

LARVAL DIVERSITY AND DEVELOPMENT IN THE SINGAPORE ANURA (AMPHIBIA)

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ABSTRACT. - Singapore is home to five families of anurans, comprising 14 genera with at least 25 species. Compared with their adult forms, the larval stages have received limited attention. This void in the faunistic studies has largely been due to the ephemeral and elusive nature of many tadpole types, especially the forest species, which represent almost 70% of all the Singapore species recorded thus far. In this study, distinctive larval types are documented for 22 anuran species, of which two (*Bufo quadriporcatus* and *Rana plicatella*) are described for the first time. Accompanying characteristic descriptions of the diverse larval forms are notes on their different microhabitats, feeding behaviour and significant developmental events throughout growth and at metamorphosis. A key to the identification of these tadpoles is provided. However, the exact larval identities of three species (*Limnonectes paramacrodon*, *Rana baramica* and *Rhacophorus cyanopunctatus*) remain to be determined.

KEY WORDS. - Larva, anura, tadpole, Singapore.

INTRODUCTION

Among amphibians, anurans clearly make up the largest Order with around 4000 described species (Stebbins & Cohen, 1995). In Malaysia (Peninsular Malaysia, Sabah and Sarawak), at least 155 species of anurans are known (Kiew, 1984b). In Singapore, there are confirmed records for 24 species (Leong & Chou, 1997). While the description and study of anurans has focused primarily on their adult stages, larval stages have not been entirely neglected.

Published work on tadpoles have varied from taxonomic descriptions (eg. Boulenger, 1903; Berry & Hendrickson, 1963; Kiew, 1984a) to biochemical or physiological analyses (eg. Deuchar, 1966; Khoo, 1971; Noland & Ultsch, 1981). Developmental aspects (eg. Alcala, 1962; Sit & Kanagasuntheram, 1973) and ecological interactions (eg. Heyer, 1973; Wassersug et al., 1981; Inger et al., 1986) have also been studied. In the East Asian region, a selection of anuran larvae has been featured to greater or lesser extents in various published works

from different parts. These areas include India (eg. Annandale & Narayan Rao, 1918; Smith, 1924), Sri Lanka (eg. Kirtisinghe, 1957), China (eg. Pope, 1931), the Indo-Australian Archipelago (eg. Kampen, 1923) and Southeast Asia (eg. Manthey & Grossmann, 1997); Philippines (eg. Alcala, 1962; Inger, 1954; Taylor, 1920), Thailand (eg. Smith, 1916a, 1916b, 1916c, 1917; Taylor, 1962; Heyer, 1973), Java (eg. Schijsfma, 1932), Borneo (eg. Inger, 1966; Inger et al., 1986; Inger & Tan, 1990).

However, studies on larval species from Peninsular Malaysia would be most relevant to Singapore. Such studies include works by Smith, 1926; Berry & Hendrickson, 1963; Khoo, 1971; Berry, 1972; Kiew, 1973; Sit & Kanagasuntheram, 1973; Yong, 1974; Gadug, 1982; Kiew, 1984a. In Singapore, contributions which included larval stages to varying extents have been by Berry, 1964; Sit, 1968; Lee & Chen, 1970; Ting, 1970; Lim & Ng, 1991; Lim & Lim, 1992.

The extreme plasticity of amphibian larvae has long been recognised by herpetologists and embryologists alike (Wilbur & Collins, 1973). The diversity of larval forms among anurans was demonstrated by Altig & Johnston (1989), who recognised a total of 24 guilds of larvae, based on developmental and ecomorphological characteristics. However, tadpoles are notoriously difficult to identify, as the seemingly unlimited variation shows little organisation on preliminary study (Orton, 1953).

In Singapore, Lim & Yang (1991) noted that a large part of the larvae collection in the Zoological Reference Collection at the National University of Singapore remains to be properly identified and catalogued. With reference to the comprehensive, popular guide book on the amphibian fauna of Peninsular Malaysia (Berry, 1975), Lim & Yang (1991) suggested that a new edition which takes into account descriptions of larval stages would certainly enhance the value of the book.

Berry (1973) admitted that our knowledge of the taxonomy and biology of tadpoles is still incomplete. She also emphasised the need for the collection of larvae and rearing them to adults so as to identify which tadpole develops to which species. Therefore, the purpose of this study was to contribute to a deeper understanding and appreciation of these transient, yet diverse life forms through achievement of the following goals:

1. Compile a comprehensive list of the known tadpole types found in Singapore with diagnostic descriptions based primarily on external morphology.
2. Construct a key to aid in the positive assignment of larval forms to their respective parental species.
3. Compare the different mouth forms among the species with their associated feeding techniques.
4. Cover the developmental process of growth and metamorphosis with emphasis on the significant stages and accompanying changes.

MATERIALS AND METHODS

Specimens previously collected locally and deposited at the Zoological Reference Collection (ZRC), of the Raffles Museum of Biodiversity Research, Department of Biological Sciences, the National University of Singapore, were examined. Additional specimens were obtained from subsequent field expeditions. Where Singapore specimens of particular species were

few or absent, specimens collected from Peninsular Malaysia were referred to, if available.

Specimen acquisition

SAMPLING SITES. - Localities where specimens were sourced for are as follows: (1) Central Catchment Nature Reserve (CCNR), eg. Nee Soon swamp forest, Upper Seletar, MacRitchie forests and Bukit Timah Nature Reserve (BTNR); (Authorisation permit #23 - National Parks Board, Singapore); (2) Areas outside of the Nature Reserves, eg. scrubland, gardens, ponds, drains; (3) Pulau Tekong, an offshore island northeast of the mainland.

In the field, the different aquatic microhabitats surveyed can be categorised into three ecologically unique systems (Heyer et al., 1994). They are (a) Lotic systems - flowing water; eg. forest streams (10 - 100 cm depths), stream banks, shingle areas, riffles; (b) Lentic systems - non-flowing water; eg. side pools of streams, rain pools, trail-side ditches, puddles, ponds, wells; (c) Phytothelmatata (Varga, 1928); eg. tree-holes, log cavities, buttress reservoirs, pitcher plant cups.

SAMPLING PERIOD. - Field surveys spanned the duration between June and December of 1996. Regularity of field trips was on a weekly basis on average, increasing shortly after any rainy spells. However, a study by Berry (1964) revealed that seven species of anurans bred throughout the year in Singapore. This could be attributed to the small annual variation and temperature range of the island, which probably has little or no effect on their reproductive activities.

SAMPLING TECHNIQUES. - Location and verification of tadpole types was by association with observations of (i) individual juveniles/adults, (ii) their characteristic call/s (Arak, 1984; Appendix 1), (iii) amplexing pairs and (iv) deposited egg masses within the vicinity. Equipment used included fine-mesh tray nets and scoop nets of varying sizes. Plastic pipettes (3 ml vol.) were used for extrication of larvae within relatively inaccessible phytothelms, such as pitcher plant cups, without damage to the larvae-containing pitchers. Containment and transportation of specimens were in assorted plastic vials. Water-filled plastic cups and sawn-off bamboo nodes were deployed between ground and waist-levels within forested areas to serve as breeding 'lures'. Such artificial collections of water in forests have been known to be utilised by certain members of the families Bufonidae (Inger, 1960), Rhacophoridae (Inger, 1985) and Microhylidae (Inger & Tan, 1996) as breeding receptacles.

Live specimens

The activity of tadpoles was observed both in the field and in captivity. This was important for recording notes concerning the following aspects: (i) live colouration, patterns, markings; (ii) feeding behaviour; (iii) locomotion; (iv) duration of metamorphosis and any accompanying changes.

REARING TECHNIQUES. - Maintaining live tadpoles in the laboratory entailed regular changes of water to prevent excessive ammonia accumulation. These were housed in plastic aquaria with dead leaves and aquatic vegetation included. Nutritional requirements of the tadpoles were provided for, using both natural and artificial food sources. Of all the species collected, all but one (*Kalophrynus pleurostigma*) were observed to feed regularly. Among these exotrophic forms, three distinct feeding strategies were identified and catered to accordingly: (1) Surface feeders - floating flakes, powdered algal pellets; (2) Suspension feeders - algae-rich water, liquid fish-fry food; (3) Substrate feeders - aquatic plants, yellowed or dead leaves, detritus, boiled lettuce, algal pellets, sinking commercial fish food.

The possibility of developmental rates and sizes of tadpoles in culture departing from that in the wild should be noted and specific series of stages which were reared are indicated in the tables of sizes. In general, metamorphosis may be delayed in captivity due to the reduction of selection pressure. However, in contrast to the artificial maintenance of tadpoles *ex situ*, Heyer et al. (1994) proposed that periodic sampling from the same aquatic habitat may be a more efficient method for ontogenetic studies.

Preserved specimens

FIXATION AND STORAGE. - Collected material comprised ova, embryos, larvae and emergents, of which representative samples were preserved at appropriate intervals throughout their developmental stages (Gosner, 1960). Fixative used was 10% buffered formaldehyde (Heyer et al., 1994). Storage solution previously used was 70% alcohol but 10% buffered formalin is currently preferred, as alcohol is known to liberate epidermal and dermal pigments. Alcohol also causes distortion and considerable shrinkage due to dehydration (Schijfma, 1932; Tyler, 1963). Tyler (1963) found that addition of the salt, cobalt nitrate, to 10% formalin was effective in maintenance of the natural appearance of the specimens. Heyer et al. (1994) and Inger (pers. comm.) also encourage the use of fresh, buffered formalin (10%) for long-term storage so as to minimise loss of structural and cytological detail. All preserved specimens used in this study are deposited at the ZRC.

MORPHOMETRICS AND MOUTHPARTS. - All measurements were taken with sliding verniers (to 0.1 mm). Fundamental parameters of the tadpoles were measured and are defined as follows: (i) Head-body Length (HBL): snout-tip to beginning of vent; (ii) Head-body Height (HBH): taken at mid-body; (iii) Head-body Width (HBW): taken at widest part of head-body; (iv) Tail Length (TL): beginning of vent to tail-tip; (v) Tail Height (TH): highest part of tail; (vi) Total Length (TTL): snout-tip to tail-tip = HBL + TL. Where applicable, such dimensions were used to calculate morphological proportions, e.g. HBL-TL ratios and also for the tabulation of ontogenetic trends, e.g. overall size increments/decrements throughout metamorphosis. For emergents (Stages 46 and later), their snout-vent lengths (SVL) were measured from the snout tip to vent.

Oral disc description is in accordance with the system devised by Altig (1970). Designation of the Labial Tooth Row Formula (LTRF) or denticle counts is determined as such: (a) rows of labial teeth are assigned a number each, beginning with the anterior-most row of each lip; (b) any rows which are discontinuous (divided) will be reflected in parentheses; with the counts for the upper and lower lips separated by a slash mark. For example, the formula denoted as 3(2-3)/3(1) indicates that there are three rows of labial teeth on the upper lip, of which the second and third rows are divided; another three rows of labial teeth on the lower lip, of which only the first row is divided.

RESULTS

A total of 22 larval types are matched with their parental species; two from the family Megophryidae, three from Bufonidae, nine from Ranidae, three from Rhacophoridae and five from Microhylidae. Descriptions for 19 species were accompanied by observation and examination of both live and preserved specimens. Three species are described based on the works of previous authors as specimens were unavailable and none were encountered in the field. A key is constructed for their identification and is focused on externally observable characteristics, e.g. position of spiracle, presence/absence of marginal papillae, position of anal tube.

