

AN ANATOMICAL REDESCRIPTION OF *PLEIODON (CAMERONIA) SPEKII*  
(PELECYPODA: MUTELIDAE: PLEIODONINAE)

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## ABSTRACT

Several anatomical features of *Pleiodon (Cameronia) spekii*, a freshwater mussel endemic to Lake Tanganyika, are confirmed, others are redescribed and still others are described anew. *P. (C.) spekii* is a unique mutelid because of its pattern of pseudotaxodont hinge dentition, lateral rugae on apically scalloped incurrent and excurrent siphons, dorsal attachment of the inner lamella of the inner demibranchs to the visceral mass for the entire length of the latter, and dimorphic spacing of interlamellar septa (comparatively distant in the outer demibranchs and more dense in the inner demibranchs of both males and females). It is related to *Mutela* by its lack of a triangular sinus at the posterior end of the hinge plate and by its long presiphonal pallial suture behind the pedal opening. It shares with some *Mutela (Mutela)* and *Aspatharia (Spathopsis)* imperforate, vertically ridgeless septa in the inner, marsupial demibranchs. It and *Mutela (M.) simpsoni* display the unionacean orientation and attachments of the labial palpi, which are posteriorly separated from the inner demibranchs. *P. (C.) spekii* lacks several features previously described as unique to this species, viz., a special sieve plate complex, lateral superior branchial pouches, and vessels in alternating marsupial septa.

## INTRODUCTION

Extant freshwater mussels characterized by secondary taxodont (i.e., pseudotaxodont, *vide* Cox, 1969) hinge dentition were long classified in the nominal genus *Iridina* Lamarck 1819 (type species by monotypy: *Iridina exotica* Lamarck 1819). Three monotypic nominal subgenera were customarily recognized: *Iridina* s.s., in which numerous small tubercles occur throughout the length of the hinge plate; *Pleiodon* Conrad 1834 (type by monotypy: *Pleiodon macmurtrei* Conrad 1834 [= *Iridina ovata* Swainson 1823, *vide* Pain & Woodward (1964) and Haas (1969a)]), with taxodont dentition strongly developed throughout the hinge; and *Cameronia* Bourguignat 1879 (type by monotypy: *Iridina (Pleiodon) spekii* S.P. Woodward 1859), in which the taxodont dentition is prominent behind the beaks but is at most weakly developed in front of the beaks.

However, Modell (1964: 85) noted that "... gehen die *Iridina [exotica]* unmittelbar aus den grossen Mutelen des Sudan-Gebietes hervor", and, because most *Mutela* possess some tubercles along the hinge (previously noticed by Germain, 1909), Pain & Woodward (1964) synonymized *Iridina* Lamarck 1819 under *Mutela* Scopoli 1777 (first done by Clessin, 1874a, 1874b) and, owing to purportedly unique anatomical features (see below), elevated *Pleiodon* to generic rank.

*Pleiodon* (sometimes as *Iridina*) have been classified in four subfamilies: Mutelinae s.s. (Thiele, 1934; Modell, 1964, for *Iridina = Cameronia* therein); Iridiniinae Swainson 1840 (Modell, 1942, 1949; = Mutelinae s.s., *vide* Modell, 1964); Aspathariinae Modell 1942 (Modell, 1964, for *Pleiodon*; Starobogatov, 1970); and Pleiodoninae Pain & Woodward 1964 (Pain & Woodward, 1964). Bourguignat (1885) erected the family taxon Iridinidae (recognized by Jousseume, 1886), and Rochebrune (1904) established Pleiodontidae, whereas all other authors beginning with Adams & Adams (1857) placed *Pleiodon* (and/or *Iridina*) in Mutelidae Gray.

