by Dr. Henry Van Hees,
of Canadian Stratigraphic Service, Ltd., who also generously supplied
information on their occurrence. Dr. Murray J. Copeland, of the Canadian
Geological Survey, measured specimens in the collection of that organiza-
tion. Specimens have been deposited and catalogued in the Museum of
Paleontology of the University of Michigan.

PREVIOUS WORK

Within the last decade, drilling of numerous oil wells in Alberta,
Saskatchewan, and North Dakota has disclosed subsurface Middle Devon-
ian strata in an elongate basin or trough, which has been named the Elk
Point basin. Although several authors have described the strata and mapped
their distribution in certain areas, the ages of the lower beds in the basin
remain in doubt. As a result, details of paleogeography of the western
plains region in Middle Devonian time must still be worked out.

The Elk Point was named as a formation by McGehee in 1949
(p. 603), based on cores and cuttings of wells in eastern Alberta and western Saskatchewan. The name was derived from the village of Elk Point (population 594), north of the North Saskatchewan River in eastern Alberta. Wells drilled in this area penetrated 1200 to almost 1500 feet of strata included in the formation. McGehee originally (1949, p. 603) considered the age of the Elk Point to be Silurian, but pointed out (p. 610) the possibility that the upper beds could be Middle Devonian. Later (1954, pp. 131, 139), he came to regard all of the beds as Middle Devonian.

McGehee's original suggestion on the age of the beds was endorsed by Webb (1951, p. 98; 1954, p. 10). In his chart (1951, p. 93, Webb correlated strata of the central and southern plains with those of the southwestern plains; he indicated that the upper part of the formation was equivalent to the Manitoban, Winnipegosan, and Elm Point formations and the lower part of the Elk Point to the Ashern and Interlake group.

Crickmay (1954) was the first to use paleontology to date certain beds in the Elk Point group and to correlate them with other rocks in western Canada and in the plains region to the east. He found two conspicuous faunas: Stringocephalus in the upper part and Atrypa arctica near the middle of the sequence. He stated (1954, p. 143): "It is a reasonable conclusion that the entire formation belongs within the Middle Devonian." Crickmay also selected the type section to be that in the Anglo-Canadian Elk Point No. 11 well in Lsd. 2, Sec. 21, T. 57, R. 5 W. 4th Mer. He divided this section into nine members. His divisions have subsequently been used in correlating beds in the plains region.

In 1956 Van Hees prepared a stratigraphic cross section of Devonian and older formations from eastern Alberta to western Manitoba (see our Fig. 3). He regarded the Elk Point as a group and divided it into the "Lower Elk Point group" and the "Upper Elk Point group." Using Crickmay's terminology for beds in Alberta and western Saskatchewan, Van Hees made the following correlations with strata in Saskatchewan and Manitoba: Member 1 = First Red, Dawson Bay, and Second Red formations; Member 2 = First salt or Prairie evaporite; Member 3 = Winnipegosis (including the Elm Point stage); Member 4 = Ashern formation; Member 5 = Second salt; Members 6 and 7 = an unnamed limestone (between Second and Third salts); Member 8 = Third salt; and Member 9 = Basal Red strata. Since the Ashern was the first bed laid down as the sea spread beyond the confines of the "Lower Elk Point" basin, Van Hees separated his Lower and Upper Elk Point groups at the base of the Ashern formation. From west to east, the Ashern overlies successively the lower Elk Point beds and older strata of the Silurian Interlake group. For the pre-Ashern beds of the Elk Point group in western Saskatchewan,
Fig. 3. Cross section through sedimentary strata from eastern Alberta to western Manitoba. Map at the base shows locations of the wells from which records were used. Datum is the base of the Ashern formation. Modified from Van Hees, 1956, pp. 30-31.
Van Hees (1956, p. 34) introduced the name “Meadow Lake beds.” He (1956, p. 36) supposed that the lower part of the Elk Point group was of “questionable Lower Devonian age” on the basis of its stratigraphic position.

Two more papers on the Devonian deposits of this area appeared in 1958, one by Buller and the other by Van Hees. Both authors considered all of the Elk Point group as Middle Devonian. Buller (1958, p. 43) employed Van Hees’ earlier (1956) term “Meadow Lake beds,” and, in one of his cross sections (p. 36), included a log of the Imperial Goodsoil
No. 8-11 well (from which our ostracods were obtained). Van Hees (1958, Fig. 5) also presented a log of the Goodsoil well and (1958, Fig. 11) a map of rocks which he regarded as equivalent (or nearly so) to the lower Elk Point deposits, with significant tectonic and paleogeographic features. He discussed the occurrence (p. 73) and figured (Figs. 9–10) the ostracod species studied here. He called the bed containing the ostracods the "Ostracod limestone" and correlated it with Crickmay's Members 6 and 7 in the type section of the Elk Point. The erosional scarp forming the southern limit of the "Lower Elk Point" basin he called the "Meadow Lake Escarpment." The cross section given by Van Hees as his Figure 5 is modified and included here as our Figure 4.

In all discussions of the lower part of the Elk Point group, no direct evidence on its age has been brought forth. As pointed out by Buller (1958, p. 44) and by Van Hees (1958, p. 76), these strata have been assigned by various workers to Ordovician, Silurian, Lower Devonian, and Middle Devonian. An estimate of Middle Devonian was arrived at by Buller (1958, p. 49) from the continuity of sedimentation throughout Elk Point time and from the known Middle Devonian age of formations included in the upper part of the group. The same conclusion was reached by Van Hees (1958, p. 76) from the occurrence of the new species of *Welleria* described here, which he presumed to be of nearly the same age as the similar Middle Devonian species *Welleria afromensis* Warthin.

