The moulting cycle of larval Amazon River prawn *Macrobrachium amazonicum* reared in the laboratory

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Abstract

The moulting cycle of *Macrobrachium amazonicum* larvae was studied in laboratory. Using the telson as main reference region and applying Drach's classification system, we checked twice daily the epidermis and cuticle and documented major structural changes such as the retraction of epidermal tissues from the cuticle and setal development. Rapid development (1-2 days or 3-4 days per larval instar at 29 and 21°C, respectively), a thin and little structured larval integument, and gradual rather than abrupt integumental changes allowed for only a coarse classification of the moulting cycle with three principal stages: A-C (postmoult and intermoult stages combined), D (premoult), and E (ecdysis). In early A-C, the cuticle is still thin and water is taken up, so that the larval body expands and rapidly attains its final size and shape. In late stages A-C, the larvae reinforce the cuticle, while the epidermis shows a conspicuous tissue growth. In D occurs a retraction of the epidermis from the cuticle (apolysis), and initiating the formation of new setae and appendages. Stage E is a very short process. It begins dorsally with a cuticular rupture between the cephalothorax and the pleon, followed by a rapid retraction of the pleon from the old exoskeleton. A-C took at both experimental temperatures ca. 40-50% of total instar duration, while stage D required slightly more than one half of the time. As larval growth is known to occur predominantly during A-C, we suggest that physiological and biochemical measurements comparing successive larval instars should be carried out near the end of this period, i.e. at ca. 30-40% of the moulting cycle.

Key words: Moulting cycle, larvae, *Macrobrachium,* freshwater prawn

Introduction

Growth and development of crustaceans appear to be discontinuous processes associated with successive moults (Hartnoll, 2001). Using histological and other morphological methods, Drach (1939) described in great detail moult-related anatomical changes occurring regularly in the integument of adult edible crabs, *Cancer pagurus.* Based on variations in the hardness of the cuticle as well as in epidermal and cuticular structures, he proposed for the moulting cycle a classification system with five principal stages (A-E) and numerous substages. This system was later further elaborated by Skinner (1962) and Drach and Tchernigovtzeff (1967), and it has been used in numerous studies on adult Decapoda and other crustaceans (Charmantier-Daures and Vernet, 2004).

Besides in anatomy and morphology, the moulting cycle implies also changes in behaviour, physiology and biochemistry, including cyclic activities of an antagonistic hormonal control system (for review, see Skinner, 1985; Chang, 1995; Charmantier-Daures and Vernet, 2004). Hence, knowledge of the course of the moulting cycle stage is highly important for the understanding

of various aspects of crustacean biology, including physiology and biochemistry (e.g. Spindler-Barth, 1976; Chang, 1995; Ahearn *et al.,* 2004; Gaxiola *et al.,* 2005), behaviour (Thompson and McLay, 2005; Mikami, 2005), food requirements (Mantelatto and Christofoletti, 2001; Giménez *et al.,* 2002; Schmidt *et al.,* 2004), reproduction (Diaz *et al.,* 2003; Tarling and Cuzin-Roudy, 2003; de Lestang and Melville-Smith, 2006), accumulation dynamics of toxic substances (Bondgaard and Bjerregaard, 2005; Norum *et al.,* 2005), as well as fisheries and aquaculture of commercially important species (Ziegler *et al.,* 2004; de Oliveira *et al.,* 2006; Brylawski and Miller, 2006).

In basic scientific investigations as well as in applied research including crustacean aquaculture, all such cyclical changes have implications for the experimental design and evaluation of data obtained from either laboratory or field studies. While the moulting cycle has been extensively studied in adult Decapoda and other crustaceans, it is much less well known for larval stages, mostly due to practical problems related to small body size, a thin and hardly structured integument, short moulting cycles, and restricted availability of materials with precisely known age within a moulting cycle (for review, see Anger, 2001).