In the description for each species, their common name/s, geographical distribution and typical habitat of the adults are listed. The known reproductive behaviour of the adults is included. This provides valuable information on typical oviposition sites, approximate clutch sizes, egg diameters. The larval microhabitat/s where tadpoles have been collected is/are also described. Descriptions of external larval morphology include variations in a set of characteristics, namely, (i) head-body shape, (ii) snout form, (iii) relative positions of nostril and eye, (iv) position of spiracle, (v) position of vent, (vi) tail profile.

Morphometrics regularly applied include Head-body Width (HBW) to Head-body Length (HBL) ratios and Tail Length (TL) to Head-body Length (HBL) ratios. Head-body Height (HBH) to Head-body Width (HBW) ratios were occasionally calculated to provide an indication as to the extent of dorso-lateral compression. The range of colour patterns, markings in the live tadpoles are reported. Oral disc descriptions include the presence/absence and arrangement of the following structures: (i) oral papillae, (ii) labial teeth and (iii) jaw sheaths. The orientation of the mouth (dorsal, terminal or ventral) is also noted.

Feeding strategy of the larvae is reported as observed in captivity and in the field. This includes the mode of food acquisition and its diet range. Development of the larvae is documented from both a qualitative and quantitative perspective. Recognisable changes in colour/markings or the appearance/disappearance of various features are recorded. Fluctuations in Head-body Lengths (HBL) and Total Lengths (TTL) of specimens at various larval stages (Stages 26 through 46, with selected intermediate stages) are tabulated for 18 species (Tables 1-19). This provides a basis for subsequent comparisons of growth and size limits. The referred materials are listed according to their assigned catalogue numbers at the ZRC, NUS. Additional remarks are appended where taxonomic, physiological or ecological notes prove to be relevant.

KEY TO THE TADPOLES OF SINGAPORE

Section A: Key to the genera and species in the Families Megophryidae, Bufonidae, Ranidae and Rhacophoridae. All larval characteristics refer to tadpoles in the Stages 26-40 (Gosner, 1960).

- | | |
|--|------------------------------|
| 1. Spiracle median ventral; jaw sheaths absent | Microhylidae (Section B) |
| - Spiracle sinistral; jaw sheaths present | 2 |
| 2. Marginal papillae absent from oral disc | 3 |
| - Marginal papillae present on oral disc | 4 |
| 3. Labial tooth row absent from both lips | 18 |
| - Labial tooth row present on upper lip only | <i>Pelophryne brevipes</i> |
| 4. Oral disc entirely fringed by papillae | <i>Leptobrachium nigrops</i> |
| - Oral disc not entirely fringed by papillae | 5 |
| 5. Vent/anal tube median | 6 |
| - Vent/anal tube dextral | 8 |
| 6. Papillae confined to lateral portions only | 7 |
| - Papillae in staggered, double row across lower lip and crowded at corners of upper lip | <i>Nyctixalus pictus</i> |

7. Labial tooth rows distinct; head-body heavily pigmented ventrally *Bufo melanostictus*
 - Labial tooth rows weak; head-body not pigmented ventrally *Bufo quadriporcatus*
8. Head-body much depressed, slightly longer than broad *Theloderma horridum*
 - Head-body oval 9
9. White spot (iridescent in life) present on snout tip *Polypedates leucomystax*
 - No such marking on snout tip 10
10. Head-body with distinct glandular patches 11
 - Head-body without such patches 12
11. Colour from golden-yellow to cream in life; cephalic markings extensive
 - Purplish-brown in life; cephalic markings reduced *Rana chalconota* form A
Rana chalconota form B
12. Head-body and caudal fins scattered with small, whitish glandules (more conspicuous in younger tadpoles); colour in life reddish-brown, speckled with dark brown patches continuing onto tail fins *Rana glandulosa*
 - Head-body and caudal fins otherwise 13
13. Tail with rusty-red splotches, lightly speckled with black; three white, longitudinal lines on dorsum of more advanced stages *Rana erythraea*
 - Pattern on tail and head-body otherwise 14
14. Tail muscle and fins with dark brown spots; head-body also dark brown *Rana cancrivora*
 - Pattern on tail and head-body otherwise 15
15. Posterior third to half of tail shaded dark grey to black, distinct from anterior portion
 - Pattern on tail otherwise *Rana limnocharis*
 - Pattern on tail otherwise 16
16. Dorsal fin beginning after anterior quarter of tail; tail speckled with black *Rana plicatella*
 - Dorsal fin beginning shortly after junction of head-body and tail; tail with black, vertical bands 17
17. Vertical bands well defined, regularly spaced, usually reaching to edges of dorsal and ventral fins; head-body slightly depressed *Limnonectes malesiana*
 - Vertical bands not as distinct, seldom reaching to edges of dorsal and ventral fins; head-body more cylindrical *Limnonectes blythii*
18. Mouth formed into funnel by dorsally-directed, expandable lips *Megophrys nasuta*
 - Mouth small, tubular, terminal; lower lip U-shaped *Occidozyga laevis*

Section B: Key to the genera and species in the Family Microhylidae.

1. Mouth terminal (anteriorly directed) 2
 - Mouth dorso-terminal (dorsally directed) 4
2. Tail with terminal filament *Microhyla butleri*
 - Tail without terminal filament 3
3. Head-body flattened above; spiracle opens through transparent sheath *Kaloula pulchra*
 - Head-body not flattened; spiracle without flap, opens beneath centre of intestinal coil *Kalophrynus pleurostigma*
4. Lower lip not expanded; fins crossed by dark, vertical band at posterior third of tail *Microhyla borneensis*
 - Lower lip expanded; fins without such banding *Microhyla heymonsi*

FAMILY MEGOPHYRIDAE

This Family is represented by two species in Singapore, namely *Leptobrachium nigrops* and *Megophrys nasuta*. Although adults of both species are largely terrestrial and appear to have similar modes of life, their larvae exhibit a pronounced divergence in niche. The different larval forms of these two species are described.

Leptobrachium nigrops Berry & Hendrickson
(Fig. 1, Table 1)

Vernacular names. - Black-eyed Ground Toad, Malay- Kodok Tanah Matah Hitam (Kiew, 1984b); Black-eyed Litter Frog (Lim & Lim, 1992).

Geographical Distribution. - Borneo, Malay Peninsula, Singapore (Inger, 1966).

Typical Habitats. - Well-drained primary, secondary, and swamp forests. Usually observed on forest floor, along jungle footpaths, along banks of small streams, seepage areas (Berry, 1975). Stable populations occur in CCNR and BTNR for Singapore.

Reproductive Strategy. - Males considerably smaller than females (1/2 to 2/3 SVL). Amplexus is inguinal. Exact site of oviposition is uncertain. Berry (1964) observed a possible month to month correlation of reproductive ripeness with 'drought' or periods of dry spells during a study at the Nee Soon Area.

Larval Microhabitats. - Various stages (Stage 26-38) of larvae were observed and collected from still waters at seepage areas. Tadpoles were also found in relatively fast-flowing, small streams, especially along stretches with dense aquatic vegetation. The overgrown banks are usually favoured hiding places. Berry & Hendrickson (1963) collected specimens from among growths of *Fimbristylis* sp. and *Eleocharis* sp. in forest streams in Singapore.

Larval Morphology. - Head-body elongate and slender, HBL 1.81-2.23 times HBW; nostrils dorsally located, midway between snout tip and eyes; eyes dorsal, not visible from below; inter-orbital distance 1.94-2.28 times inter-narial distance; spiracle sinistral, nearer the eye than vent; vent dextral, opening at margin of ventral fin. Tail bluntly pointed; dorsal fin slightly deeper than ventral, not extending onto back of head-body; TL 1.26-1.63 times HBL.

Colour/Markings. - (In life) Uniform black on dorsum and lighter shade on venters; caudal fins dusky; no observable markings in all developmental stages; lateral line pores distinct.

Oral Disc. - Mouth sub-terminal, width 0.39-0.48 of HBW, divided into indistinct anterior, posterior, and lateral lobes, bordered entirely by a single marginal row of large, conical papillae; infra-marginal papillae not observed; jaw sheaths heavy, strongly arched and entirely black, edges coarsely serrated.

LTRF. - 3(1-3)/4(1-3).

Feeding Strategy. - As evidenced from its large size, stream-lined head-body form and powerful tail, this tadpole is capable of propelling itself against relatively strong currents, swimming upstream to survey different feeding sites. A generalised bottom-feeder, it

Table 1. Developmental changes in Head-body Length (HBL) and Total Length (TTL) of larval *Leptobrachium nigrops*. Stages 38-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
25	20	3.9-10.8	10.4-24.1
26	9	11.9-15.8	29.7-38.0
27	4	10.2-16.3	26.8-40.2
30	1	14.5	36.5
34	2	16.0-19.4	38.0-43.1
37	3	19.5-21.5	41.4-44.8
38	1	20.7	46.6
40	2	20.9-21.9	50.0-53.4
42	2	17.7-18.8	38.9-40.5
45	1	18.3	20.5
46	1		SVL=17.5mm

consumes both living and dead plant matter, together with detritus along the stream banks. Larvae in the field were observed to be active both by day and night.

Development. - The youngest larvae (Stages 25, 26) collected (TTL 10-12 mm) were translucent-grey and developing lungs were visible from the dorsum. Their colour becomes increasingly darker with age. Total time required for the full developmental period is uncertain. However, judging from the relatively permanent water bodies it inhabits and the great biomass increments required from pre-limb to emergent stages, the entire larval stage could span from two to three months or longer.

In captivity, late four-limbed larvae (Stages 42, 43) were observed to take up to one week for total tail resorption. This is the longest time observed for the complete disappearance of tail among the Singapore larvae studied. A likely explanation is the relatively large biomass involved during cellular re-organisation of caudal musculature. New emergents (Stage 46 onwards) are entirely black on the dorsum and dermal reticulations only appear after the first week from metamorphosis. The eye remains entirely black throughout adulthood.

Material examined. - (n = 46); ZRC.1.1794-1800, ZRC.1.2222, ZRC.1.1544, ZRC.1.3403, ZRC.1.3404, ZRC.1.3405, ZRC.1.3406, ZRC.1.3407, ZRC.1.3408.

Additional Remarks. - Berry (1972) pointed out that Bornean larvae of '*Leptobrachium nigrops*' (Inger, 1966) do not agree with the Peninsular Malaysian (and Singapore) forms. Differing characteristics of the Bornean forms include: (i) a rounded tail tip, (ii) pale-yellowish colouration, with gold chromatophores and black bands present, (iii) dissimilar labial tooth counts. She proposed that the 'tentative identification' of the tadpoles by Inger (1966) as belonging to '*L. nigrops*' be re-assigned the parental species of *L. pelecyptoides* Boulenger instead. However, Inger (1983, 1985) continued to describe the Sarawak larval material as belonging to *L. nigrops* Berry & Hendrickson, but agreed that they differed markedly from Malayan larvae assigned to *L. nigrops* in terms of head-body shape, colouration, LTRF and that association with adults was not certain (Inger, 1985). Berry's proposal remains doubtful due to the differences between the larvae of *Leptobrachium* and *Leptolalax* (Inger, 1983).