### Occurrence of Specimens

*Locality.*—All specimens were enclosed in fragments of core from the following well:

Imperial Oil Company, Goodsoil No. 8-11 well, Lsd. 8, Sec. 11, T. 62, R. 22 W. 3d Meridian, Saskatchewan Province, Canada. Well commenced November 17, 1956, and completed December 16, 1956, drilled to depth of 3461 feet. Schlumberger radioactivity log. Record of well in Central Canadian Stratigraphic Service, Ltd., Log No. CC-898, in which lithology and tops were checked against electric log. Ostracods in samples from interval between 2541 and 2546 feet. A generalized section of this well shown in Figure 4.

*Stratigraphic position.*—The ostracods occur in the Meadow Lake beds in the lower part of the Elk Point group. They are presumed to be Middle Devonian. In Van Hees's terminology (1956, pp. 30–31), the ostracod-bearing strata lie below the Second salt and above the Third salt in his "Lower Elk Point group." In 1956 (p. 30) Van Hees identified the beds as Members 6 and 7 of Crickmay's (1954) classification, and in 1958 (Figs. 4, 5) he called them the "Ostracod limestone."
Paleogeography.—The new ostracods are found in an unusual setting. They constitute the only species that has been discovered in a thin limestone between thick salt beds. Nevertheless, they are exceedingly abundant.

To explain this enigmatic occurrence, it is necessary to point out certain paleogeographic features of the region during the Devonian period.

For a long time preceding the deposition of the Elk Point group, the plains region of western Canada was above sea level. During this interval,
FIG. 6. Cross section through sedimentary strata in the Meadow Lake area, parallel to the Meadow Lake escarpment. Datum is the base of the Ashern formation. Locations of wells used in this section and in those in Figures 4 and 5 are shown in the map. Modified after Van Hees, 1958, Figure 4.
erosion produced a mature topography. In southeastern Alberta and southern Saskatchewan, a thick sequence of Cambrian sandstones capped by the resistant Upper Ordovician Red River dolomite dipped gently toward the south (Fig. 5). This cuesta has been termed the “Prairie Plateau” by Van Hess (1958, Fig. 11). The most conspicuous topographic feature in the region was the escarpment along the eroded face of the cuesta (Map I and Fig. 5). This cliff, called the Meadow Lake escarpment (Van Hess, 1958, Fig. 11), was several hundred feet high. Subsequently, it was buried under younger strata (Figs. 4, 6). Only in recent years have drilling records revealed its magnitude and location.

In Devonian time, marine waters invaded several basins in western Canada. The basal deposits, mostly red beds from reworked residual soil, covered over Cambrian and Ordovician formations (Fig. 3), forming the “Sub-Devonian unconformity” (Harker et al., 1954). In Alberta and western Saskatchewan, the Meadow Lake escarpment blocked the southward spread of the sea. The Lower Elk Point basin (Map II) was bounded on the south by the escarpment, on the west by high ground between the Sweetgrass arch and the Peace River high, and on the north by the Peace River—Athabaska arch. As in other basins in western Canada (Map I), the basal red beds in the Lower Elk Point basin were succeeded by evaporites (Figs. 3–5). Salt was precipitated and formed thick beds. The chief replenishment of marine water to the basin came through a trough (called the “Meadow Lake Basin” by Buller, 1958, p. 50) along the base of the Meadow Lake escarpment (Map I). Deposits in this trough constitute the Meadow Lake beds in the type locality and the surrounding area.

The “Ostracod limestone” lies in the upper part of the Meadow Lake beds (Figs. 4–6). It consists of carbonates and salt precipitated from marine water flowing into the highly concentrated solution in the evaporite basin. In the Goodsoil well core, the bed consists of thin layers of limestone alternating with laminae of salt. Without doubt, some calcium sulphate was also precipitated with the calcium carbonate and salt, but its presence in the core was not verified. The only fossils discovered in the bed are ostracods of the new species. When the “Ostracod limestone” was deposited, there was an auxiliary trough connecting the northern end of the basin to the open sea (Map II). Ostracods have been found in wells there, too. As would be expected, the carbonate ratios in the troughs increase toward the east, away from the basin.

Soon after the “Ostracod limestone” was laid down, the Lower Elk Point basin was filled to the level of the Meadow Lake escarpment (Fig. 5). The highly saline sea in the basin spilled over the escarpment and spread southeast in an elongate trough, which extended through the
MAP I. Distribution of rocks thought to be equivalent (or nearly so) to the lower part of the Elk Point formation of Alberta and Saskatchewan. A few significant tectonic and paleogeographic features have been added. Lithologies are generalized, and only the dominant rock type of the sequence is indicated. Numbered lines are isopachs. Modified only slightly from Van Hees, 1958, Figure 11.
Map II. Isopachs and generalized lithologies of members 5, 6, and 7 of the Elk Point formation. These beds yield numerous specimens of Welleria in the carbonate facies. Limestones are restricted to two narrow zones, the channels that admitted normal marine waters into the evaporite basin. One (labeled "Carbonate beds") is just south of Beaver River, along the base of the Meadow Lake escarpment, and the other (labeled "Carbonates") is about 50 miles south of the Clearwater River. The encircled $\times$ marks the location of the Imperial Goodsoil well from which the ostracods described in this paper were obtained. Adapted from a map supplied by H. Van Hees.
site of Saskatoon to the Williston region of North Dakota (Map III). The Ashern formation, the initial deposit of the upper part of the Elk Point group, was laid down uniformly over the Meadow Lake beds and older strata toward the south (Fig. 5) and east (Figs. 3, 6). Above the