In Brazil, the Amazon River prawn, *Macrobrachium amazonicum* Heller 1862 is commercially fished (Odinetz Collart, 1993) and also has a high potential for aquaculture (Kutty *et al.,* 2000; Kutty, 2005; New, 2005). Technologies for hatchery and grow-out are presently under development (see New and Valenti, 2000; New, 2005). Populations of this species live in both freshwater and brackish estuarine habitats (Moreira *et al.,* 1986; Magalhães and Walker, 1988; Odinetz-Collart, 1991a, b, 1993; Bialetzki *et al.,* 1997). *M. amazonicum* shows an extended type of larval development with ca. 9-11 free-swimming stages (Guest, 1979; Magalhães, 1985), requiring at optimal rearing conditions (30°C, salinity 10‰; Valenti, unpubl. data) about 18-21 days from hatching to metamorphosis. The larval physiology of *M. amazonicum* has been experimentally studied by only a few authors. McNamara *et al.* (1983) and Zanders and Rodríguez (1992) described effects of temperature and salinity on respiration rates of the two earliest zoeal stages, and Moreira *et al.,* (1986) studied effects of salinity on the upper thermal limits for their survival. In these investigations, however, changes during the moulting cycle have not been considered. The present study provides the first information about the course of the moulting cycle in the larval Amazon River prawn, *M. amazonicum.*

Material and Methods

Ovigerous females of *M. amazonicum* were obtained from the Aquaculture Center (CAUNE-SP) in São Paulo State University, Brazil. The broodstock came originally from the vicinities of Belém, in the state of Pará, northern Brazil (01°13'S 48°17'W). Prawns were transported to the Helgoland Marine Biological Laboratory, Germany, where they were maintained in individual aquaria (30 L) with freshwater, aeration, constant 29°C, and an artificial 12:12 h daylight:darkness regime. The adults were fed daily with fish meat and grated carrots.

After hatching, ca. 500 larvae were mass-reared in gently aerated 1-L glass beakers filled with brackish water (salinity 10‰) kept at constant 21°C and 29°C, under the same conditions of light. The larvae were fed daily with freshly hatched *Artemia* sp. nauplii, the water was changed, and dead individuals were removed. The successive larval stages (in order to avoid confusion with the term "stage" in the context of the moulting cycle, from hereon referred to as larval "instars"; for review of terminology, see Anger, 2001) were microscopically identified using the morphological description provided by Guest (1979). When moults occurred, the larvae were separated according to their instar, so that each rearing beaker contained exclusively individuals being in the same instar and with the same age within a given moulting cycle.

Samples of 3-5 larvae were taken twice daily from the cultures and examined under a BH2-NIC (Olympus) photo-microscope equipped with differential interference contrast. Changes in the epidermal structures were recorded and photographically documented. We used primarily the larval telson as a reference region, and we also used the uropods in advanced stages (from zoea III) (cf. Anger, 1983, 2001), because these body parts are thin and transparent, so that changes occurring in the epidermis and cuticle could easily be seen. As all larval stages presented in principle the same sequence of anatomical modifications, we describe in this paper the moulting cycles only for the two earliest instars (zoea I-II).

Results

The duration of development through successive larval instars depended greatly on temperature. While the average time for each moulting cycle varied from ca. 3-4 days at 21°C, only 1-2 days were required at 29°C. Although late instars (from zoea V) tended to develop at a slightly slower speed than the earliest ones, the duration of the moulting cycle was generally too short to allow for a high temporal resolution of sampling and microscopic examination. Another problem preventing a precise moult-staging was that the larval integument was found to be thin and little structured, and morphological changes were often indefinite. Thus, transitions between stages and substages could not be identified with a comparably high accuracy and a precise timing as in Drach's classical system (elaborated for adult crabs with thick and multi-layered structures). We therefore decided to combine the principal stages of postmoult (A-B) and intermoult (C), where gradual rather than abrupt changes occurred. After the combined stages A-C, premoult (stage D) and the moulting process (E) could be identified. Although our de-