Megophrys nasuta (Schlegel)

(Fig. 2, Table 2)

Vernacular Names. - Horned Frog (Yong, 1976); Nose-horned Frog (Hendrickson, 1966); Common Horned Toad, *Malay-* Kodok Tanduk Biasa (Kiew, 1984b); Malayan Horned Frog or Horned Toad (Lim & Lim, 1992); Asian Horned Toad (Mattison, 1993); Asian Horned Frog (Walls, 1995).

Geographical Distribution. - Brunei, Sabah, Sarawak, Kalimantan, Sumatra, Java, Philippines, southern half of Malay Peninsula, Singapore (Inger, 1966; Das, 1995; Lim & Lim, 1992).

Typical Habitats. - Primary forests, usually on forest floor beside fast-flowing streams. Excellent camouflage among dead leaves. Occasionally found well away from water. Found from lowlands up to montane altitudes of 2200 m a.s.l. (Inger, 1966). In Singapore, confined to CCNR and BTNR.

Reproductive Strategy. - Eggs, numbering up to 700, are deposited in gelatinous packets attached to the roof of low 'caves' formed by rock, log or bark. The cave roof is usually damp and just above water level. Fertilised ova hatch in 10 to 12 days and larvae drop or slide into the water upon hatching (Mattison, 1993; Walls, 1995).

Larval Microhabitats. - Usually collected from streams of moderate to strong currents, where larvae exhibit the tendency to 'beach' themselves onto sandbanks on either side of the stream. Also regularly observed in the slow, backwaters of small streams. Habitats often sandy to silty with accumulation of dead leaves and other plant material on the bottom. Plankton, which forms the diet of these larvae are apparently more abundant in these portions than where the current is faster (Inger, 1966).

Larval Morphology. - Head-body elongate to ellipsoidal, cross-section almost circular, HBW 0.55-0.56 of HBL; eyes located laterally, visible from ventral aspect; nares open, rim projecting mid-dorsally; spiracle sinistral, low on left side, tube free from head-body at tip, snout-spiracle 0.51-0.54 of HBL; anal tube median, unattached to ventral fin. Tail slender, tapering gradually from centre to slightly rounded tip; tail muscle strong, deeper than caudal fins except near tip; fins originating at root of tail, margins sub-parallel, ventral fin not as deep as dorsal; TL 1.85-2.15 of HBL.

Colour/Markings. - (In life) Head-body and tail muscle overall dark brown; throat with much darker (almost black) pigmentation fading gradually towards posterior; thin yellow/cream band running from lateral extremities of funnel mouth through the eyes on to anterior half of tail; tail scattered with dark spots on posterior half of tail; margin of funnel mouth and both fins edged with orange/red.

Oral Disc. - Mouth dorso-terminal. Lips expanded into funnel as wide as head-body when fully opened; anterior margin (edge of raised lower lip) sinuate, lateral corners pointed; lower lip deeper than upper lip, lips without denticles but possessing numerous short, low ridges (corrugations) radiating from the centre; marginal papillae absent but lower lip with low, rounded infra-marginal papillae; both jaw sheaths weak, edged with long, fine, pointed serrae.

Table 2. Developmental changes in HBL and TTL of larval *Megophrys nasuta*. Stages 25-32 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
25	6	5.4-8.3	15.9-24.5
26	1	10.6	29.5
27	7	10.7-10.9	30.3-35.8
28	2	12.9-13.0	35.4-37.3
32	1	13.5	40.0
36	5	13.1-14.8	38.8-41.5
38	1	15.7	42.7
42	1	14.8	43.6
46	1		SVL=14.5mm

LTRF. - Not Applicable (N.A.)

Feeding Strategy. - In the field, individuals were observed to feed in a position almost parallel to the surface of the water. A similar position was adopted by tadpoles in captivity if shallow water (<1 cm) was provided. However, if the water was deeper, feeding tadpoles would still 'hang' perpendicular from the surface or any other angle depending on the water level. Its funnel mouth, the most peculiar part of the larval anatomy, is well adapted for obtaining food from the water surface. Altig & Johnston (1989) regarded such mouth types as being 'umbelliform'.

Observations of its feeding behaviour are comparable with that described in Smith, 1926. In captivity, the larvae responded eagerly to powdered algal pellets sprinkled over the water. Smith (1926) obtained similar reactions from his tadpoles by using 'fragments of vegetable dust'. Once at the water surface, the lips attain their fully expanded form which is flushed with the surface along the margin. The tadpole then begins to imbibe mouthfuls of water at a rapid pace, creating a shallow meniscus inside its mouth. The corrugations of the mouth serve as filters for food particles. Larger pieces of floating debris are prevented from entry and only finer particles are ingested. In the wild, its diet consists mainly of surface film plankton (Yong, 1974).

As previously noted by Annandale (1903), the mouth of these tadpoles is capable of assuming two distinct forms: (i) the rhomboidal, expanded 'float' as described earlier when feeding and (ii) a collapsed, upward-curving form which is adopted when the tadpole is at rest on the bottom and not feeding.

Development. - After emerging from the egg membranes and entering the water, the young larvae are able to swim against the current almost immediately. The yolk sac is prominent and its feeding apparatus has not fully developed yet. By the first week, the lateral 'horns' of the upturned funnel mouth would have enlarged significantly and most of the yolk absorbed by the larva. Newly hatched larvae are dark grey in colour without any noticeable markings. By the second week, the brown colouration on the head-body and tail has appeared. In the later stages (Stages 36-42), the characteristic pair of dorsal, longitudinal dermal ridges begin to appear, as reported in Inger, 1985. From Stage 42 onwards, the white axillary glands are noticeable on the venters. In the emergent, the dermal projection over the eyelids and snout are still not pronounced yet.

Material examined. - (n = 25); ZRC.1.1543, ZRC.1.3235-3239, ZRC.1.1522-1523, ZRC.1.3338, ZRC.1.3409, ZRC.1.3410.

FAMILY BUFONIDAE

The larval characteristics of three bufonid species are highlighted, with that of *Bufo quadriporcatus* possibly being described for the first time. The authors did not observe, nor rear the larvae of *Pelophryne brevipes*.

Bufo melanostictus Schneider

(Fig. 3, Table 3)

Vernacular Names. - "Indian Toad", "Javanese Toad", "Formosan Toad" (Sit, 1968); Common Toad, Malay- Kodok Paru Biasa (Kiew, 1984b); Asian Common Toad (Karsen et al., 1986); Black-spined Toad (Mattison, 1993); Asian Toad (Lim & Lim, 1992).

Geographical Distribution. - India, Sri Lanka, Himalayas, South China, Hainan, Hong Kong, Sumatra, Java, Bali, Philippines, Sarawak, Kalimantan, Malay Peninsula, Singapore (Kampen, 1923; Bourret, 1941; Kirtisinghe, 1957; Inger, 1966; Berry, 1975; Karsen et al., 1986; Lim & Lim, 1992).

Typical Habitats. - Cosmopolitan inhabitant of disturbed forest to agricultural and urban areas (Lim & Lim, 1992). In Singapore, well distributed island-wide and on offshore islands.

Reproductive Strategy. - Amplexus is axillary. Eggs are released as a single file in each of the two mucilaginous strings, often laid in stagnant puddles, pools or drains. Water from clear to muddy. In captivity, a coupling pair of the adults produced a large mass (>700) of eggs (1.0-1.5 mm diameter) in shallow water (1.5 cm depth). Blair (1972) regarded this strategy of laying large quantities of small eggs as a 'primitive' trait and an adaptation to egg-laying in conditions where the mortality of the tadpoles is usually high. Apart from using freshwater bodies, *Bufo melanostictus* has also been reported to breed in brackish water (Kirtisinghe, 1957).

Larval Microhabitats. - Tadpoles are usually found in temporary to semi-permanent, lentic waters of rain-filled pools or choked drains. Larvae have also been encountered in drains within tidal influence (Lim & Lim, 1992) and even a lagoon (Kirtisinghe, 1957). Strahan (1957) found that tadpoles of *B. melanostictus* can survive salinities of up to 0.75%, though not in the first days of life.

Larval Morphology. - Head-body ellipsoidal, HBW 0.56-0.67 of HBL; snout rounded; nostrils dorsal, much nearer to eye than tip of snout; eyes superior, inter-orbital width about twice inter-narial and about equal to oral-disc width; spiracle sinistral, directed posteriorly, visible from above and below, nearer to vent than to snout tip; vent median. Tail with broadly rounded tip; both crests nearly equal in depth, deeper than tail muscle for posterior 3/4 of tail; dorsal fin slightly convex and not extending onto back; TL 1.05-1.21 of HBL.

Colour/Markings. - (In life) Dorsum and sides jet-black to blackish-brown, evenly distributed with fine, golden-yellow iridocytes; venter grey, pigmented; tail musculature same colour as head-body; both fins clear to pale grey.

Table 3. Developmental changes in HBL and TTL of larval *Bufo melanostictus*. Stages 25-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
25	10	3.1-3.6	8.1-9.3
27	5	4.9-5.8	11.7-12.5
30	5	6.1-7.7	13.2-14.7
32	3	6.0-7.9	12.8-15.3
34	4	6.3-8.2	13.3-15.6
36	5	7.2-10.0	16.5-21.4
38	7	7.7-10.3	15.8-21.2
41	4	7.9-8.1	15.2-20.2
42	2	6.8-7.8	16.5-18.2
44	2	7.6-7.7	14.9-16.9
45	1	7.8	8.9
46	3	SVL=7.9-9.3mm	

Oral Disc. - Mouth ventral, subterminal; lips with papillae confined to lateral margins; jaw sheaths smooth and white, black at edges only.

LTRF. - 2(2)/3; second labial tooth row on upper lip nearly as long as first row, narrowly interrupted in the middle; those of lower lip almost equal in length, with the innermost row being the longest and the outermost row the shortest.

Feeding Strategy. - In captivity, the larvae of this toad were indiscriminate feeders, consuming all manner of food offered (both natural and artificial) rapidly. These tadpoles were observed to be highly adaptable in their sourcing for food, exploring all levels of the water column (bottom, mid-water, surface) and devouring any available food at each of these levels.

Development. - Sit & Kanagasuntheram (1973) provided an excellent account of the chronological sequence of development together with photographic detail. They also described the developmental changes occurring in the nervous and digestive systems. Time-size comparisons were made for various stages with two other anuran species, namely *Rana pipiens* and *Xenopus laevis*.

Material examined. - (n = 51); ZRC.1.1369-1375, ZRC.1.2251-2620, ZRC.1.2878-2891, ZRC.1.3411, ZRC.1.3412.

Bufo quadriporcatus Boulenger
(Fig. 4, Table 4)

Vernacular Names. - Four-ridged Toad, Malay- Kodok Jambul Empat (Kiew, 1984b); Swamp Toad (Inger & Tan, 1996).

Geographical Distribution. - Sabah, Sarawak, Kalimantan, Sumatra, Malay Peninsula, Singapore (Inger, 1966; Lim & Lim, 1992).

Typical Habitats. - Primary forest inhabitant, found on forest floor or near small streams. Occurs in peat swamp forests as well (Berry, 1975; Inger & Tan, 1996). In Singapore, occurs within CCNR.