MAP III. Isopachs of all Devonian formations in Alberta and Saskatchewan. The Peace River high and the Sweetgrass arch remained positive elements throughout the Devonian. A low arch between the Peace River high and Lake Athabaska separated the 1000-foot isopachs of the Elk Point basin and the Hay River basin. The heavy dashed lines represent the approximate limits of evaporites. Adapted from Webb, 1951, Figure 5.

Ashern, the Elk Point group contains another thick salt bed, the First salt or Prairie evaporites.

At the present time, the Meadow Lake escarpment has high relief, as determined from well records (Fig. 4), but this was not its expression during early Elk Point time. If the cross sections are plotted with the base
of the Ashern formation as datum (Figs. 3, 5, 6), they show the relationships of beds at the close of early Elk Point time. In Figures 4 and 5, the same cross section has been plotted twice: first, with the base of the Cambrian as datum, showing approximately the present attitude of beds, and, second, with the base of the Ashern as datum. It is obvious from a comparison of these figures that much of the relief of the escarpment developed after the Ashern was deposited. During late Elk Point time, basins formed north and south of the crest of the escarpment; in them the Prairie evaporites were laid down (Fig. 3). Undoubtedly, some of the increase in relief can be attributed to settling of sediments on the fore and back slopes of the escarpment.

As pointed out by Van Hees (1958, p. 70), the Meadow Lake escarpment is aligned with the boundary between the Churchill and Superior provinces of Precambrian rocks and is parallel to the Kisseymew lineament (Map I). No conclusive evidence has been presented to show that the escarpment was formed, even in part, by faulting. Van Hees (1958, Fig. 2) has shown that the structural contours at the top of the Precambrian continue across the line of the escarpment without interruption or bending. Thus, it appears that the Meadow Lake escarpment was an erosional rather than a structural feature, and that the extension of the sea at the beginning of Ashern time resulted from sedimentary filling of the basin rather than from diastrophism.

The Lower Elk Point basin in Devonian time appears comparable to the Gulf of Kara Bogaz today. The Gulf receives water from the Caspian Sea, which has lower salinity than normal sea water. Nevertheless, the annual deposition of evaporites, mostly anhydrite, exceeds two feet (Twenhofel, 1932, p. 501). Just as today the Gulf of Kara Bogaz lies in the Desert of Kara-Kum, so, we believe, during Devonian time the Lower Elk Point Basin lay in an arid region.

Consideration of the process of evaporite precipitation leads us to the conclusion that influx of sea water to the Lower Elk Point Basin (Map II) was very sluggish during the time that the “Ostracod limestone” was being deposited. The red beds around the periphery (between the 0- and 50-foot isopachs) were undoubtedly laid down before the brine was sufficiently concentrated to yield carbonates. Exclusive of the area covered by red beds, the basin extended over about 92,000 square kilometers. While the limestone was being deposited, there is no reason to doubt that the basin was approximately in equilibrium, whereby evaporation loss was compensated by inflow of normal sea water to maintain constant volume, and precipitation of \( \text{CaCO}_3, \text{CaSO}_4, \) and \( \text{NaCl} \) was compensated by influx of these minerals in solution to maintain constant salinity. Briggs (1958,
p. 51) estimated net evaporation loss for the Silurian Salina sea to have been 5 feet per year, and King (1947, p. 475) estimated that for the Permian Castile Sea to have been 9.5 feet per year. It is reasonable to assume that evaporation in the Lower Elk Point Basin resulted in an annual net loss of 2 meters in depth, or 184 cubic kilometers of water. The two troughs through which sea water replenished the basin had a combined width of about 184 kilometers. If the troughs averaged only 2 meters deep, the rate of flow sufficient to offset evaporation would have been only 500 km/year, 1.6 cm/sec or .035 miles/hour.

With such an insignificant rate of inflow, it is possible that the Lower Elk Point Basin and its channels were shut off from the open ocean by sand bars across the mouths of the channels, and that sea water entered the basin by seepage. Thus, the basin may have been comparable to the modern marine salina near Larnaca on the Island of Cyprus, which receives sea water from the Mediterranean through a sand barrier; since this salina has very little fresh water entering from streams, its brine is valuable for the extraction of salt (see Twenhofel, 1932, pp. 496–97). More likely, the channels leading to the Lower Elk Point Basin had restricted openings, wide enough to admit a continuous and sufficient supply of sea water but narrow enough to prevent loss of basinal brine to the open sea by currents and large-scale mixing. Unfortunately, such postulations cannot be checked, for the open sea during Meadow Lake time lay east of the present boundary with Precambrian rocks (Map I), and all record of the entries into the two channels has been removed by erosion.