Pain & Woodward (1964) recognized three Recent species: *Pleiodon (P.) ovatus* Swainson 1823 and *P. (P.) waterstoni* Pain & Woodward 1964 of western Africa, and *P. (Cameronia)*

*spekii* S.P. Woodward 1859, which is endemic to Lake Tanganyika. Verdcourt (1963) recorded *Pleiodon* from Miocene deposits in Kenya, Modell (1964) listed Upper Cretaceous "Iridina" (*Iridina* s.s. = *Cameronia* therein) and *Pleiodon* from Egypt, and Haas (1969b) cited *Pleiodon* s.s. from the Upper Pliocene or Pleistocene and *Cameronia* as only Recent. *Pleiodon priscus* von Ihering, from the Cretaceous of Brazil, has been reclassified as a species of Mycetopodidae: *Paxydon* Schumacher (cf. Parodiz & Bonetto, 1963), and the presence of pseudotaxodont dentition in Anthracosiidae: *Pseudomutela verneuili* Amalitzky, from the Permian of Africa, has been interpreted as a case of parallel evolution (Pain & Woodward, 1964).

The anatomies of *Pleiodon* s.s. are unknown, and the soft-part structure of *P. (Cameronia) spekii* was described previously by Pelseneer (1886), Meyer (1958) and Pain & Woodward (1964); according to Pilsbry & Bequeart (1927), Deshayes' (1827) anatomical description of "Iridine du Nil" concerned *Mutela (M.) nilotica* (Cailliaud), and Troschel's (1847) account of *Iridina coelestis* Lea concerned *Mutela (M.) rostrata* (Rang). Each of those three accounts on *Pleiodon spekii* differed from the others by containing descriptions of features overlooked by the other workers. There follows a composite description based upon those reports.

Animal with pigmented, papillated, muscular incurrent and excurrent apertures, a pallial suture above the latter but lacking a separate supra-excurrent opening, and a comparatively long pallial suture anterior to the former; diaphragm separating the posterior ends of the branchial and suprbranchial chambers incomplete, with intercommunication accomplished through a sieve plate complex (see below); outer demibranchs with a lateral "superior branchial pouch" resulting from an overfold of the outer lamella dorsal to the sieve plate complex; presence of a densely ciliated "sieve plate complex" that serves to extract food particles from water passing through the branchial chambers; inner demibranchs dorsally attached to the visceral mass along the entire length of the latter, and anteriorly to the labial palpi; marsupia contained in the inner demibranchs; inner demibranchs of gravid but not nongravid females with a vertical ridge on each side of the interlamellar septa, separating the interlamellar space into a water-tube near the inner lamella and a brood space near the outer lamella; septa of gravid animals with numerous minute perforations of irregular distribution; and lacunae (vessels) in the inner demibranchs of gravid females located in alternating septa.

The purposes of this report are to both confirm and correct features in those prior descriptions, to add further details about several structures, and to compare *Pleiodon (Cameronia) spekii* to other mutelacean mussels.

#### MATERIAL STUDIED

*Pleiodon spekii* (S.P. Woodward): one gravid female (132 mm long) and one male (117 mm) collected by J.J. and S.T. Landye on 26 September 1974 from Kigoma Bay of Lake Tanganyika, just north of a tributary stream near Kigoma, Tanzania (4°53' S lat. x 29°39' E long.). Voucher shells are in the Museum of Zoology, The University of Michigan.

Additional species for comparison: *Aspatharia (Spathopsis) nyassaensis* (Lea), *A. (S.) petersi* (von Martens), dioecious *A. (S.) wahlbergi* (Krauss), *Mutela (Mutela) alata* (Lea) and *M. (M.) simpsoni* Ancey from Malawi; monoecious *A. (S.) wahlbergi* from Zimbabwe (Rhodesia); and *A. (S.) trapezia* (von Martens), *M. (M.) bourguignati* Bourguignat and *M. (M.) rostrata* (Rang) from Lake Victoria (all Mutelacea: Mutelidae); and *Anodontites (Anodontites) carinatus* (Dunker), *A. (A.) trapesialis* form *exotica* (Lamarck) and *A. (A.)* sp. from Colombia, and *A. (A.)* spp. from Mexico (all Mycetopodidae).