Reproductive Strategy. - Inger and Tan (1996) reported that eggs are deposited in small ponds in forest. This was verified when a pair in axillary amplexus was sighted in a forest pool at late morning (16 June, 1996). The male was about 2/3 the size of the larger female. This pool was approximately two metres from the nearest stream, and measured 150 cm long by 70 cm wide and not more than 10 cm at its deepest. The water was clear, with abundant leaf litter. Long, continuous strands of eggs (1.3-1.5 mm diameter) had already been laid and were distributed over an area about 50 by 50 cm inside the pool. This indicated that the pair might have been moving about actively while mating. When first sighted, the pair had both their heads above the water but when alarmed, quickly submerged themselves below the surface, remaining motionless. About five minutes later, it began to rain heavily. Hence, this species may be able to detect any forthcoming rains or periods of wet weather and increase its breeding activity accordingly, as such forest pools are highly ephemeral and can only be supplied with reasonable amounts of water through such downpours and/or from adjacent, overflowing streams.

Larval Microhabitats. - Eggs, together with larvae at various stages were found and collected from similar forest pools with clear to slightly turbid waters and heavy leaf litter beds. Other anuran larvae known to occur together with this species include those of *Occidozyga laevis* and *Rana chalconota*. Fishes inhabiting such sites include *Betta pugnax* and *Monopterus albus*.

Larval Morphology. - Head-body ovoid, HBW 0.57-0.68 of HBL; slightly depressed, HBH 0.58-0.73 of HBW; widest region of head-body just behind eyes; snout broadly rounded; nostrils and eyes dorsal, nostrils nearer to eye than tip of snout; inter-orbital about twice inter-narial and about the same as mouth width; spiracle sinistral, low on the left side, visible from dorsal and ventral aspects, slightly nearer to vent than snout tip; anal tube median. Tail tapering gradually towards rounded tip; tail musculature weak, shallower than fin height for posterior 3/4 of tail; dorsal and ventral fins approximately equal in height, margins sub-parallel, highest point at anterior quarter of tail; TL 1.25-1.45 of HBL.

Colour/Markings. - (In life) Head-body and tail muscle a uniform pinkish- to reddish-brown; blackish eyes prominent from dorsal aspect; venters translucent and unpigmented; dorsal and ventral fins clear.

Oral Disc. - Mouth ventral, sub-terminal; marginal papillae at lateral portions only; jaw sheaths serrated, edged with black.

LTRF. - 2(2)/3; second row on upper lip with narrow gap, sometimes overlapping at the centre; labial teeth and jaw sheath edges significantly worn off in advanced stages.

Feeding Strategy. - Larvae reared in captivity subsisted well on a diet of flaccid, decaying leaves obtained from the same pools in which the larvae were collected. When feeding, the larvae grazed over the epidermal layers of the brown leaves with rapid, rasping movements of the upper and lower labia.

Table 4. Developmental changes in HBL and TTL of larval *Bufo quadriporcatus*. Stages 26-32, 40-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
26	5	3.9-4.5	9.4-10.5
28	4	4.2-6.0	10.2-14.4
30	1	6.1	15.2
32	2	6.7-6.9	14.9-15.1
33	4	5.9-6.8	13.0-15.2
34	1	6.8	16.4
35	3	7.1-7.5	16.2-16.7
36	3	7.8-8.9	16.9-19.5
38	2	8.1-8.3	18.4-19.1
40	3	7.7-8.5	17.3-18.5
43	2	6.9-7.3	12.3-13.0
46	4	SVL=6.4-7.5mm	

Development. - Pigmented ova collected from the field successfully completed embryological development by the twelfth day but were not reared to metamorphosis. Later stages were also collected from similar microhabitats and a few individuals proceeded to metamorphose in captivity. In the emergents, the cephalic ridges are not developed yet, but cross-bands on the limbs are already visible.

Material examined. - (n = 34); ZRC.1.3413, ZRC.1.3414, ZRC.1.3415, ZRC.1.3416, ZRC.1.3417, ZRC.1.3418, ZRC.1.3419, ZRC.1.3420, ZRC.1.3421, ZRC.1.3422, ZRC.1.3423, ZRC.1.3424.

Pelophryne brevipes (Peters)

Vernacular Names. - Dwarf Toad (Hendrickson, 1966); Short-legged Toadlet, Malay-Kodok Kaki Pendek (Kiew, 1984b); Saint Andrew's Cross Toadlet (Lim & Lim, 1992).

Geographical Distribution. - Brunei, Sabah, Sarawak, Kalimantan, Mindanao, Sumatra, Mentawai Islands, Natuna Islands, Aur Island, Tioman Island, Malay Peninsula, Singapore (Hendrickson, 1966; Inger, 1966; Das, 1995).

Typical Habitats. - Primary forest inhabitant, usually found on low vegetation, e.g. leaves of saplings (Das, 1995), tree trunks or bases (Lim, 1990) or the forest floor (Inger, 1960). This diminutive toad is restricted to BTNR and is locally endangered (Lim, 1994).

Reproductive Strategy. - Preference for using small, rain-filled depressions as sites of oviposition, exhibiting 'increasing terrestriality' as compared to the other bufonids (Inger, 1960). Denzer (1994) observed that this species occupies an arboreal niche. Calls of this toad were localised in the trees after downpours but its call was not described. In 1991, Denzer encountered a pair of adults at the foothills (100 m) of Gunong Santubong (Sarawak) in a tree hole 1.5 m above the ground. The tree hole was 6 cm wide, 10-12 cm deep and found to contain about 20 ml of water. A batch of 26, ivory-coloured eggs were attached



Fig. 1. Lateral (a) and dorsal (b) aspects of *Leptobrachium nigrops* larva (Stage 26).

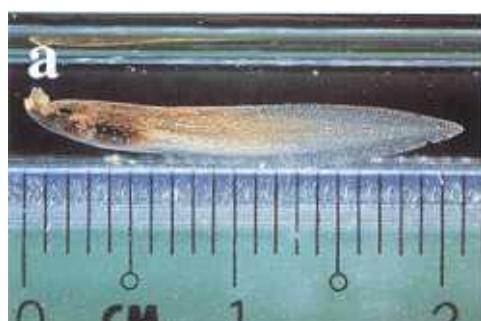


Fig. 2. Lateral (a) and dorsal (b) aspects of *Megophrys nasuta* larva (Stage 26).



Fig. 3. Lateral (a) and dorsal (b) aspects of *Bufo melanostictus* larva (Stage 26).

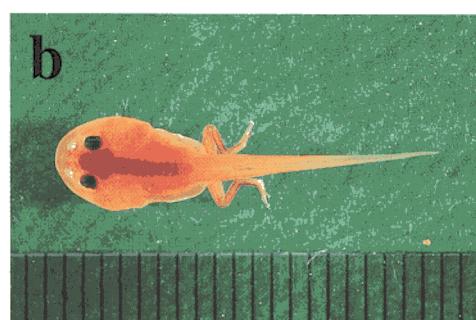


Fig. 4. Lateral (a) and dorsal (b) aspects of *Bufo quadriporcatus* larva (Stage 39).

to the back of the tree hole. Adults were collected and in captivity, oviposition occurred 2-3 times a year and the average clutch size was 16. Eggs were laid in small pools of water or water-filled bamboo segments (simulating tree holes).

Larval Microhabitats. - Inger (1960) first described five larvae collected from a 'deeply shaded, broken bottle' at 3000 ft. on Mount McKinley, Davao Province, Mindanao. Alcala and Brown (1982) collected five groups of ova and larvae from Dapitan Peak, Zamboanga Peninsula, Philippines. All were found in the leaf axils of screw pines (*Pandanus* sp.). The volume in such reservoirs ranged from 15-80 ml.

Larval Morphology. - (After Inger, 1985) Head-body ovoid, widest part at centre of visceral mass; gut with at most two coils; HBW 0.6 of HBL; eyes dorsolateral, eyeball 0.11 of HBL; nostril apparently not open; spiracle not tubular, a simple concave slit near left ventro-lateral border, slit just posterior to level of developing fore limb, snout-spiracle distance 0.46 of HBL; vent median, attached to ventral fin, opening not evident. Tail narrow, margins straight, tapering in distal fourth to broadly rounded tip; fins originating at end of head-body; TL 1.5 of HBL, HBL 4.2 mm, HBW 2.4 mm, TL 6.3 mm, TTL 10.5 mm.

Colour/Markings. - (In preservative) Pale, straw coloured, head-body and root of caudal muscle dusted with melanophores; fins unpigmented. Stage 45 possessing a cream band from above axilla to below front of eye. Capillary network on tail fins distinct in specimens observed by Alcala and Brown (1982) but not so in specimens examined by Inger (1985).

Oral Disc. - Mouth ventral, sub-terminal and circular; width 0.36 of HBW; lips wide, without lateral indentations, entire margin with very short fringe; upper lip adorned with single row of 7-26 spaced denticles, none on lower lip; jaw sheaths weak, darker at margins and finely serrated.

LTRF. - N.A.

Feeding Strategy. - Inger (1960) proposed that the tadpole subsists entirely on its yolk. This is suggested by the feebly coiled gut in larvae of limb bud stages. Also indicating such a mode of nutrition are its degenerate mouthparts and large size of the ova. This unique strategy was subsequently verified by Alcala and Brown (1982). A similar strategy is observed in the diminutive larvae of *Kalophryne pleurostigma* (Microhylidae).

Development. - Inger (1960) successfully reared four larvae until eruption of their fore limbs. SVL of the emergents ranged from 4.6-4.8 mm. Their hands and feet resembled the characteristic form of *Pelophryne* and their dorsum displayed the distinctive 'hourglass figure'. Denzer (1994) recorded that larvae exhibited muscular response and were able to swim after four days. Complete development required 30-40 days and was dependant on water temperature.

Material examined. - None.

FAMILY RANIDAE

This is the largest anuran family in Singapore, with 11 species recorded so far. The larval types of nine species are described, while those of *Rana baramica* and *Limnonectes*

paramacrodon remain unknown. Of the nine known species, two representative body forms are recognised. Based on the system of morphological guilds (Altig & Johnston, 1989), the larvae of *Occidozyga laevis* belong to the 'lentic-macrophagous' type while those of the other eight ranids can be classified as the 'lentic-benthic' type. Nomenclatural changes in this Family as proposed by Dubois (1987, 1992) were recently reviewed by Inger (1996), whose opinions will be adhered to in this paper.

Occidozyga laevis (Günther)
(Fig. 5; Table 5)

Vernacular Names. - Common Puddle Frog, Malay- Katak Limbah Biasa (Kiew, 1984b); Puddle Frog, Yellow-bellied Frog (Lim & Lim, 1992); Yellow-bellied Mud Frog (Inger & Stuebing, 1996).

Geographical Distribution. - Brunei, Sabah, Sarawak, Kalimantan, Luzon, Negros, Mindanao, Malay Peninsula to Flores, Sulawesi, Bali, Singapore (Inger, 1966; Lim & Lim, 1992; Whitten & McCarthy, 1993). Altitudinal range from sea-level to over 1000 metres (Inger, 1966).

Typical Habitats. - Primarily aquatic inhabitant of undisturbed forests or clearings, usually in still, shallow pools (Berry, 1975). Occasionally in forest streams (Lim & Lim, 1992). Main populations in Singapore located within CCNR.

Reproductive Strategy. - As observed in the field, in captivity and reported by Alcala (1962), amplexus in adults is axillary. Eggs of this species were not encountered in the field but Alcala (1962) suggested that 'the few eggs in a clutch may be lost from view when submerged at the bottom'. Clutch size was estimated to be between 100 and 140 eggs (Alcala, 1962).