Deposition of the “Ostracod limestone” probably occupied centuries rather than years. Since the limestone is continuous, we infer that conditions were uniform (or nearly so) from the start to the completion of deposition. Thus, all of the carbonates in the replenishing sea water were precipitated, and their accumulation proceeded at the same rate that a fresh supply was brought in solution. Otherwise, salinity would have changed, and the deposition of limestone would have been interrupted. From data on the composition of sea water (Twenhofel, 1932, Table 63), we calculate that sea water one meter deep would supply the following layers: .0024 cm of pure CaCO₃, .0261 cm of CaCO₃ mixed with CaSO₄, .0391 cm of pure CaSO₄, 1.0955 cm of NaCl mixed with CaSO₄, and .1695 cm of pure NaCl, with rare salts remaining in solution at a density of 1.31. In other words, a basin in equilibrium with an annual net evaporation of 2 meters would have precipitates sufficient each year to cover the entire area with about .01 cm of limestone, .14 cm of anhydrite, and 2.52 cm of salt. Since salinity increases from the inlet to the center of the basin, however, precipitation does not proceed evenly over the whole basin. For example, the limestone
is first removed from solution, and is laid down in the channels and in
tonguelike extensions into the basin. Since it covers only about one-tenth
of the total basin, it could accumulate at .1 cm/year. These figures are
based on present-day sea water, but there is no reason to believe that
Devonian sea water was of very different composition. Therefore, the
deposition of the "Ostracod limestone" must have taken over ten thousand
years, probably much longer. The sample that yielded the ostracods
described here, from five feet of core, may have required over a thousand
years to accumulate.

Several important factors in the paleogeography remain in doubt.
These include the age of the Meadow Lake beds, the details of the connection
of the evaporite basin with the open sea, and the possible correlation
of the Meadow Lake beds with other evaporite deposits.

Are the Meadow Lake beds Ulsterian or Erian in age? The age can only
be determined within certain limits. The Meadow Lake beds are younger
than any of the Cambrian, Ordovician, or Silurian rocks on which they
rest (Fig. 3). Specifically, they are younger than the Silurian Interlake
group. The Meadow Lake beds are older than the Winnipegosis formation
above them. If the *Stringocephalus* fauna found in the Winnipegosis is the
same as the *Stringocephalus* fauna of Europe, then the formation is
Givetian (in North American stratigraphic terms, upper Cazenovia to
Taghanic stages of the Erian series). Hence, by stratigraphic position the
Meadow Lake beds are younger than the Interlake group and older than
upper Cazenovian; thus, they could be Upper Silurian, Ulsterian, or Lower
Erian (Eifelian). Because the Elk Point group forms a continuous sedimentary
sequence, and because the *Welleria* species in the Meadow Lake beds
differs only in minor details from that in the upper Erian (Givetian)
of Michigan, we conclude that the Meadow Lake beds are Devonian rather
than Silurian.

From a correlation of the Elk Point group with the Devonian sequence
in Michigan, we infer that the Meadow Lake beds were probably Ulsterian.
The Winnipegosis formation, by its *Stringocephalus* fauna, can be correlated
with the Rogers City limestone of Michigan. The Rogers City limestone is underlain by the Dundee limestone and this in turn by the Detroit
River group, which in subsurface contains evaporite deposits. In similar
arrangement, the Winnipegosis is underlain by the Ashern formation and
this in turn by the Meadow Lake beds, which in subsurface contain evaporite deposits. In the absence of conclusive evidence, we suggest that
the Meadow Lake beds are equivalent to the Detroit River group, which is
dated as the Onesquethaw stage of the Ulsterian series.

How far did the trough containing the Meadow Lake beds extend
toward the east? Erosion has removed all direct evidence. From the area covered by this trough and the one to the north, it seems highly unlikely that the “Ostracod limestone” extended much beyond its present limits. In our opinion, the known extent of the “Ostracod limestone” (Map II, Figs. 4–6) as compared to the size of the evaporite basin is sufficient to account for all or nearly all of the carbonates brought in by replenishing sea water.

Were the Meadow Lake beds contemporaneous with other evaporites in Canada and the northern part of the United States? Probably, but proof is lacking. Van Hees (1958, pp. 76–77) has discussed certain possibilities of correlation of the Meadow Lake beds (his Lower Elk Point) with the Burnais gypsum of the Kootenay Basin, the Chinchaga formation (mostly anhydrite) of the Hay River Basin, the St. Martin gypsum of Manitoba, and the Abitibi River formation of the Moose River Basin. His Figure 11 (here modified as our Map I) illustrated his “Tentative Framework of Possible Lower Elk Point Equivalents.”

According to our interpretation, the late Ulsterian sea invaded from the north, across central Canada, to the Michigan Basin, and farther south to Illinois. It came into regions of mature topography, in which the low areas became basins, such as the Ft. Nelson, Hay River, Lower Elk Point, Kootenay, Moose River, and Michigan Basins. The first deposits were reworked detritus. They included the basal red beds in the Hay River Basin and the Lower Elk Point Basin, the Sextant formation in the Moose River Basin, and the Sylvania sandstone in the Michigan Basin. Some of the basins were connected with the open sea through channels, along the old stream valleys and the bases of erosional escarpments. Whenever these channels became restricted, evaporites developed in the basins. In the Moose River Basin, for example, the lower part of the Abitibi River formation consists of fossiliferous limestone, the middle part of unfossiliferous thin-bedded limestones, gypsum, and shale, and the upper part of fossiliferous limestones with coral reefs. Thus, the deposition of evaporites or normal marine strata depended upon the nature of the connection with the open sea at a particular time.