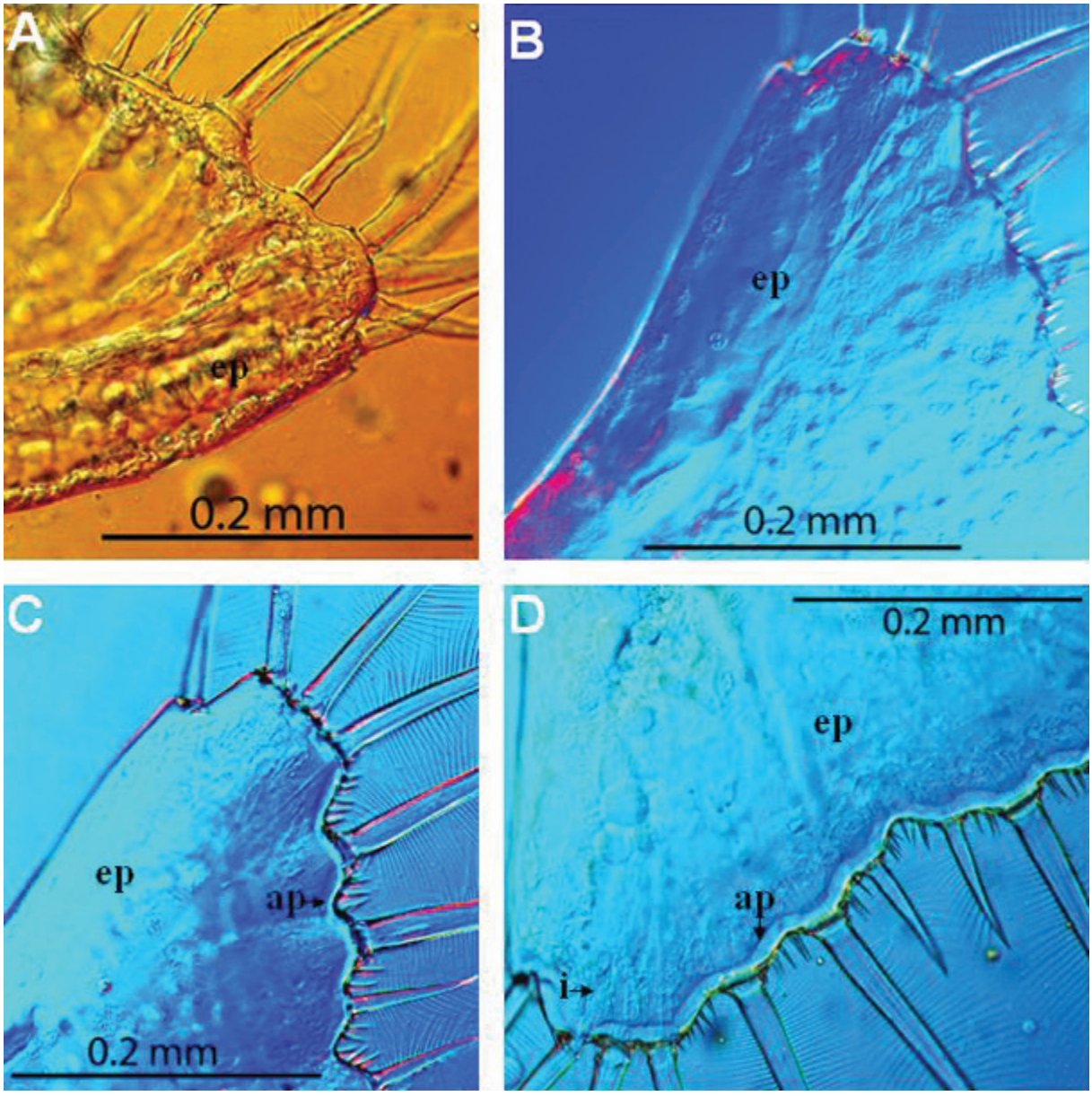

Figure 1. Telson of *Macrobrachium amazonicum,* larval instar zoea I: A, Early postmoult (stage A), with spongy epidermal tissue structure, large hemolymph-filled spaces (lacunae); B, intermoult (stage C), with epidermal growth, tissue concentration along the inner surface of the cuticle, reduced lacunar spaces; C, early premoult (stage D, substage D_0), with beginning epidermal retraction from the cuticle (apolysis); D, intermediate premoult (substage D_1), with advanced apolysis, beginning epidermal invaginations at the setal bases; ap, apolysis; ep, epidermis; i, invagination.

scription also provides some details including those of the important premoult substages D_0 and D_1, a precise schedule of their timing cannot be provided.