#### METHODS

The Colombian *Anodontites* and *Mutela simpsoni* from Malawi were placed directly into formalin, whereas the animals of the other mutelaceans studied here were narcotized with either menthol crystals (Mexican *Anodontites*) or sodium nembital (mutelids) and fixed in 10% formalin; all animals were preserved in 70% ethyl alcohol. Gross dissection revealed most features, and histological preparations were

made (see Heard, 1975) in order to identify the sex of each individual and to determine the structure of the demibranchs from frontal and transverse sections. Student's *t*-test was used to statistically interpret differences in septal spacing.

## OBSERVATIONS

### Mantle, siphons and pigmentation

Mantle sheets conjoined dorsally, and by a pallial suture above the excurrent siphon (without a separate supra-excurrent opening dorsal to it), between the excurrent and incurrent siphons, and anterior to the incurrent siphon for 27.9-28.8% of the length of the animal (Fig. 1). Apex (posterior margin) of both incurrent and excurrent siphons scalloped, presenting a superficial appearance of papillae; lateral (but not medial) surface of both siphons rugose and with rare, small tubercles. Both lateral and medial surfaces of each siphon flecked with moderate concentration of dark brown pigment (less dense on medial surface). Outer (ventral) surface of the pallial suture between the incurrent siphon and the pedal slit with a very dense dusting of dark brown pigment that forms a wide band. (Descriptions of pigmentation are based on preserved specimens, and other pigments and colors, if present in live animals, might have been leached by fixation and preservation.)

### Labial palpi

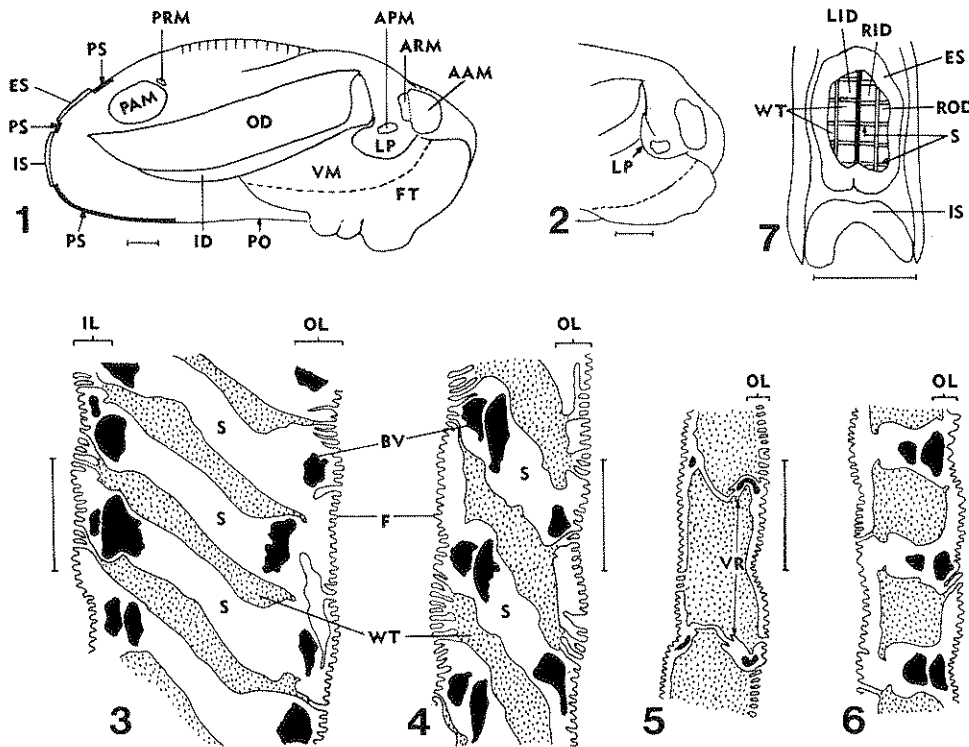
Palps 18.9-21.4% as long as the inner demibranchs, their height 51.8-56.1% of their length. Palpi of *Pleiodon spekii*, as of *Mutela simpsoni*, oriented in an anteroposterior direction (Fig. 1), with posterior 8.7-14.0% of their length free from the apposing mantle sheet and distinctly separated from the inner demibranchs; members of each palp posteriorly free from each other for 13.8-26.8% of their length. Contrasting conditions in the other mutelids examined are: strong dorsal curvature of the palpi (Fig. 2); posterior end nearly contiguous with the anteroventral border of the inner demibranchs; and union of the palp members and also of the outer member with the mantle sheet for their full length.