We have stated without presenting evidence that the late Ulsterian marine invasion extended to Illinois. At another time the senior author plans to describe the occurrence of Anderdon (late Detroit River) fossils in a well in eastern Illinois. In drilling operations, the drill suddenly dropped several inches through a subterranean cavity. Pumping brought up gallons of weathered debris mixed with fossil ostracods and snails. Although most of the thousands of ostracods were only steinkerns, the snails were well-preserved and could be readily identified as species present
in the Anderdon limestone in outcrops in northwestern Ohio. The thin angular particles of debris appear to be residues of thin laminae of limestone. The presence of the cavity suggests that the Anderdon equivalent in Illinois consisted of alternating laminae of limestone and soluble evaporites. It will suffice at this time to say that there is no doubt that at least part of the Detroit River group reached Illinois.

**SYSTEMATIC DESCRIPTION**

Order **OSTRACODA**

Suborder **PALEOCOPA**

Family **Kloedeniidae**

Genus *Welleria* Ulrich and Bassler, 1923

*Welleria meadowlakensis*, sp. nov. (Pl. III, Figs. 1–10; Pl. IV, Figs. 1–16; Pl. V, Figs. 1–8)

*Welleria* sp. Buller, 1958, p. 44. Van Hees, 1958, p. 74, Figs. 9–10.

**Adult female.**—Carapace subelliptical in lateral view, subquadrate in anterior view, and subovate in dorsal view. Hinge line straight. Antero-dorsal and posterodorsal borders nearly straight, anteroventral and postero-ventral borders subround, and ventral border smoothly curved.

Two short sulci dividing the dorsal part of each valve into three unequal lobes. *L1* very low, about the same width as *L2* and separated from it by a shallow groove, *S2*. *L2* relatively small, subround, set below the hinge line, ventrally nearly confluent with the brood pouch. *L3* large, dorsally round and extending above the hinge line. *S2* deeper than *S1* but dorsally confluent with it, relatively shallow, the sulci forming a narrow horseshoe-shaped depression, ventral end of *S2* curved forward but not joined to *S1*. Brood pouch elongate, corresponding to the ventral lobe in the male, dorsally confluent or nearly so with the lobes, ventrally projecting slightly beyond the free edge.

Velate ridge on each valve, low, extending from corner to corner. Submarginal ridge, very low, parallel to the free edge in the left (overlapping) valve; submarginal ridge, if any, overlapped in the right valve in all specimens.

Corners slightly protuberant, the posterior directed backward and the anterior directed forward. Anterior cardinal angle about 110°, very slightly greater than the posterior cardinal angle. Surface smooth.

**Adult male.**—Shape, size, lobation, velar and submarginal ridges like those of the female, except for convexity of the ventral lobe (brood pouch

Immature instars.—Carapaces of six immature instars recognized (Tables IX and X). Characters like those of adult male, differing only in

| TABLE IX |
| MEASUREMENTS OF CATALOGUED SPECIMENS OF Welleria meadowlakensis, sp. nov. |

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* Specimen has a small chip out of posterodorsal corner; figure given is actual weight.

size and in proportions of the lobes. During ontogeny, $L_3$ increasing in size and all lobes shifting progressively forward.

Remarks.—A comparison of Welleria meadowlakensis, sp. nov., with the very similar $W$. aitonensis Warthin, from the Middle Devonian Gravel Point formation in Michigan, is offered in Table XI. Both species are illustrated in Plate III. They have the same general form, lobation, and smooth valves. Welleria meadowlakensis is larger, it has proportionately less height and width, its $L_2$ is smaller, and its $L_3$ more nearly symmetrical. The most conspicuous difference, however, is in the anterior corner and cardinal angle. In $W$. meadowlakensis the anterior corner has a tip
### TABLE X
**Summary of Average Measurements and Their Growth Ratios For Each Population and Instar of Welleria meadowlakensis, sp. nov.**

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<td>147.8</td>
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<td></td>
<td>5</td>
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<td>.66</td>
<td>.63</td>
<td>.409</td>
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<td></td>
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<td>1.30</td>
<td>.84</td>
<td>.79</td>
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<td>590.6</td>
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<tr>
<td><strong>Average</strong></td>
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<td>1.27</td>
<td>1.28</td>
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<td>2</td>
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<td></td>
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<td>.45</td>
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<td>1.32</td>
<td>1.34</td>
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<td>4</td>
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<td>.700</td>
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<tr>
<td>7</td>
<td>3</td>
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<td>1.25</td>
<td>1.83</td>
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</tr>
<tr>
<td><strong>Average</strong></td>
<td>1.25</td>
<td>1.27</td>
<td>1.26</td>
<td>2.01</td>
<td>2.01</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* The number in this column is the number of specimens measured, including uncatalogued specimens in The University of Michigan (measured by R. V. Kesling) and in the Geological Survey of Canada (measured by Dr. M. J. Copeland). The number in the last column is the number of specimens weighed (see Table IX).

† Specimen has a small chip out of posterodorsal corner; figure given is actual weight.
protuberant forward and its cardinal angle is 110° or less, whereas in *W. aftonensis* the anterior corner is blunt and the cardinal angle about 130°. When carapaces are seen in ventral view, the L3 lobes of *W. meadowlakensis* are visible, but those of *W. aftonensis* are hidden below the strongly convex ventral lobes.