Larval Microhabitats. - Local specimens were collected in low numbers (despite frequent sightings of the adults) from forest pools and at the banks of streams. Heyer (1973) noted previously that the tadpoles 'were never abundant'.

Larval Morphology. - Head-body depressed, dorsal surface flattened, HBL 2.36-2.54 of HBH, HBL 1.38-1.78 of HBW, HBH 0.33-0.50 of HBW; snout tip pointed; nostrils nearer eye than tip of snout; eyes dorso-lateral, inter-orbital twice inter-narial distance; spiracle sinistral, in form of long, protrusive tube directed posteriorly, much closer to vent than snout tip; anus median, opening via a short tube. Tail with pointed tip, TH slightly greater than HBH; caudal fins shallower than muscle at its deepest points, dorsal fin low and originating behind base of tail, ventral fin much lower than dorsal; TL 1.88-1.91 of HBL.

Colour/Markings. - (In life) Olive-brown above, with light-golden and dark variegations; a distinct, dark band through the eye to snout tip; a creamy-white patch on dorsal region of snout; venter densely speckled with dark and light pigments.

Oral Disc. - Mouth small, tubular, terminal in position; oral papillae and labial teeth entirely absent, but upper and lower jaw sheaths present; both jaw sheaths serrated and edged with black; lower lip consisting of a 'U'-shaped, protrusible structure which is interrupted dorsally; upper lip much smaller, fitting into dorsal gap of the 'U'.

LTRF. - N.A.

Table 5. Developmental changes in HBL and TTL of larval *Occidozyga laevis*. Stages 42-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
29	1	2.1	6.8
31	1	3.7	10.5
40	1	6.5	23.2
42	1	6.4	18.7
44	1	6.7	10.9
46	1		SVL=7.6mm

Feeding Strategy. - This species has been described as a carnivorous feeder, preying on mosquito larvae and even other small tadpoles (Smith, 1916c). In a comparative study of larval gut lengths, Heyer (1973) found those of *O. laevis* to be the shortest among 17 species examined. This report seems to confirm the report by Smith (1916c), as shorter guts indicate a primarily carnivorous diet. However, Heyer (1973) failed to find any remains of larval mosquitoes or other arthropods among the gut contents of *O. laevis* tadpoles, but indications of a herbivorous diet instead. Thus, it was suggested that this species must be facultatively carnivorous and able to operate as omnivores when necessary.

Development. - Heyer (1973) estimated the length of larval period to be around 27 days from time of egg deposition. Early specimens (Stages 29-31) were reared unsuccessfully in captivity, but a two-limbed larva (Stage 40) erupted its fore limbs after 12 days. Its tail was entirely resorbed after two days. Emergents clearly exhibit the adult characteristics, such as dilated, oval toe discs and fully webbed hind feet.

Material examined. - (n = 6); ZRC.1.3370, ZRC.1. 3371.

Additional Remarks. - In captivity, the larvae usually remained motionless at the bottom, as described by Smith (1916c), Alcala (1962) and Heyer (1973). Smith (1916c) remarked that the larvae 'have a habit of sprawling out their hind-limbs in an ungainly manner, and of using them as a means of locomotion, preferring to crawl slowly about by their aid, rather than use their tails.' Heyer (1973) described its movement as inching along the bottom 'in a very methodical fashion.'

Limnonectes blythii (Boulenger) (Fig. 6; Table 6)

Vernacular Names. - Giant Frog (Yong, 1978); Malayan Giant Frog, Blyth's Frog (Lim & Lim, 1992); Malay- Katak Demam (Kiew, 1984b).

Geographical Distribution. - Brunei, Sabah, Sarawak, Kalimantan, Sumatra, Peninsular Malaysia, Singapore (Inger, 1966; Lim & Lim, 1992; Das, 1995).

Typical Habitats. - Primary forest streams and banks. Stream types may vary in size, depth and clarity of water. Also found in well-shaded, secondary forest streams (Inger, 1966). Healthy populations occur in both BTNR and CCNR.

Table 6. Developmental changes in HBL and TTL of larval *Limnonectes blythii*. Stages 41-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
28	5	5.0-6.5	15.8-19.3
36	1	7.0	22.3
37	1	7.9	22.9
41	1	9.2	24.2
43	1	8.5	22.4
46	1		SVL=8.7mm

Reproductive Strategy. - A pair was observed in amplexus at midstream during a night survey. The male was noticeably larger than the female and his forelimbs were encircled around her at the axillary region. Both were in a crater-shaped depression about 30 cm in diameter and 2 cm deep. Upon closer inspection, both adults leapt away. No ova were found in the depression. This sighting was very similar to previous descriptions of nest-building behaviour in *Limnonectes blythii* (Inger, 1966; Dring, 1979; Inger & Stuebing, 1989; Emerson, 1992). Emerson (1992) further described, in detail, the alternating bouts of low calling, circling round the crater, kicking and burrowing with hind feet and then pausing. Subsequently, the unpigmented eggs were found interspersed among the pebbles within the crater. Matsui (1995) also recorded calls produced by adults of this apparently 'voiceless' species.

Larval Microhabitats. - Larvae were collected in forest pools isolated from the main current of the adjacent stream by sand or gravel bars. Such pools were often cluttered with dead leaves. Hatching larvae could wriggle through the shallow gravel layer and reach these protected pools (Inger, 1966).

Larval Morphology. - Head-body oval, HBW 0.53-0.57 of HBL, slightly flattened at the back, HBW 1.23-1.46 of HBH, rounded below; eyes dorso-lateral, not visible from below; nostrils dorsal, open, midway between eye and snout-tip, inter-narial smaller than inter-orbital; spiracle sinistral, ventro-lateral, midway between vent and snout-tip; vent dextral, attached to ventral fin. Tail lanceolate, both margins weakly convex, tapering gradually to narrow tip; TL 1.70-2.20 of HBL; caudal muscle deeper than either fin in proximal half of tail, dorsal fin originating behind end of head-body, deeper than ventral fin except towards tip.

Colour/Markings. - (In life) Head-body olive-brown mottled with black, irregular, indistinct black bands/patches on tail, seldom extending onto fins; venters translucent, unpigmented; dark bars radiating from eye.

Oral Disc. - Mouth ventral, sub-terminal, width 0.31-0.36 of HBW; upper lip with papillae at the lateral corners only; lower lip with single, staggered row of papillae, narrow median gap in centre; jaw sheaths serrated, edged with black, upper jaw sheath with wide, weak median convexity, lateral margins curving towards the posterior rather abruptly.

LTRF. - 1/3(1-2), n = 5; extreme distal row of lower lip 1/3-1/2 length of middle row.

Feeding Strategy. - The tadpoles are known to graze over the surfaces of dead leaves and larval intestinal smears have revealed that their diet consists of diatoms, green and blue-green algae, fragments of higher plant epithelium (Inger, 1966).

Development. - A complete developmental series is not available. However, diagnostic features of metamorphosing tadpoles include fully-webbed hind feet, relatively short fourth toes and flap of skin on outer edge of the fifth toes (Inger, 1966). A dark, canthal streak is clearly visible in the new emergents.

Material examined. - (n = 10); ZRC.I.1545, ZRC.I.3358, ZRC.I.3359, ZRC.I.3360, ZRC.I.3361.

***Limnonectes malesiana* (Kiew)**

(Fig. 7; Table 7)

Vernacular Names. - Malesian Frog (Lim & Lim, 1992); Malaysian Frog, Malay- Katak Malaysia (Kiew, 1984b).

Geographical Distribution. - Borneo, Sumatra, Java, Natunas, Peninsular Malaysia, Singapore (Kiew, 1984a). Inger (1985) noted that larvae have not been reported from Borneo.

Typical Habitats. - Normally associated with seepage areas and small streams (< 2 m wide) of forest, belukar and rubber plantations (Kiew, 1984a). Regularly encountered in BTNR and CCNR in Singapore.

Reproductive Strategy. - Kiew (1984a) describes the eggs as being laid individually in a loose cluster in still waters (< 3 cm depth). The thick jelly coating of the eggs readily pick up adjacent sand particles and debris, thereby acquiring camouflage and anchorage.

Larval Microhabitats. - Larvae were collected in both non-flowing waters and slow-flowing streams. Waters were clear to slightly murky.

Larval Morphology. - Head-body ovoid, HBW 0.51-0.59 of HBL; slightly depressed, HBW 0.57-1.50 of HBH; eyes and nostrils dorso-lateral, inter-orbital distance twice inter-narial, nostrils midway between eye and snout tip; spiracle sinistral, opening midway between snout tip and vent; anal tube is clearly dextral, as observed in all the specimens, and *not* median, as reported by Kiew (1984a). Inger (1985) also pointed out that 'the position of the anal tube by Kiew is unusual for a ranid tadpole not living in swift water'. The tail possesses well-developed musculature, with margins tapering gradually to a narrow tip, TL 1.70-1.90 of HBL; dorsal fin deepest at mid-point to two thirds from head-body, slightly deeper than ventral fin.

Colour/Markings. - (In life) Earlier stages (Stages 22-24) characterised by four dorso-lateral patches on head-body (Kiew, 1984a). In later stages, head-body golden-brown with brownish-black pigments; dark bars radiating from eye; one behind, one below and one toward snout tip; brown inter-orbital bar and 'W'-shaped marking on pectoral region visible in advanced stages (Stage 42 onwards); venter white to pale-yellow and translucent, throat region increasingly pigmented with black (Stage 27 onwards).

Table 7. Developmental changes in HBL and TTL of larval *Limnonectes malesiana*. Stages 36-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
25	15	3.9-4.3	11.1-14.4
27	1	5.4	14.6
31	1	8.2	22.5
35	1	8.5	23.6
36	1	7.0	22.8
37	1	9.5	24.8
38	1	9.6	26.7
42	2	7.0-9.8	20.1-21.5
46	1		SVL=10.8mm

Oral Disc. - Mouth ventral, sub-terminal, width 0.26-0.42 of HBW; single row of marginal papillae from lateral corners of upper lip with a narrow median gap; both jaw sheaths serrated, edged with black, lateral margins of upper jaw sheath curving gradually towards the rear.

LTRF. - 0/0, n = 21; 0/1, n = 1; 0/2, n = 1; 1/2(2), n = 1; 1/3(2), n = 1. Despite the great variation in denticle row counts, it can clearly be seen that the majority of larvae possessed inconspicuous, weak labial teeth which were often shed, agreeing closely with observations by Kiew, 1984a.

Feeding Strategy. - The foraging and rasping of foods provided (both natural and artificial) was typically ranid in behaviour.

Development. - Kiew (1984a) collected tadpoles from Selangor and successfully reared them to metamorphosis (TTL up to 22.9 mm). A series of larvae (Stages 25-46) were obtained from various localities and is presented in Table 7.

Material examined. - (n = 24); ZRC.1.3362, ZRC.1.3363, ZRC.1.3364, ZRC.1.3365, ZRC.1.3366, ZRC.1.3367, ZRC.1.3368.

***Rana cancrivora* Gravenhorst**
(Fig. 8; Table 8)

Vernacular Names. - Crab-eating Frog, Mangrove Frog (Lim & Lim, 1992); Malay- Katak Bakau (Kiew, 1984b).

Geographical Distribution. - From Peninsular Malaysia to Flores in the Lesser Sundas; from Java to Luzon; Sabah, Sarawak, Kalimantan (Inger, 1966).