### Demibranchs

All four demibranchs in both specimens of a uniformly dark tan color. Outer demibranchs 0.6-1.6 mm shorter than the inner demibranchs. Outer (ascending) lamella of the outer demibranchs dorsally attached to the inner surface of the apposing mantle sheet for the entire length of the former; dorsal margin of the inner (descending) lamella of each outer demibranch joined to the dorsal margin of the outer (descending) lamella of the inner demibranch of the same ctenidium for its entire length; inner (ascending) lamella of each inner demibranch attached anteriorly to the visceral mass for the length of the latter, and posteriorly (behind the visceral mass) to the inner lamella of the apposing inner demibranch of the other ctenidium for 27.5% of the length of the inner demibranchs of the female and for 38.8% of that of the male. Posterior end of all four demibranchs united to the pallial suture separating the two siphons.

Height of outer and inner lamellae of the outer demibranchs greater than that of their corresponding lamellae in the inner demibranchs (by 1.1-2.2 mm and 1.4-2.4 mm, respectively); height of outer lamella greater than that of the inner lamella in both outer (by 3.8-4.1 mm) and inner demibranchs (3.0-5.4 mm). Height of interlamellar septa in the outer demibranchs greater by 1.5 mm than that of septa in the inner demibranchs of the female, but 0.7 mm shorter than septa in the inner demibranchs of the male.

Interlamellar septa of outer and inner demibranchs of both female and male imperforate; septa in the inner, marsupial demibranchs of the female without vertical ridges (compare Fig. 3 to Fig. 5). Septa comparatively distantly spaced throughout the outer demibranchs of both sexes (female:  $16.5 \pm 1.3$  filaments along each side of 10 water-tubes examined; male:



FIGS. 1, 2. General anatomical features of *Pleiodon (Cameronia) spekii* and *Aspatharia nyassaensis*. FIG. 1. Right side of *P. (C.) spekii*, with the mantle sheet removed from the branchial chamber. FIG. 2. Right side of the anterior end of *A. nyassaensis*, showing the orientation of the labial palpi. Scale for Figs. 1 and 2: 10 mm.

FIGS. 3-6. Camera lucida drawings of frontal sections of part of different demibranchs of *Pleiodon (Cameronia) spekii* and other mutelaceans. FIG. 3. Right inner (marsupial) demibranch of the gravid female *P. (C.) spekii*. FIG. 4. Right outer (non-marsupial) demibranchs of the same female *P. (C.) spekii*. FIG. 5. Right inner (marsupial) demibranch of a nongravid hermaphroditic *Anodontites trapesialis* form *exotica*. FIG. 6. Right inner (marsupial) demibranchs of a nongravid female *Aspatharia nyassaensis*. Scale for Figs. 3-6: 1 mm.

FIG. 7. Dorsoposterior end of the ctenidia (i.e., the four demibranchs behind the visceral mass) of *Aspatharia nyassaensis*, as viewed through the excurrent siphon. (This perspective shows the "sieve plate complex" that Pain & Woodward (1964) reported to be unique to *Pleiodon (Cameronia) spekii*.) Scale: 5 mm.