The course of the moulting cycle was similar in all successive larval instars. We therefore show here only some typical integumental chang-

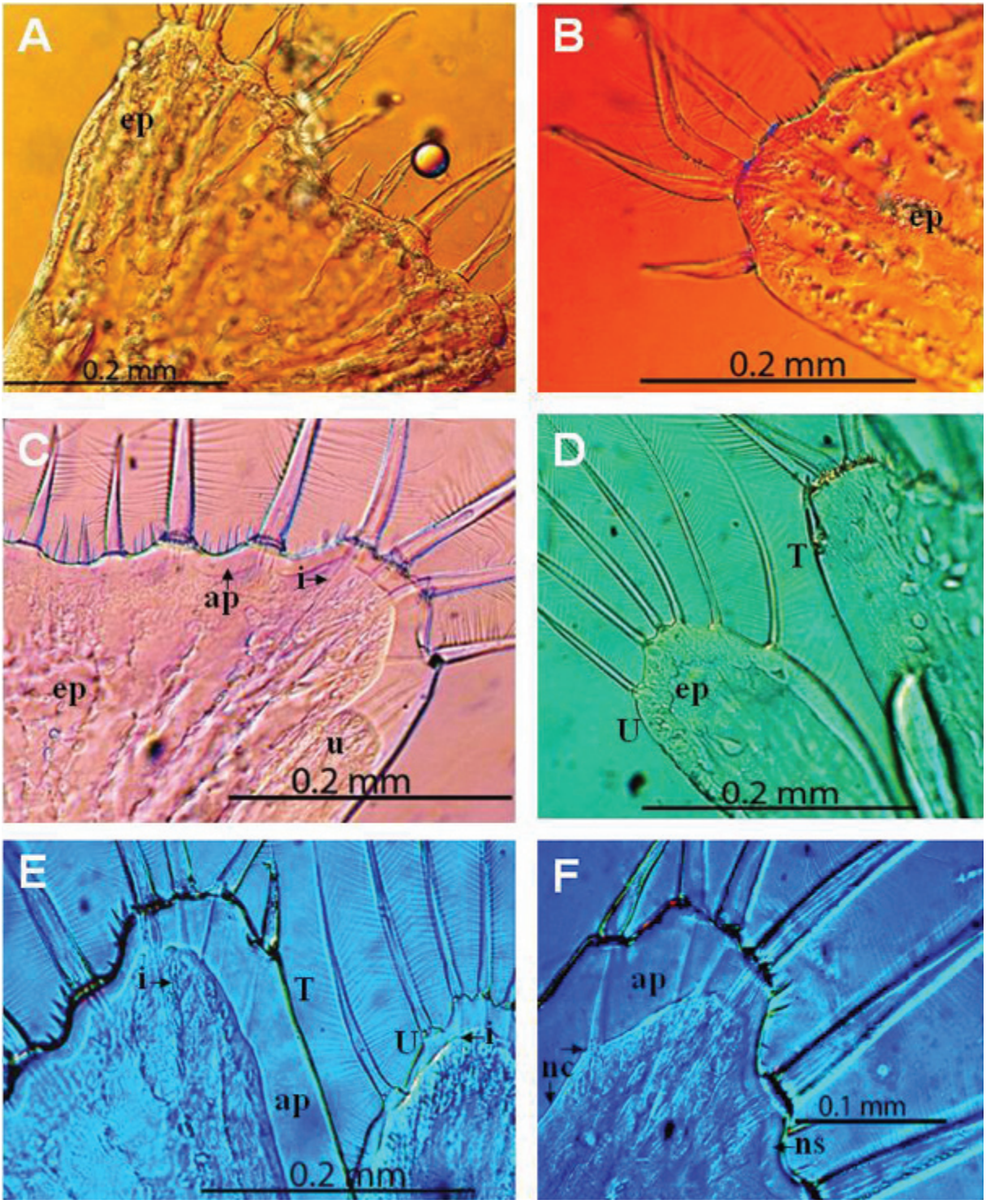

Figure 2. *Macrobrachium amazonicum,* larval instars zoea II (A-C) and zoea III (D-F): A, zoea II, early postmoult (stage A); B, zoea II, late postmoult (stage B), with advancing tissue concentration along the inner surface of the cuticle; C, zoea II, intermediate premoult (substage D_1), with uropod formation (u) inside the telson of the zoea II; D, zoea III, postmoult (stage B), with telson (T) and newly appearing uropod (U); E, zoea III, intermediate premoult (substage D_1); F, zoea III, late premoult (substages D_{2-4}), with formation of a thin new cuticle (nc); ap, apolysis; ep, epidermis; i, invagination, ns, new setae.

es, using micrographs taken from the telson (see Fig. 1, 2) and uropods (see Fig. 2) of the first three zoeal instars as examples. The process of ecdysis is documented with photos showing the moult from the zoea I to the zoea II instar.