Typical Habitats. - Never found in rain forest. Instead, coastal areas, disturbed forest, agricultural areas, marsh land, canals, mangroves and prawn ponds (Lim & Lim, 1992). In Singapore, occurs in Sg. Buloh, Pulau Ubin, P. Tekong.

Table 8. Developmental changes in HBL and TTL of larval *Rana cancrivora*. Stages 27-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
26	14	6.5-8.1	13.9-20.0
27-28	9	8.6-9.5	19.7-23.8
29-30	11	9.7-11.0	20.6-26.4
31-33	13	9.7-11.7	22.6-27.2
34-36	9	11.6-13.7	28.0-32.5
37-38	10	11.0-12.9	27.3-33.3
39-40	4	13.3-13.6	31.8-34.1
41	4	13.5-14.6	32.5-35.9
44	1	14.8	25.0
46	4	SVL=10.7-16.0mm	

Reproductive Strategy. - Amplexus in the adults is axillary. Eggs are in the form of oblong or circular rafts (from 1-15 cm diameter) on the surface of the water. Each mass may have a few to several hundred, but usually between 50 and 70 eggs. Attachment of egg rafts to vegetation or other floating objects is with the help of sticky outer capsules. Once such attachments are broken, the egg mass sinks to the bottom of the ponds. The eggs average 1.2-1.3 mm in diameter (2.0 mm including the gelatinous layers) and are pigmented in the animal hemisphere (Alcala, 1962).

Larval Microhabitats. - Larvae specimens were obtained from coastal areas (eg. Sungai Buloh) and a hot spring on an off-shore island (Pulau Tekong), indicating a tolerance of not only salinity but high temperatures (average 43°C) also. Laboratory tested larvae of *R. cancrivora* have demonstrated a tolerance of up to 3.9 % salinity, which is around 120 % of normal sea-water concentration (Gordon et al., 1961).

Larval Morphology. - Head-body oval, HBW 0.52-0.56 of HBL; snout broadly rounded; nostrils midway between eye and snout tip; eyes dorso-lateral, inter-orbital around twice inter-narial distance; spiracle tube-like, low on left side, midway between tip of snout and vent, in line with mouth and ventral edge of tail muscle; anal tube dextral. Tail of moderate depth, deepest at mid-point, tip sharply pointed; upper fin originating on head-body anterior to base of tail, gradually rising to highest point and then sloping towards tail tip; dorsal fin twice depth of ventral fin; tail musculature weak; TH 0.16-0.29 of TL; TL 1.35-1.79 of HBL.

Colour/Markings. - (In life) Back, sides and tail muscle dark grey to chocolate brown, with even darker spots extending onto fins; venters lightly coloured.

Oral Disc. - Mouth ventral; marginal papillae bordering lower lip and lateral corners of upper lip; infra-marginal papillae on lower lip only, lower lip with narrow median gap; jaw sheaths serrated, narrowly edged with black.

LTRF. - 2(2)/3; the length of the outer most denticle row on the lower lip is 2/3-3/4 of second row.



Fig. 5. Lateral (a) and dorsal (b) aspects of *Occidozyga laevis* larva (Stage 26).

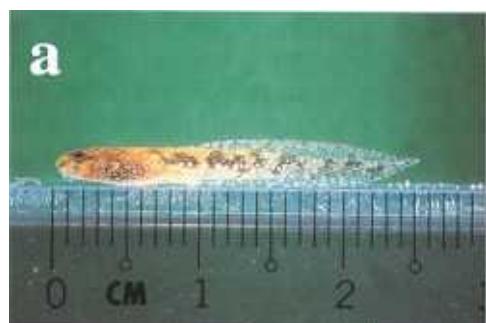


Fig. 6. Lateral (a) and dorsal (b) aspects of *Limnonectes blythii* larva (Stage 36).

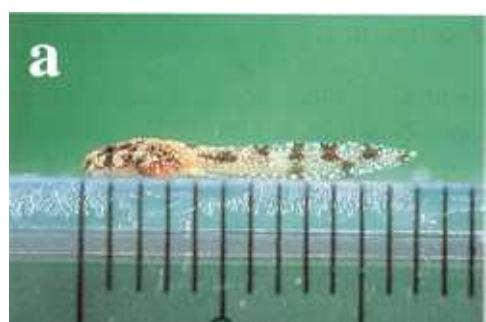


Fig. 7. Lateral (a) and dorsal (b) aspects of *Limnonectes malesiana* larva (Stage 26).

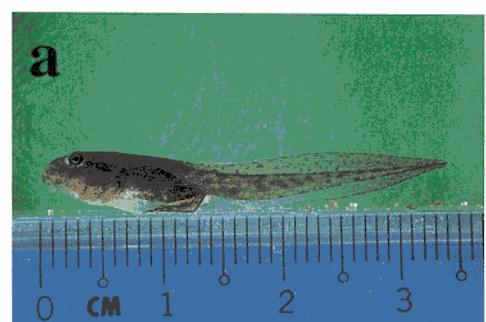


Fig. 8. Lateral (a) and dorsal (b) aspects of *Rana cancrivora* larva (Stage 41).

Feeding Strategy. - Larvae collected at hot springs were maintained on a diet of blue-green algae, dead leaves and detritus obtained from the area. Alcala (1962) observed necrophagy among larvae reared in aquaria but true cannibalism was not recorded.

Development. - Alcala (1962) recorded that the operculum is complete about 70 hrs after oviposition and fertilisation. It was also estimated that the total larval period up to metamorphosis can take between 50 and 82 days. A stage 35 larva collected from the hot spring was maintained at about 35-40°C and completed metamorphosis after two weeks. The late stages (Stage 39 onwards) already exhibit complete webbing on their hind feet up to the toe tips. New emergents possess tubercles scattered on the dorsum.

Material examined. - (n = 79); ZRC.1.3372, ZRC.1.3377.

Additional Remarks. - As previously noted by Schijsfma (1932) and Bourret (1941), the tadpoles of *Rana cancrivora* are deceptively similar to those of *Rana limnocharis*. Inger (1985) distinguished the two species based on characteristic markings: in *R. cancrivora*, the tail possess dark, round spots whereas in *R. limnocharis*, the tail is heavily pigmented in the posterior third; later stages (Stage 38 onwards) of *R. cancrivora* also have a well defined, dark stripe on the developing hind limb. Schijsfma (1932) pointed out other differences: larvae of *R. cancrivora* are generally larger than those of *R. limnocharis*; the third row of labial teeth on their lower lip is relatively longer in *R. cancrivora* than in *R. limnocharis*. In the emergents, the hind feet of *R. cancrivora* are more extensively webbed than in *R. limnocharis*, just as they are in the adults (Lim & Lim, 1992).

***Rana chalconota* (Schlegel)**

(Figs. 9 & 10; Tables 9 & 10)

Vernacular Names. - Malayan Bush Peeper (Hendrickson, 1966); Malay- Katak Tembaga (Kiew, 1984b); Copper-cheeked Frog, White-lipped Frog (Lim & Lim, 1992).

Geographical Distribution. - From Peninsular Thailand to Java, Bali and Sulawesi. Also found in Borneo (Inger & Stuebing, 1997).

Typical Habitats. - Known to occur along small streams of both primary and secondary forests and around swampy areas at the edge of clearings (Inger, 1966). Most successful and widespread of the forest species in Singapore.

Reproductive Strategy. - In the field, mating pairs were not observed, but egg masses were regularly found (50-100 eggs per clump) at the water surface of small quiet pools in the vicinity of forest streams.

Larval Microhabitats. - Larvae were encountered in both lentic and lotic habitats, eg. still forest puddles, stagnant pools, small to medium sized streams and along their banks.

During the field surveys, two discernible forms of this species were discovered. Both forms were found to occur within the same vicinities. The more commonly encountered morph, referred to as *Rana chalconota* Form A (Fig. 9) differs from *Rana chalconota* Form B (Fig. 10) in terms of colour, markings and LTRF. Form B also appears to be comparatively smaller

Table 9. Developmental changes in HBL and TTL of larval *Rana chalconota* Form A. Stages 25-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
25	5	2.3-6.5	5.6-12.7
26	3	6.2-7.1	13.9-14.9
27	8	7.2-8.6	18.7-20.3
29	4	8.6-9.5	20.2-24.8
31	5	9.7-11.6	23.7-26.4
36	6	11.7-13.5	29.4-33.8
39	2	10.3-11.5	26.5-31.3
40	1	13.6	34.7
41	16	14.0	30.1-34.8
42	5	11.5-15.1	23.8-34.5
43	1	15.2	18.3
46	5	SVL=12.7-14.8mm	

Table 10. Developmental changes in HBL and TTL of larval *Rana chalconota* Form B. Stages 36-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
27	1	6.3	15.9
28	1	6.8	18.7
34	1	8.0	22.5
36	4	8.9-9.1	22.2-25.0
37	2	9.6-9.7	23.3-24.3
38	4	10.0-10.6	24.3-29.2
43	1	11.4	14.8
44	1	11.2	13.0
46	2	SVL=10.6-11.0mm	

in size. Form A is the prevailing form, while Form B was collected from only two different localities.

Larval Morphology. - (Both forms) Head-body oval, HBW 0.53-0.65 of HBL; snout rounded, nostril equidistant between eye and snout tip; eyes dorso-lateral, inter-orbital one and a half to twice inter-narial; spiracle sinistral, directed upwards and backwards, visible from above and below, midway between snout tip and vent; vent dextral, tubercular, opening at margin of ventral fin. Tail pointed, fins convex, deepest point a third to halfway from tail root, dorsal fin deeper than ventral; TL 1.24-1.53 of HBL. Distinct glandular patches visible in up to four regions; (i) a round one behind each eye, (ii) an oblong one at each of the tail base, (iii) two round ones (confluent in older specimens) beside each other, behind the oral disc and (iv) an elongated one at each side of the belly. Individual glands polygonal in shape, forming a mosaic.

Colour/Markings. - (In life) *Form A.*- Dorsum of head-body and tail muscle buff to golden-yellow; venters and fins clear; extensive cephalic markings, including (i) a black spot below nostril, (ii) a black bar below eye, (iii) a curved, vertical black line laterally behind the head, (iv) a longitudinal black patch dorsolaterally behind head (more prominent on the right flank), (v) a narrow, mid-dorsal black streak from behind head to base of tail, (vi) inter-orbital markings between and just behind the eyes. (In life) *Form B.*- Head-body and tail muscle uniform dark brown; venters lightly pigmented; both fins clear; cephalic markings reduced to (i) a lateral black bar behind head, (ii) inter-orbital marking behind eyes only, (iii) faint mid-dorsal streak. Lateral line pores conspicuous on dorsum. Individual glands of glandular patches with inner ring of black pigments.

Oral Disc. - (Both forms) Mouth ventral, sub-terminal; marginal papillae in a continuous series across lower lip and at corners of upper lip; infra-marginal papillae present; jaw sheaths finely serrated, edged with black.

LTRF. - *Form A.* 4(2-4)/3(1); second to fourth row on upper lip widely separated by jaw sheaths; median gap of first row on lower lip very narrow. *Form B.* 3(2-3)/3(1).

Feeding Strategy. - Larvae of this species are active feeders, as observed in the field and in captivity. All forms of food were readily accepted, eg. dead leaves, aquatic plants, commercial fish food. Necrophagy was observed in the larvae of Form A. Their extensive denticle rows are well suited for this mode of feeding where much time is invested in grazing activity.