### TABLE XI
**COMPARISON OF CARAPACES OF TWO SPECIES OF Welleria**

<table>
<thead>
<tr>
<th></th>
<th><em>W. aftonensis</em> Warthin*</th>
<th><em>W. meadowlakensis</em>, sp. nov.†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Population A</td>
<td>Population B</td>
</tr>
<tr>
<td>Length</td>
<td>1.33 mm</td>
<td>1.35 mm</td>
</tr>
<tr>
<td>Adult Male Height</td>
<td>.89 mm</td>
<td>.90 mm</td>
</tr>
<tr>
<td>Adult Male Width</td>
<td>.84 mm</td>
<td>.85 mm</td>
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<tr>
<td>Ultimate Length</td>
<td>.97 mm</td>
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<tr>
<td>Immature Height</td>
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<tr>
<td>Instar Width</td>
<td>.64 mm</td>
<td>.79 mm</td>
</tr>
<tr>
<td>Height/Length</td>
<td>.67</td>
<td>.64</td>
</tr>
<tr>
<td>Width/Length</td>
<td>.63</td>
<td>.59</td>
</tr>
<tr>
<td>Anterior corner</td>
<td>Blunt, never protuberant</td>
<td>Sharp, tip protuberant forward</td>
</tr>
<tr>
<td>Cardinal angle</td>
<td>About 130°</td>
<td>105 to 110°</td>
</tr>
<tr>
<td>Ventral lobe</td>
<td>Strongly convex</td>
<td>Moderately convex</td>
</tr>
<tr>
<td>L2</td>
<td>Large</td>
<td>Small</td>
</tr>
<tr>
<td>S2</td>
<td>Deep, narrow</td>
<td>Relatively shallow</td>
</tr>
<tr>
<td>L3</td>
<td>Hump inclined forward</td>
<td>Dorsally round</td>
</tr>
</tbody>
</table>

* Averages from uncatalogued specimens, some in the Museum of Paleontology of The University of Michigan (measured by R. V. Kesling) and others in the Geological Survey of Canada (measured by Dr. M. J. Copeland).

Specimens can be assigned to instars by their length, height, and width. Although 23 specimens were in instar 5 and 33 in instar 6, no specimen was found to have a length between 1.12 and 1.18 mm. Since this constituted the greatest hiatus or gap within the series for length, it appeared to mark the boundary between instar 5 and instar 6. This boundary was also separated from that between instar 6 and the adult by about a factor of
1.26, the ideal increase per dimension per instar. The boundaries between younger instars had similar but less conspicuous gaps in the series of measurements.

To determine the limits of height and width, measurements were plotted for length vs. height and for length vs. width. We found the boundaries between instars to be: for length, 0.46, 0.58, 0.73, 0.92, 1.16, and 1.46; for height, 0.29, 0.37, 0.46, 0.58, 0.73, and 0.92; and for width, 0.28, 0.35, 0.44, 0.56, 0.71, and 0.89 mm. Six immature instars and the adults have been identified (Tables IX and X). Whether these include all the immature instars of the species is not known; more extensive collecting will be required to confirm or extend this figure. It will be seen in Table X that the growth ratios for height are more consistent than those for length or width. Probably, the deformation of small carapaces affects length and width more strongly than height. This is indicated by the fact that the growth ratios for products of length, height, and width (Table X) deviate very little from a constant figure, 2.

Types.—Holotype, a female carapace (not weighed or measured), No. 30493. Paratypes (all weighed and measured, see Table IX), 1 carapace in instar 1, No. 42255; 4 carapaces in instar 2, Nos. 42256–42259; 3 carapaces in instar 3, Nos. 42260–42262; 6 carapaces in instar 4, Nos. 42263–42268; 3 carapaces in instar 5, Nos. 42269–42271; and 2 carapaces in instar 6, Nos. 42272–42273.

Weights of specimens

Weights were determined for nineteen specimens by the technique described in Part 1, pp. 15–17. The weights (Table IX) fall remarkably close to the series 18, 37, 50, 60, 73, 100, 120, 146, 200, 292, 400, 584 μg. As one can see at a glance, each number in this series varies from at least one other number by approximately a factor of 2 or a multiple of 2. We have interpreted the weights to signify three distinct populations within the species.

For convenience, the populations are referred to as A, B, and C. Population C is the smallest, A the intermediate, and B the largest in each instar. The ostracods weighed in population C seem to be part of the following series, from first instar to adult: 15, 30, 60, 120, 240, 480, and 960 μg; those in population A: 18, 37, 73, 146, 292, 584, and 1168 μg; and those in population B: 25, 50, 100, 200, 400, 800, and 1600 μg.

As can be seen in Table X, the growth ratios for weight vary less than the growth ratios for the product of length, height, and width. This was expected, since linear dimensions are too variable to be used in separating
populations within instars. Presumably, some of the variations in young instars may be attributed to the ease with which the thin-walled valves could be deformed during burial. Inasmuch as the weight (and, therefore, the volume) changed very little, it appears that the deformation of the immature carapace was comparable to that of a balloon—that is, if compressed in one direction, it expanded in others, so that the volume remained about the same. Thus, ontogenetic series of instars can be better established and defined by weights than by linear dimensions.

We find that the weights of the ostracods in each population agree very well with Przibram’s Law.