Stages A-C combined (postmoult-intermoult)

Stage A (early postmoult). Immediately after hatching from the egg (zoea I) or moulting (later instars), the cuticle is thin and wrinkled, and the lar-

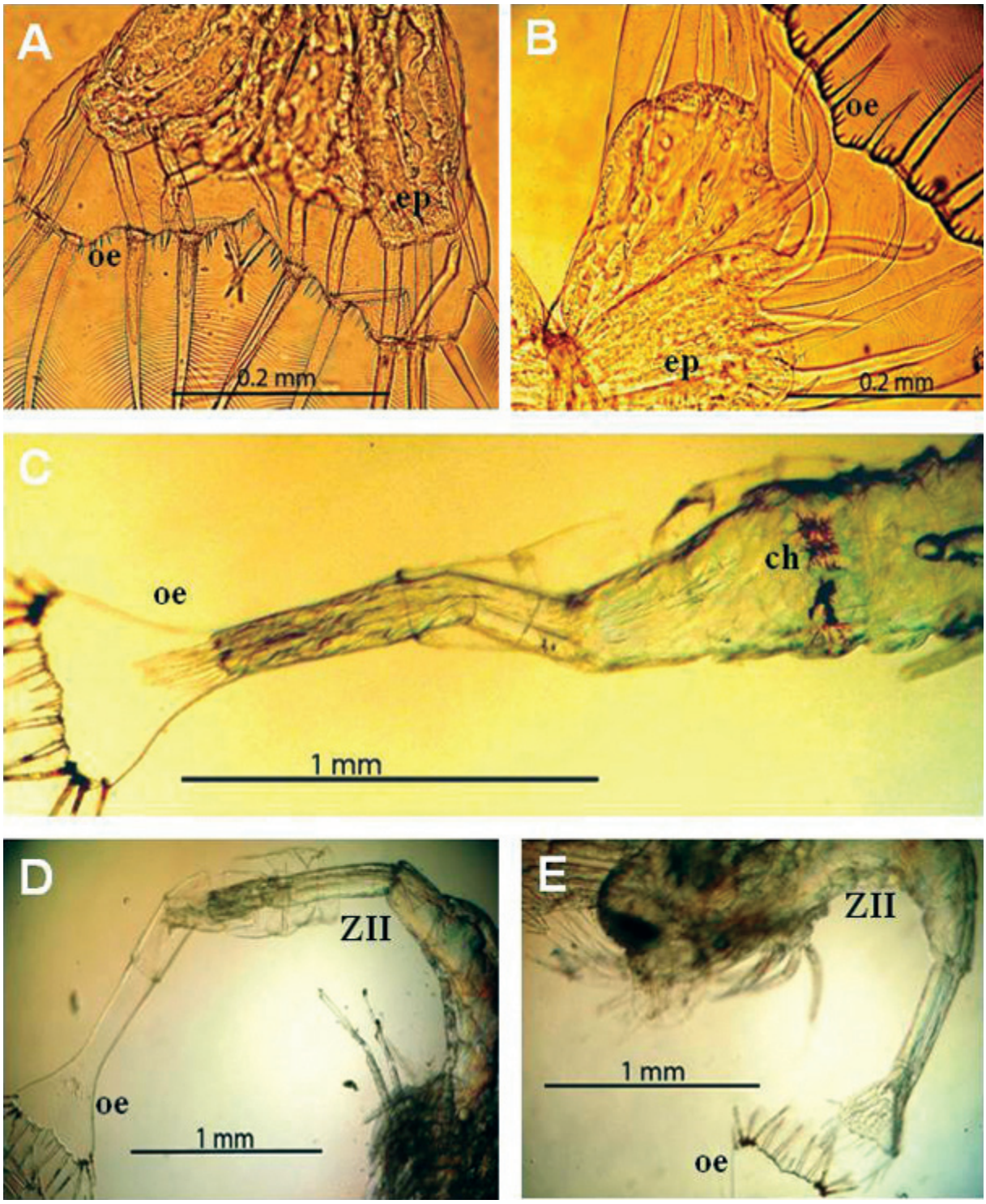

Figure 3. *Macrobrachium amazonicum,* moulting (ecdysis) of larval instar zoea I to zoea II: A-C, retraction of the telson from the old exoskeleton (oe), epidermis (ep); chromatophore (ch); D, shedding of the exuvia, appearance of the zoea II (ZII); E, zoea II with shed exuvia; ch, typical dorsal chromatophore on larval pleon.

val body is completely soft (ascertained by probing with delicate forceps). Microscopic examination revealed a spongy epidermal tissue structure with numerous large and irregularly shaped lacunar spaces. Figures 1A and 2A illustrate this condition for the telson of the zoeal instars I and II, respectively. Within a few minutes during and after ecdysis, the larva takes up water, so that the integument is rapidly stretched, previously invaginated setae and appendages are evaginated, wrinkles disappear, and the body attains its final size and shape (cf. below, Figs. 3D, E).

Stage B (late postmoult). The cuticle becomes more rigid, and the epidermal tissues begin to concentrate along the inner surface of the cuticle (as examples, see telson of the zoea II, Fig. 2B; uropod of the zoea III, Fig. 2D).

Stage C (intermoult). Both the reinforcement of the cuticle and the condensation of the epidermis tissues continue to a maximum, accompanied by a gradual reduction of lacunar spaces and conspicuous tissue growth (see zoea I, Fig. 1B).

The average duration of stages A-C combined was ca. 2.5 days at 21°C and slightly less than 1 day at 29°C, representing ca. 40-50% of the total time of the moulting cycle.

Stage D (premoult)

Substage D_0 (early premoult). Substage D_0, the onset of the premoult period, is well characterized by the beginning retraction of the epidermal matrix from the cuticle. This conspicous process (termed apolysis; Jenkin and Hinton, 1966) is first visible at the bases of the terminal setae of the telson (Fig. 1C), proceeding only later through other body regions and appendages.