Development. - A developmental series was recorded for both forms of this species (Tables 9 & 10). In the emergents, the characteristic features of the adults are clearly seen and cross-bars may be present on the limbs. Two weeks after metamorphosis, the conspicuous iridescent white stripe on the upper lip becomes noticeable.

Material examined. - *Form A* (n = 61); ZRC.1.1801-1823, ZRC.1.2098-2106, ZRC.1.3390, ZRC.1.3391, ZRC.1.3392, ZRC.1.3393, ZRC.1.3394, ZRC.1.3395, ZRC.1.3396, ZRC.1.3397, ZRC.1.3398. *Form B* (n = 17); ZRC.1.3399, ZRC.1.3400, ZRC.1.3401, ZRC.1.3402.

Rana erythraea (Schlegel)

(Fig. 11; Table 11)

Vernacular Names. - Common Greenback, Green Paddy Frog (Lim & Lim, 1992); Malayan Pond Frog, Malay- Katak Pisang (Kiew, 1984b).

Geographical Distribution. - Known from eastern India and Burma to Sumatra, Java, Sulawesi and the Philippine Islands (Boulenger, 1920).

Typical Habitats. - Usually found in forest clearings and agricultural lands (Lim & Lim, 1992).

Reproductive Strategy. - No mating pairs were observed in the field. However, clumps of their eggs were found attached onto mats of aquatic vegetation lying just beneath the water surface.

Table 11. Developmental changes in HBL and TTL of larval *Rana erythraea*. Stages 26-43 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
26	2	7.1-8.5	18.2-23.1
27	3	9.6-10.4	27.5-25.1
28	1	8.9	24.8
31	1	11.6	33.7
35	1	13.3	36.4
36	2	14.5-15.5	39.2-40.2
37	2	13.7-16.8	36.2-42.9
38	1	17.0	41.5
40	2	17.2-18.8	44.5-45.6
41	1	18.4	40.9
43	1	16.7	32.3

Larval Microhabitats. - In the field, larvae were collected from streams and their grassy banks at the edge of swamp forest. Kiew (1972) reported tadpoles of this species to be associated with reeds and *Utricularia* plants.

Larval Morphology. - Head-body ovoid, HBW 0.40-0.59 of HBL; head sloping gradually from eyes to a narrowly-rounded snout; nostrils nearer to tip of snout than eye; eyes dorsolateral, equidistant between snout tip and spiracle; inter-orbital more than twice inter-narial distance, which is slightly less than mouth width; spiracle sinistral, directed upwards and backwards, slightly nearer to vent than to snout tip; vent dextral, close to lower border of tail. Tail pointed, originating from posterior of head-body; dorsal fin often deeper than ventral; TL 1.40-1.85 of HBL; TL 2.93-4.28 of TH.

Colour/Markings. - (In life) Head-body and tail muscle olive-brown to golden-brown, marbled with dark brown and scattered with iridocytes; throat translucent to grey; belly white, mottled with reddish-brown splotches; a dark streak running through wine-red eyes towards snout. Tail fins clear to translucent, with dapplings of rusty-red spots. More advanced tadpoles (Stage 38 onwards) begin to exhibit a thin, light vertebral stripe flanked by dorso-lateral lines running from behind the eyes toward the tail muscle. The characteristic green on the dorsum is noticeable at Stages 42 and later.

Oral Disc. - Mouth ventral, sub-terminal; sides and lower border of lips with papillae, marginal papillae on lower lip long and narrow, infra-marginal short and conical, no median gap; jaw sheaths edged with black.

LTRF. - 1/2(1); length of second labial tooth row on lower lip 2/3 that of first row.

Feeding Strategy. - In captivity, larvae remained largely inactive for the most part, either perched upon submerged aquatic plants or resting on the bottom. Instead of grazing casually on the substratum as is typical of most ranids, the tadpoles appear to be 'nibbling' away at detritus or soft vegetable matter, changing positions occasionally by darting away. This form

of diet agrees well with its low LTRF count of 1/2(1) as compared with the larger number of denticle rows in actively rasping tadpole types.

Development. - In captivity, larvae required two to three months to reach metamorphosis. In this species, the four-limbed period was longer than most other ranids as more time was required for the absorption of a comparatively larger tail. A developmental series is provided in Table 11.

Material examined. - (n = 17); ZRC.1.1793, ZRC.1.2223-2226, ZRC.1.3379, ZRC.1.3380, ZRC.1.3381, ZRC.1.3382.

Rana glandulosa Boulenger

Vernacular Names. - Glandular Frog, Malay- Katak Kelenjar (Kiew, 1984b); Rough-sided Frog (Inger & Stuebing, 1989; Inger & Tan, 1996).

Geographical Distribution. - Sabah, Sarawak, Peninsular Thailand, Peninsular Malaysia, Sumatra (Inger, 1966), Singapore (Rajathurai & Teo, 1997).

Typical Habitats. - Primary and secondary forests, large clearings and swamps; along stream banks; on forest floor, sometimes far from vicinity of any water (Berry, 1975). Also known from coastal areas (Inger & Stuebing, 1989). In Singapore, occurs in CCNR swamp forests.

Reproductive Strategy. - Unknown.

Larval Microhabitats. - Berry (1972) collected specimens from a stream at 1280 m, Gunong Bunga Buah, Pahang. A developmental series was reared in the laboratory and preserved at various stages.

Larval Morphology. - (Based on Berry's description of 10 individuals) Head-body oval, HBL 1.75-2.0 of HBW; snout rounded, external nostrils only visible just before metamorphosis. Inger (1985) regarded this appearance of external nares as a unique feature among Indo-Malayan ranid larvae. Spiracle sinistral, not produced into a tube, situated nearer vent than snout tip; anus dextral, covered by large, skin flap, opening onto right side of ventral fin. Tail accutely pointed; dorsal fin higher than ventral. TTL around 55 mm.

Colour/Markings. - Head-body and caudal fins covered with small, scattered whitish glandules, especially conspicuous in younger tadpoles. In life, back and sides of head-body and tail reddish brown, speckled with dark brown patches continuing onto tail fins; ventral surface light. Emergents reddish to olive-brown above and speckled with black; venters whitish; limbs with distinct dark bars; throat of young specimens brownish with white spottings.

Oral Disc. - Mouth ventral; sides fringed with single row of rounded papillae, lower border with two rows; jaw sheaths white, serrate and broadly edged with black.

LTRF. - 3(2)/3(1) in three specimens. In one 16.3 mm larva, labial teeth were entirely absent and jaw sheaths were poorly developed.

Feeding Strategy. - No information was supplied on the types of food provided for the larvae reared by Berry (1972).

Development. - Berry (1972) did not provide any indication of the time span or growth rates from pre-limb bud stages to metamorphosis.

Material examined. - None.

***Rana limnocharis* Boie, in Wiegmann**
(Fig. 12; Table 12)

Vernacular Names. - Padi-field Frog, Malay- Katak Sawah (Kiew, 1984b); Paddy Frog (Karsen et al., 1986); Field Frog, Grass Frog (Yong, 1980; Lim & Lim, 1992).

Geographical Distribution. - India, Sri Lanka, Malay Peninsula and Archipelago, Philippines, Borneo, China, Japan (Kirtisinghe, 1957).

Typical Habitats. - Disturbed vegetation, forest edge, gardens, parks, roadsides, lawns (Inger & Stuebing, 1989; Lim & Lim, 1992).

Reproductive Strategy. - (After Pope, 1931) Both sexes pair off at the edges of quiet ponds or ditches. Amplexus is axillary. At regular intervals, females duck their heads and, as their vents reach the water surface, eject ova upon it. The eggs subsequently sink to the bottom.

Larval Microhabitats. - Larvae were collected from shallow rain-filled pools in open areas of gardens, scrubland, forest edges.

Larval Morphology. - Head-body oval, HBW 0.54-0.58 of HBL; snout bluntly pointed; nostril nearer to snout tip than eye; eyes dorso-lateral, inter-orbital more than twice internarial distance; spiracle sinistral, visible from above and below, equidistant between snout tip and vent; anus dextral. Tail with tip attenuated; fins deeper than muscle, dorsal margin convex, ventral margins straight; TL 1.54-1.81 of HBL.

Colour/Markings. - (In life) Dorsum olive, speckled with black or brown; venters white, posterior half of tail often dark grey to black, sometimes with reddish tinge.

Oral Disc. - Mouth ventral, sub-terminal; single row of papillae on lateral corners of upper lip, marginal and infra-marginal rows on lower lip, with median gap approximately equal to width of outer-most labial tooth row; jaw sheaths edged with black.

LTRF. - 2(2)/3; the distal, third labial tooth row of the lower lip has a length about a third to half of the second row.

Feeding Strategy. - Typical ranid rasping behaviour was observed in captive larvae, which fed readily on both natural and artificial foods. Smith (1916b) reported that the tadpoles fed upon 'vegetable and dead animal matter.' Heyer (1973) found diatoms, filamentous algae and protozoans among the gut contents of the tadpoles.

Table 12. Developmental changes in HBL and TTL of larval *Rana limnocharis*. Stages 27-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
27	2	5.8-6.0	14.0-16.1
28	4	6.3-6.4	16.1-16.2
31	3	7.1-7.7	16.6-19.5
33	2	8.3-8.6	20.4-22.5
35	3	8.6-10.0	22.2-24.7
36	2	7.8-8.9	18.5-22.3
37	4	8.7-9.2	19.0-22.9
40	1	10.6	27.0
41	1	11.4	28.8
42	2	10.3	14.5-30.9
43	2	10.4-11.8	11.9-19.8
44	1	12.9	13.9
46	1	SVL=10.2mm	

Development. - Lee and Chen (1970) reported that operculum development is complete 64 hours after fertilisation. At this stage, feeding began. The entire larval stage was estimated to be 23 days by Heyer (1973) and 28 days by Pope (1931). Accompanying the protrusion of fore limbs is the development of prominent, longitudinal folds on the dorsum, as noted by Smith (1916b). At the same time, a dark inter-orbital bar and other dorsal patterns become distinct; dark spots become visible on the hind limbs.

Material examined. - (n = 28); ZRC.I.2688-2701, ZRC.I.3373, ZRC.I.3374, ZRC.I.3376.

Rana plicatella Stoliczka
(Fig. 13; Table 13)

Vernacular Names. - Rhinoceros Frog, Malay- Katak Badak (Kiew, 1984b).

Geographical Distribution. - Thailand, Burma (?), Peninsular Malaysia, Singapore (Bourret, 1941; Taylor, 1962).

Typical Habitats. - Always found in close proximity to forest streams. Occurs in isolated localities at BTNR and CCNR.

Reproductive Strategy. - Males were regularly heard calling along forest streams but amplexing pairs were not sighted. However, an adult female (SVL 28 mm) was observed along an overgrown stream bank together with her batches of spawn. She was seated within a crater (3.5 cm diameter, 0.5 cm depth) of fine sand. On her right was a similar-sized crater containing early embryos (Stages 18-20). Towards her left was another crater with a gelatinous mass of freshly deposited ova (16 eggs counted). The eggs were relatively large (1.8-2.1 mm) and lightly pigmented at the animal pole. This oviposition site was just adjacent to the water's edge.