PALEOECOLOGY

Certain factors in the occurrence of Welleria meadowlakensis point to an unusual ecology: (1) it is the only species of animal that is known from the Meadow Lake beds; (2) the ostracods are abundant; (3) the ostracods were deposited in a trough connecting an evaporite basin with the open sea, most of them in limestone and some in thin salt stringers interbedded with the limestone; and (4) three distinct populations of the species occur within a few feet of strata.

Since Welleria meadowlakensis is the only kind of animal found in the Meadow Lake beds, we infer that the environment precluded other organisms, except possibly microorganisms on which the ostracods fed. Possibly, the mouths of the channels were blocked by sand bars (as pointed out in Paleogeography above), shutting out invasions of marine animals except those swept over by storm waves; more probably, salinity acted as the barrier, killing most animals that were brought into the concentrated brine. Undoubtedly, the first specimens of W. meadowlakensis came into the channels from the open sea.

In being the only species in the strata and in occurring in great numbers, Welleria meadowlakensis resembles the morphologically similar W. afromensis Warthin in the Middle Devonian Gravel Point formation of Michigan. The latter species was studied by Kesling and Soronen (1957), who concluded that it lived in a lagoon. It now seems reasonable to postulate that the lagoon had higher salinity than the surrounding sea, thus preventing other animals from living there.

Specimens of Welleria meadowlakensis are abundant in the “Ostracod limestone,” giving certain bedding planes a pebbly texture. If we assume, as above, that the limestone accumulated no slower than .1 cm per year, the ostracods must have swarmed in the brine during Meadow Lake time. The species was prolific in this environment. For whatever food supply
that was available, there was no competition with other metazoans. Certain microorganisms may also have lived in the brine and served as food for the ostracods. Or the ostracods may have thrived on organic detritus brought into the channels, possibly scavenging on animals killed by the high salinity.

The ostracods probably lived close to the area where they were buried. We believe that they thrived in brine with salinity of about 65 to 160, the range in which $\text{CaCO}_3$ is precipitated. Today, another crustacean, a small brine shrimp, lives in Great Salt Lake, which has brine of such high salinity that no $\text{CaCO}_3$ remains in solution. Thus, at least one other crustacean is known to inhabit waters more concentrated than those postulated for the Meadow Lake area when *Welleria meadowlakensis* lived there. Undoubtedly, some ostracods were carried farther toward the center of the basin by occasional currents; however, the normal flow into the basin was very slow (see discussion of Paleogeography pp. 33–43), too weak to move the ostracods far.

The occurrence of three populations in a few feet of strata poses a perplexing problem. Since the sample was broken up when received, we have no way of determining whether the populations were contemporaneous or lived at different times. If, as we believe, this sample accumulated during several centuries, the populations could have evolved, one from another. There was enough time.

It is quite possible, however, that the three kinds of *Welleria meadowlakensis* developed in response to temperature differences, either seasonal or climatic, so that they may not have been genetically isolated in time. If the three kinds occurred in a sequence of generations that was repeated annually, for example, then they were not true populations according to the definition used in zoology. Living ostracods appear to reach a size that is related to the temperature of the water in which they live. In *Cytherura nigrescens* (Baird) from one locality in the Baltic (Table XII), specimens collected in winter are about 8 per cent larger in each dimension than those collected in summer. Since the ostracods in this species normally complete their ontogeny in 30 to 35 days (Elofson, 1941, pp. 396–97), the summer and winter collections do not show differences in two seasonally isolated breeding populations but, instead, the effects of temperature in individuals of one continuously breeding population. In his experiments with the marine species *Xestoleberis aurantia* (Baird), Elofson (1941, p. 447) selected 16 specimens hatched on July 14. He removed eight of them to an aquarium maintained at $18^\circ$C, and the other eight to an aquarium at $6^\circ$C, and provided both groups with equal food and oxygen. On August 13, he found that each of the eight ostracods kept at $18^\circ$ had
attained the fourth instar, whereas six of those kept at 6° were in the second instar and the other two were still in the first—they had not molted once. Elofson's observations on *Xestoleberis* and *Cytherura*, therefore,

### TABLE XII

**VARIATIONS IN POPULATIONS OF OSTRACOD SPECIES**

(All measurements in millimeters)

<table>
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<tr>
<th>Locality</th>
<th>Adult</th>
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<th>Instar 4</th>
<th>Average</th>
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<td>1.90</td>
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<tr>
<td>Gullmarfjord</td>
<td>2.41</td>
<td>2.09</td>
<td>1.59</td>
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<tr>
<td>Ratio</td>
<td>1.25</td>
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<td>.300</td>
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<tr>
<td>Summer</td>
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<tr>
<td>Ratio</td>
<td>1.05</td>
<td>1.11</td>
<td>1.07</td>
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Carapaces of Middle Devonian *Welleria meadowlakensis*, sp. nov.‡

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<td>B</td>
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</tr>
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<td></td>
<td>C</td>
<td>1.23</td>
<td>1.00</td>
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<tr>
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<td>.68</td>
<td>.56</td>
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</tr>
<tr>
<td></td>
<td>C</td>
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<td>.60</td>
<td>.46</td>
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</tr>
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<td>1.13</td>
<td>1.22</td>
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<tr>
<td>Width</td>
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<td></td>
<td>C</td>
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<td>.60</td>
<td>.45</td>
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</tr>
<tr>
<td>Ratio</td>
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<td>1.17</td>
<td>1.13</td>
<td>1.15</td>
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</tbody>
</table>

* Median values from data of Elofson (1941, p. 399).
‡ Data of Elofson (1941, p. 400).
† Averages from uncatalogued specimens, some in The University of Michigan (measured by R. V. Kesling) and others in the Geological Survey of Canada (measured by Dr. M. J. Copeland).

indicate that ostracods in cold water develop much slower but reach a larger size than those in warm water.