Abbreviations: AAM, anterior adductor muscle; APM, anterior pedal protractor muscle; ARM, anterior pedal retractor muscle; BV, blood vessel; ES, excurrent siphon; F, filament; FT, foot; ID, inner demibranch; IL, inner lamella; IS, incurrent siphon; LID, left inner demibranch; LP, labial palp; OD, outer demibranch; OL, outer lamella; PAM, posterior adductor muscle; PO, pedal opening; PRM, posterior pedal retractor muscle; PS, pallial suture; RID, right inner demibranch; ROD, right outer demibranch; S, (interlamellar) septum; VM, visceral mass; VR, vertical ridge; WT, water-tube (interlamellar space).

$16.0 \pm 2.3$  filaments/10 water-tubes); septa more densely spaced throughout the inner demibranchs of both sexes (female:  $11.8 \pm 1.8/10$  water-tubes; male:  $12.0 \pm 1.0/10$  water-tubes). (Compare septal spacing in Figs. 3 and 4.) Septal spacing in the outer demibranchs was significantly different from that in the inner demibranchs in both female ( $t = 7.86$ ;  $P < .005$ )

and male ( $t = 6.17$ ;  $P < .005$ ), but there was no significantly different spacing in the outer demibranchs of female and male ( $t = 0.64$ ;  $P > .05$ ) and also none in septal spacing in the inner demibranchs of female and male ( $t = -0.31$ ;  $P > .05$ ). Lacunae and vessels were found in all septa in both inner (Fig. 3) and outer demibranchs (Fig. 4), and not only in alternating septa.

#### Diaphragm, sieve plate complex, and lateral superior branchial pouches

The diaphragm separating the posterior region of the branchial chamber from the posterior region of the suprabranchial chamber (i.e., the cloaca) is complete, formed in part by the anterior extension of the pallial suture between the incurrent and excurrent siphons and in part by the posterior ends of the outer demibranchs (attached by the outer lamellae to the mantle).

A unique sieve plate complex, i.e., a structural organization that would contribute to an incomplete diaphragm, was not found in either sex.

Purportedly dorsal to the sieve plate complex, an overfold of the outer (ascending) lamellae of the outer demibranchs that contributes to a lateral superior branchial "pouch" was not confirmed.

#### Larvae

The single female *Pleiodon spekii* (collected 26 September 1974), several monoecious *Aspatharia wahlbergi* (collected 17 July 1972), several *Mutela bourguignati* (collected 7 October 1974), one *M. rostrata* (collected 10 September 1974) and some *M. simpsoni* (collected 10 December 1965) were gravid, but none contained mature larvae.

## DISCUSSION

#### Discrepancies

The present findings agree with those in prior accounts on *Pleiodon spekii* except for: descriptions of "les orifices palleanx" (Pelseneer, 1886), "Ingestions- und Egestionsoffnung" (Meyer, 1958) and "inhalent and exhalent apertures" (Pain & Woodward, 1964) ornamented with papillae; Meyer's (1958) claims of vertical ridges in the inner, marsupial demibranchs of only gravid and not nongravid females, perforations in these marsupial septa in gravid animals, and "Lakunen-Systems" (circulatory vessels) in alternating marsupial septa; and Pain & Woodward's (1964) report of a unique sieve plate complex and also lateral superior branchial pouches.

*Pleiodon spekii* lacks the comparatively simple incurrent and excurrent "openings" that are not separated by a pallial suture in non-hyriid Unionacea (e.g., *Anodonta*, *Caelatura*, *Elliptio* and *Unio*) and instead possesses the short, muscular siphons that in part characterize Mutelacea: Mutelidae (*Aspatharia* and *Mutela*) but not Mycetopodidae (e.g., *Anodontites*; and *Etheria elliptica* Lamarck, *vide* Heard & Vail, 1976a). In addition, the incurrent opening of Unionacea (see Kokai, 1977) and Mutelacea: Mycetopodidae (Heard & Vail, 1976a; this study) is flanked by at least one row of a variety of kinds of papillae, none of which occur in *P. spekii*, *Aspatharia* and *Mutela*.