Substage D_1 (intermediate premoult). The beginning of this substage is indicated by the occurrence of epidermal infoldings or invaginations (Figs. 1D-C, 2E). This internal enlargement of the tissue surface is a prerequisite for morphological reconstruction processes (morphogenesis) including the lengthening of already existing setae (setal growth), the formation of new setae (setogenesis; Fig. 2F), and the appearance of other completely new organs (organogenesis). During these sub-surface reconstruction processes in the epidermal tissues, the cuticle (i.e. the external shape and size of the larval body) does not change. As an example, Figure 2C shows the formation of uropods. These appendages appear externally only after the moult to the zoea III instar (Fig. 2D), but they can already be seen inside the telson of the zoea II instar (Fig. 2C).

Substages D_{2-4} (late premoult). When morphogenesis has been completed, a very thin new cuticle is secreted on the surface of new epidermal structures such as setae and appendages, while the gap between the old and the new cuticle increases (Fig. 2F). No resorption processes or other changes in the cuticular layers, as observed in adult crabs (Drach, 1939), were found during this period, so that no further distinction between substages D_{2-4} of Drach's classification system was possible. The average duration of complete Stage D was ca 3-4 days at 21°C and about 1 day at 29°C, corresponding to ca. 50-60% of the moult-cycle duration.

Stage E (ecdysis)

The moulting process (ecdysis) takes normally at most a few minutes. It is initiated by larval flexing movements, followed by a dorsal rupture of the cuticle between the cephalothorax and the pleon. First, the telson is retracted from the old exoskeleton (Figs. 3A-D). Subsequently, the larva sheds also the anterior parts of its exuvia, so that a new larval instar appears, and a new moulting cycle begins (Fig. 3E).