In recent ostracods, the effects of temperature on geographically separated populations of an ostracod species are striking. Populations of
Philomedes globosus (Lilljeborg) from the cold waters near Greenland are about 20 per cent larger than those from the somewhat warmer waters of Gullmarfjord (Table XII). In fact, the differences between the two are so great that the ultimate immature instar from Greenland is about the same size as the adult from Gullmarfjord.

The difference between the largest (population B) and smallest (population C) groups in Welleria meadowlakensis is about 15 per cent in each dimension, nearly midway between the 8 per cent difference in Cytherura nigrescens and the 20 per cent in Philomedes globosus. No direct evidence is available on the time involved in the ontogeny of Welleria meadowlakensis. If the ostracods developed slowly, requiring several years to attain maturity as do certain recent marine species, then the groups of different size may have belonged to three distinct populations living at the same time but breeding at different seasons of the year.

As we analyze the occurrence of three size groups of Welleria meadowlakensis, then, there are three possible explanations: (1) the three groups were different populations that were not contemporaneous, but one evolved from another; (2) the three groups were one continuous population in which young hatched at different seasons developed to different sizes according to the temperature of the water; or (3) the three groups were different populations that lived contemporaneously but each bred at a different time during the year.

In conclusion, Welleria meadowlakensis, like its relative W. aftonensis, could live in the open sea but, being saliniphilous, thrived best in brine that eliminated its enemies and competitors. In the channels leading to the Lower Elk Point Basin the species was prolific. Three size groups existed; (1) as populations in an evolutionary sequence, or (2) with different breeding seasons, or (3) as groups of one population that were strongly influenced by seasonal temperatures.

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Submitted for publication June 2, 1960
EXPLANATION OF PLATE I

Fig. 1. Cartesian diver, first model (without air chamber). Note the three weights near the base. × 2.

Figs. 2–3. Cartesian divers, improved models (with air chambers), made on glass blower's lathe. × 1.

Fig. 4. Cartesian diver, improved model, made solely by hand methods. × 2.

Fig. 5. Apparatus used in this study. After the photograph was taken, insulation was added around the bottles for canned atmosphere. Compare with Figure 1 in the text (p. 5). Scales on the manometer tubes are each 1 meter long. About × 0.087.
EXPLANATION OF PLATE II

(All figures × 1)

**Fig. 1.** Cartesian diver, improved model (with air chamber), very sensitive, thin-walled. Note short length of fine platinum wire wrapped around base to achieve most advantageous weight. This diver at equilibrium at 985 mbs. pressure with a bubble less than 1 mm².

**Figs. 2–9.** Cartesian divers, improved models. Those shown in Figures 3 and 5 made solely by hand methods; all others made on glass blower's lathe.
EXPLANATION OF PLATE III

(All figures × 30)

Welleria meadowlakensis, sp. nov. ............................................ 43

Figs. 1–10. Right lateral and dorsal stereograms of five carapaces of Population A: Figs. 1–2, No. 42272, sixth instar; 3–4, No. 42269, fifth instar; 5–6, No. 42265, fourth instar; 7–8, No. 42256, second instar; and 9–10, No. 42255, first instar. All specimens from core of Imperial Oil Company Goodsoil No. 8–11 well, in interval between 2541 and 2546 feet.

Welleria aftonensis Warthin .......................................................... 44

Figs. 11–16. Right lateral stereograms of six carapaces: No. 33679, first instar; No. 33716, second instar; No. 33701, third instar; No. 33704, fifth instar; No. 33714, fifth instar; and No. 33676, adult female. All specimens from Gravel Point formation of Michigan, illustrated for comparison with Welleria meadowlakensis, sp. nov.
EXPLANATION OF PLATE IV

(All figures × 30)

*Welleria meadowlakensis*, sp. nov. .................................................. 43

**Figs. 1–4, 7–10.** Right lateral and dorsal stereograms of four carapaces of Population B: Figs. 1–2, No. 42271, fifth instar; 3–4, No. 42268, fourth instar; and 7–10, Nos. 42258 and 42259, second instars.

**Figs. 5–6, 13–16.** Right lateral and dorsal stereograms of three carapaces of Population A: Figs. 5–6, No. 42261, third instar; 13–14, No. 42270, fifth instar; and 15–16, No. 42273, sixth instar.

**Figs. 11–12.** Right lateral and dorsal stereograms of carapace in Population C, No. 42263, fourth instar.
EXPLANATION OF PLATE V

(All figures × 30)

Welleria meadowlakensis, sp. nov. ................................................. 43

Figs. 1–6. Right lateral stereograms of six carapaces: No. 42266, fourth instar, Population A; No. 42267, fourth instar, Population B; No. 42264, fourth instar, Population C; No. 42262, third instar, Population B; No. 42260, third instar, Population C; and No. 42257, second instar, Population B.

Figs. 7–8. Right lateral and dorsal stereograms of adult female carapace, with valves agape, No. 30493. Note anterodorsal structures, apparently marginal denticles.