Although Ortmann (1921) reported that vertical ridges on marsupial septa occur only in gravid and not in nongravid Mutelacea (=Mutelidae + Mycetopodidae *sensu* Parodiz & Bonetto, 1963) and Meyer (1958) described that same relationship for *Pleiodon spekii*, our gravid *P. spekii* lacked such ridges (Fig. 3). Moreover, these ridges were found here on marsupial septa of nongravid *Anodontites carinatus*, one species of Mexican *Anodontites*, and some but not all *A. trapesialis* form *exotica* (Fig. 5) and *Aspatharia petersi*. Some but not all gravid *Aspatharia wahlbergi* and *Mutela bourguignati* lacked marsupial septal ridges, whereas septa in the outer, non-marsupial demibranchs of some *Anodontites trapesialis* form *exotica* possessed these ridges. The vertical ridges of the mycetopodids were sharp and well defined, and

those of the mutelids gave the appearance of bulges or swellings in both gravid and nongravid animals (see Fig. 6). Further study of more, seasonal material is needed to interpret the presence and significance of these structures.

Perforated marsupial septa, common in such primitive Unionacea as *Caelatura* of Africa, *Diplodon* of South America, *Hyridella* of Australia and *Pseudodon* of Asia (Heard, 1974), have been illustrated for Mutelidae: *Mutela (Chelidonopsis) hirundo* (see Germain, 1909) and described for *Pleiodon spekkii* (Meyer, 1958), but were not found here in *P. spekkii*, *Aspatharia*, *Mutela* and *Anodontites*. The unionacean perforations are present in both nongravid and gravid females and are not of seasonal occurrence (Heard, pers. observ.), but the nature of mutelacean perforations is not as well understood.

Meyer's (1958) fig. 2A was claimed to portray lacunae in alternating marsupial septa of *Pleiodon spekkii*, but it did not. See Figs. 3 and 4 here for the distribution of vessels in a ctenidium of *P. spekkii*, and Figs. 5 and 6 for that of vessels in some other mutelaceans.

Pain & Woodward's (1964: figs. 2, 7) illustrations of the sieve plate complex reveal that this structural organization is not unique to *Pleiodon spekkii*. This "complex" simply constitutes the dorsal region of the posterior end of all four demibranchs united to the pallial suture between the incurrent and excurrent siphons, and is common to the other Mutelacea that we have examined (see Fig. 7) as well as to the Unionacea: Hyriidae that lack a perforation in the pallial suture (see McMichael & Hiscock, 1958).

Of the 16 *Aspatharia nyassaensis* that we examined, six (three females and three males) had an overfold of the dorsal part of the outer lamella of just one of the outer demibranchs, a condition that we interpret as due to contraction upon fixation prior to complete narcotization of the animals. Perhaps the same condition occurred in Pain & Woodward's (1964) specimens of *Pleiodon spekkii*. If so, there is created no unique lateral superior branchial "pouch"; which space in *A. nyassaensis* comprised the dorsal part of the interlamellar space that was forced out of normal position. Finally, an enigma in Pain & Woodward's (1964) figs. 10, 12 and 13 is that the arrow from M.P. ("marsupial pouch") goes to an outer demibranch, to an inner demibranch, and to both an outer and inner demibranch, respectively.