Discussion

The course of epidermal and cuticular changes observed during moulting cycles of larval Amazon River prawn, *Macrobrachium amazonicum,* is generally similar to those previously described for other decapod crustacean larvae (Freeman and Costlow, 1980; McNamara *et al.,* 1980; Anger, 1983, 1984). Comparison with adult life-history stages (e.g. Drach, 1939; Peebles, 1977; Dexter, 1981) is difficult, because technical constraints such as very short moult-cycle duration and a thin and little structured larval integument do not allow for a comparably high resolution in the description of larval moulting cycles (for review, see Anger, 2001). For practical purposes in applied re-

search including crustacean aquaculture, however, the lack of numerous precisely defined substages may not be a serious problem, as an identification of a few major moult stages should be sufficient to allow for a separation of fairly homogeneous materials taken from large cultures, e.g. for subsequent experiments, physiological measurements, or biochemical analyses. Our study may therefore provide a simple and practical guide for the identification of the major moult stages in larval *M. amazonicum,* aiding the selection of materials for studies of larval metabolism, growth, biochemical composition, or other relevant aspects of crustacean aquaculture.

Various structures can be used for moult-staging in larval decapods. Freeman and Costlow (1980) used for this purpose the antennae of the larval mud crab *(Rhithropanopeus harrisii),* while Anger (1983, 1984) used mainly the telson, but also pereiopods, antennae, and dorsal spines, to describe changes in the integumental structures of larval spider crabs *(Hyas araneus).* In early juvenile crayfish *(Parastacoides tasmanicus, Astacus leptodactylus)* and penaeid prawns *(Penaeus esculentus),* the uropods were most commonly used, at least in addition to the telson (Mills and Lake, 1975; Herp and Bellon-Humbert, 1978; Smith and Dall, 1985). In the present work, the description of the moulting stages was principally based on microscopic examination of the larval telson, because this body part is plane, thin and transparent, so that changes in the epidermal tissues can be easily observed. Similar observations were made in a study by McNamara *et al.,* (1980) with larvae of a congener, the shrimp *Macrobrachium olfersii.* The uropods appear in these palaemonid species only from the zoea-III instar, providing an additional reference region for studies of later larval development.

Tayamen and Brown (1999) proposed criteria for the evaluation of larval quality in *Macrobrachium rosenbergii,* based on characteristics of body coloration, setation, muscles, swimming behaviour, etc. An opaque appearance of the muscles in the pleon, for example, along with sluggish behaviour, represent a poor condition. However, the same characteristics occur also during early postmoult, when the larval body is limp and the larvae tend to sink towards the bottom due to weak swimming activity. A "healthy" colour and behaviour, e.g. a positive response to light, are rapidly recovered during later postmoult and intermoult. This shows that the moulting cycle must be taken into consideration when the health condition of shrimp larvae is evaluated.

The same applies to larval feeding and growth, which cease from late premoult through ecdysis and early premoult, re-starting only in late postmoult or intermoult (Anger, 2001). Stage C seems to be a period without dramatic structural and metabolic changes, characterized only by substantial tissue growth. During the premoult period, by contrast, the rates of growth and feeding decrease, while numerous structural changes occur in the integument, and the mass-specific metabolic rate increases (Anger, 2001). As stage C is the metabolically and morphologically most stable period within the moulting cycle, physiological experiments or biochemical analyses comparing successive larval instars of a species, or equivalent instars of different species, should preferably be conducted during this phase. In the larvae of *M. amazonicum,* the most suitable reference point for such comparisons may thus be found at ca. 30-40% of total moult-cycle duration, i.e. near the end of stage C and shortly before the transition to substage D_0, where apolysis occurs.

Besides intrinsic hormonal control factors, extrinsic variables such as temperature, food, water chemistry, or photoperiod may affect the moulting cycle in crustaceans (Chang, 1995; Ismael and New, 2000; Kulum and Ku, 2005). Also in the present study, it was accelerated by higher temperature (29° vs. 21°C), shortening the absolute time spans for each stage of the moulting cycle. Preliminary observations suggested, however, that variation in temperature might change also the temporal proportions of individual stages within the moulting cycle, with an apparently increasing duration of stages A-C combined in relation to stage D. However, further studies with a substantially enhanced temporal resolution of sampling and microscopic observation are necessary to evaluate the extent and significance of such an effect. Also, successive larval instars might differ in their response to environmental factors, which requires more detailed studies with various instars exposed to differential experimental conditions.

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