#### Comparisons to other Mutelidae

The comparatively long presiphonal pallial suture behind the pedal opening, the absence of vertical ridges and perforations associated with the marsupial septa, and the lack of a triangular sinulus at the posterior end of the hinge plate are features of *Pleiodon spekkii* that are shared with *Mutela* s.s. and *M. (Chelidonopsis)* (Deshayes, 1827; Rang, 1835; Troschel, 1847; Clessin, 1874a; Germain, 1909; Ortmann, 1910; Pilsbry & Bequeart, 1927; Bloomer, 1932; Mandahl-Barth, 1968; present study). In contrast, the presiphonal pallial suture is short in *Aspatharia (Spathopsis)* and absent in *Aspatharia* s.s., the hinge posteriorly possesses a triangular sinulus in *Aspatharia* s.l., and septal spacing is comparatively distant in all four demibranchs of male, female and hermaphroditic *A. (Spathopsis)* and *Mutela* s.s. (Ortmann, 1918; Pilsbry & Bequeart, 1927; Mandahl-Barth, 1968; present study). The anatomies of Mutelidae: *Arthropteron* and *Chambardia* are unknown.

Features that distinguish *Pleiodon spekkii* from other mutelids are pseudotaxodont hinge dentition, rugae on the siphons, attachment of the inner lamella of the inner demibranchs along the full length of the visceral mass, and the peculiar difference in septal spacing between the outer and inner demibranchs of both sexes. Dimorphic septal spacing is widespread among non-margaritifera Unionacea, with comparatively distant septa in non-marsupial demibranchs and non-marsupial parts of marsupial demibranchs, and densely spaced septa in the marsupia (Ortmann, 1911, 1921; Heard, 1975; Heard & Vail, 1976b); exceptions are *Modellinaia siamensis* Brandt (see Heard & Hanning, 1978), and *Megaloniais* Utterback and *Pseudodon* Conrad (Heard, pers. observ.). The condition in the female *Pleiodon spekkii* is equivalent to that in most unionaceans, but the same state in the male is enigmatic. Consequently, examination of more specimens is needed in order to determine the constancy of

this phenomenon. In addition, the *Aspatharia* (*Spathopsis*) and *Mutela* s.s. examined here possessed a few irregularly distributed tubercles, not papillae and not scalloping, at the apex of the siphons; *M. (Chelidonopsis) hirundo* evidently has simple siphonal apices (see Germain, 1909: 15-17, including fig. 14).

The comparatively wide gap between the palpi and inner demibranchs and also the incomplete attachments of the palps, which features are newly reported here for any mutelid, are features of unionaceans. Moreover, although Ortmann (1921) reported that the palpi of Mutelacea: Mycetopodidae are contiguous with the inner demibranchs, a gap between these structures was found here in all *Anodontites* examined.

Pain & Woodward (1964) expressed doubt that *Pleiodon* s.s., presumably predominantly fluviatile in western Africa (Cosumance River in Senegal, the Niger River drainage and Lake Chad), have the same anatomy of the lacustrine *P. (Cameronia) spekii*. However, as reported here, the sieve plate complex is not an unique structure, and the lateral superior branchial pouches are probably an artifact. Nevertheless, because of dimorphic septal spacing and attachment of the inner demibranchs to the visceral mass in *P. (C.) spekii* and of pseudotaxodont dentition in *Pleiodon* s.l., we retain the subfamilial name Pleiodoninae Pain & Woodward.

#### Reproduction

Meyer (1958) reported gravid *Pleiodon spekii* from a 17 September collection, although he did not indicate whether mature larvae were present. Our gravid female, collected on 26 September, contained only immature embryos in the upper half of the middle 2/3 of the length of the inner demibranchs. *P. spekii* and possibly also *Aspatharia* s.l. presumably produce haustorial larvae (for description of which in *Mutela bourguignati*, see Freyer, 1961) and neither lasidia of Mycetopodidae (described by Ihering, 1891; Bonetto, 1951; Parodiz & Bonetto, 1963) nor any of the various kinds of unionacean glochidia (see Ortmann, 1911; Parodiz & Bonetto, 1963). The duration of brooding of developing young (i.e., "breeding season" *sensu* Ortmann, 1911; tachytictic = short-term, or bradytictic = long-term) is unknown for any species of Mutelidae.

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