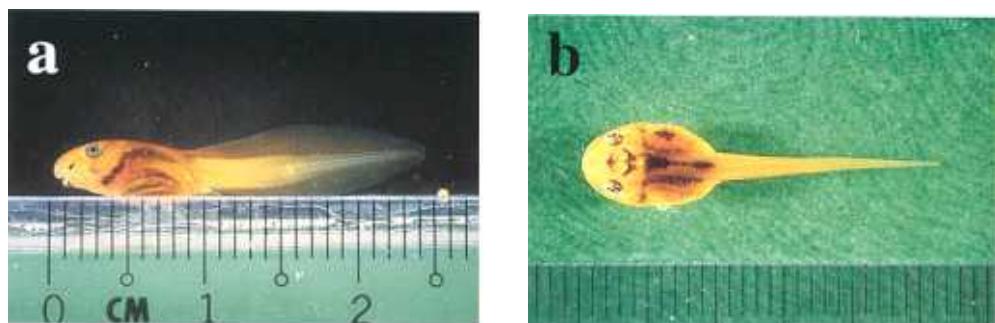


Fig. 9. Lateral (a) and dorsal (b) aspects of *Rana chalconota* form A larva (Stage 28).

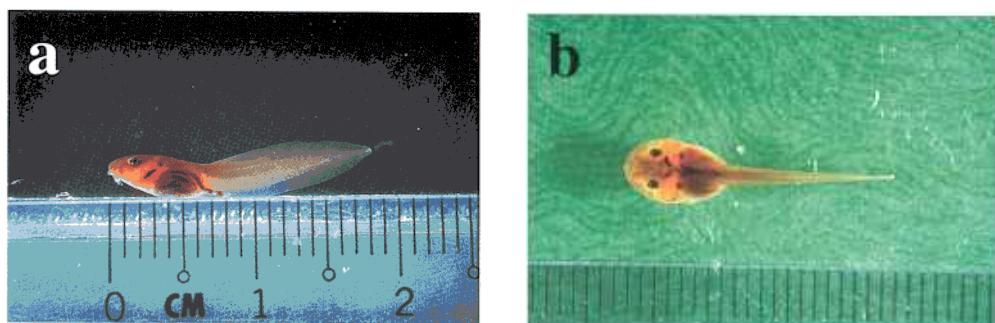


Fig. 10. Lateral (a) and dorsal (b) aspects of *Rana chalconota* form B larva (Stage 28).

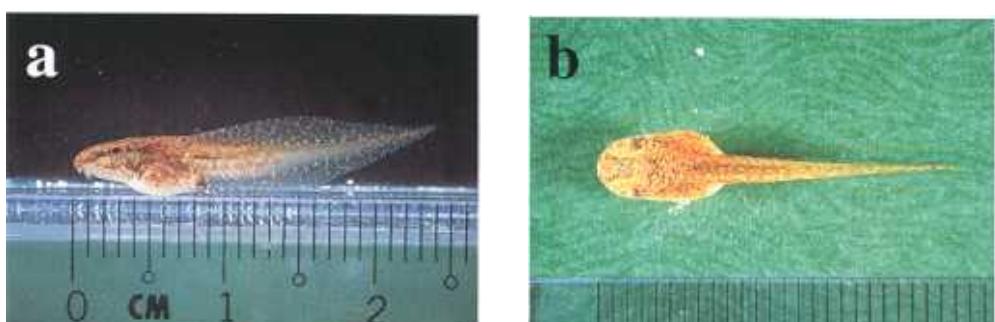


Fig. 11. Lateral (a) and dorsal (b) aspects of *Rana erythraea* larva (Stage 26).

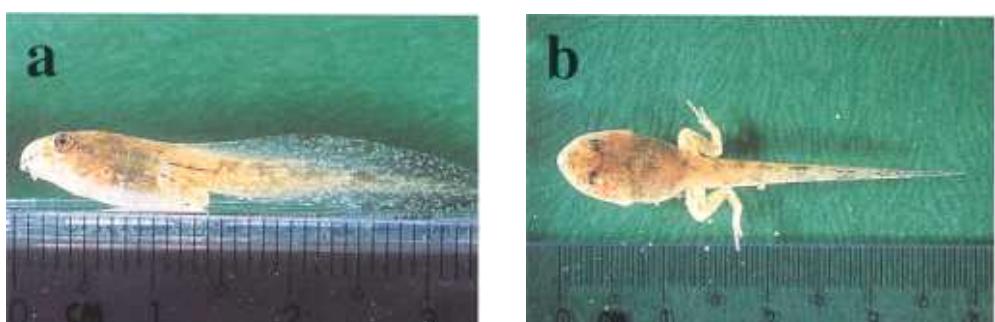


Fig. 12. Lateral (a) and dorsal (b) aspects of *Rana limnocharis* larva (Stage 41).

Table 13. Developmental changes in HBL and TTL of larval *Rana plicatella*, Stages 25-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
25	2	2.9-3.3	8.3-10.1
26	3	5.5-5.7	17.2-17.8
27	2	6.3-6.9	20.5-21.3
30	1	7.5	21.5
34	2	7.4-7.9	22.7-23.4
36	2	7.5-7.7	22.2-24.2
38	3	8.1-8.8	25.8-29.2
40	3	8.3-9.0	25.4-29.1
42	1	8.2	21.4
43	1	8.6	22.9
44	1	7.9	15.0
46	4	SVL=7.1-8.9mm	

Larval Microhabitats. - Larvae were often observed in the quiet, shallow (0.5-1.5 cm depth) side pools of streams with clear water over a sandy substrate. Although the larvae have excellent camouflage against the sand bottom, they are also known to hide among rubble and under dead leaves in water.

Larval Morphology. - Head-body ovoid, HBW 0.51-0.56 of HBL, back slightly depressed, HBH 0.65-0.82 of HBW; snout rounded; nostrils dorsal, nearer to eye than snout tip; eyes dorso-lateral, midway between snout tip and spiracle, inter-orbital 1.2-1.5 times inter-narial; spiracle sinistral, slightly nearer to tip of snout than vent; vent dextral, anal tube fused with ventral fin, opening posteriorly towards the right side. Tail gently sloping towards pointed tip; caudal musculature strongly developed; fins with sub-parallel margins, dorsal fin originating after anterior quarter of tail, deeper than ventral fin; TL 2.21-2.38 of HBL, TL 4.43-5.78 of TH.

Colour/Markings. - (In life) Head-body and tail light- to golden-brown with randomly distributed black spots and blotches; distinct black bands around eye, one running laterally behind eye, one towards the snout tip, one vertically below the eye and another directly posterior to this. Fins clear but interspersed with fine, black and iridescent pigmentation.

Oral Disc. - Mouth ventral, sub-terminal; papillae bordering lateral corners of upper lip and onto lower lip except for a narrow, median gap; infra-marginal papillae present; jaw sheaths serrated, with broad, black edges.

LTRF. - 2(2)/3(1-2); second row on upper lip broadly interrupted by upper jaw sheath; third row on lower lip less than a quarter of second row.

Feeding Strategy. - In captivity, larvae were seen to pick up detritus from the bottom with their mouths and hardly scraping away on any substrate matter. The transparent intestinal coils contained fine sand grains mixed with detritus of possibly decaying vegetable matter.

Development. - Fertilised ova successfully developed from embryo to larval stages in captivity. Stage 18 was attained after four days, Stage 20 after eight days and Stage 25 by the twelfth day. Pigmentation of head-body and tail steadily increased beginning from day 10 onwards. At the advanced stages (Stage 43 onwards), characteristics of the adult become noticeable. These include dilated finger and toe tips, cross-bars on the limbs, longitudinal skin folds on the dorsum and two dark, dorsal chevron marks: one pointing towards the posterior from between the eyes, the other pointing towards the anterior from the pectoral region. A developmental series (Table 13) is provided.

Material examined. - (n = 25); ZRC.1.3383, ZRC.1.3384, ZRC.1.3385, ZRC.1.3386, ZRC.1.3387, ZRC.1.3388.

FAMILY RHACOPHORIDAE

Among the four species of tree frogs recorded in Singapore, three are strictly inhabitants of primary to mature secondary forests, namely *Nyctixalus pictus*, *Rhacophorus cyanopunctatus* (Manthey & Steiof, 1998) and *Theloderma horridum*. Adults of *N. pictus* have been sighted occasionally within BTNR and CCNR, but their larvae have only been recently encountered. *T. horridum* is recently recorded from Singapore, but its tadpoles have yet to be reported from there. The exact identity of larval *R. cyanopunctatus* remains uncertain and sightings of the adults have been few and far between. By far, the most frequently observed rhacophorid is *Polypedates leucomystax*, whose breeding behaviour and larval stages have been well documented. Except for *R. cyanopunctatus*, larval forms of the other three species are described.

Nyctixalus pictus (Peters) (Fig. 14; Table 14)

Vernacular Names. - Spotted Tree Froglet, Malay- Katak Pokok Bintik (Kiew, 1984b); Spotted Tree Frog (Lim & Lim, 1992); Cinnamon Tree Frog (Inger & Tan, 1996).

Geographical Distribution. - Palawan Island (Philippines), Brunei, Sabah, Sarawak, Kalimantan, Sumatra, Peninsular Malaysia, Singapore (Inger, 1966; Brown & Alcala, 1994, Das, 1995).

Typical Habitats. - Primary forest inhabitant, found in both swamp forest and well drained areas; largely arboreal in habit but found from ground level to about 1.5 m above (Inger, 1966). Evenly distributed within BTNR and CCNR in Singapore.

Reproductive Strategy. - Known to breed in water-containing tree holes, log cavities and even in large, hollow fruit; which implies that 'steepness of the terrain does not affect the ability of this species to reproduce' (Inger & Tan, 1996). In this species, a small number of eggs (8-15) are covered by a gelatinous substance and deposited on the walls of such phytotelmata. Foam nests are not found, as indicated by the absence of convoluted Wolffian ducts in males (Liem, 1970).

Previous accounts of tree hole breeding (eg. Inger, 1966, 1985, Kitching & Orr, 1996) were verified when the larvae of this species were encountered in the cavity of an old, fallen tree

Table 14. Developmental changes in HBL and TTL of larval *Nyctixalus pictus*. Stages 27-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
27	1	17.5	45.3
34	1	18.3	42.6
40	1	19.9	46.3
43	1	20.2	45.1
46	1		SVL=19.8mm

in the middle of swamp forest (1.2.1996). The hole was approximately 15 cm wide by 8 cm high, 1.2 m above the forest floor. Only four to five larvae were observed attached to, or dangling from the ceiling and back wall of the cavity. An individual was suspended, head-down, by a highly viscous, mucilaginous slime and on the verge of dropping into the shallow, tea-coloured water below. It was collected for developmental studies.

Larval Microhabitats. - Phytotelm inhabitant of shallow, stagnant waters in the various forms of cavities earlier described. Other co-inhabitants include insect larvae (O. Diptera) equipped with posterior breathing tubes. A rusty, water-filled oil-drum within forest was found to be inhabited by at least 8-10 mature larvae. They were swimming amongst the many dead leaves on the inside of this disused drum. A recent emergent was also encountered here.

Larval Morphology. - Head-body ovoid, HBW 0.68-0.69 of HBL; depressed, HBH 0.61-0.67 of HBW, and almost circular from plan view in earlier stages; maximum HBW just behind the eyes, snout broadly rounded; nostrils and eyes dorsally situated, not visible from below; inter-narial slightly narrower than inter-orbital; inter-orbital almost 1/3 of HBW; spiracle sinistral, ventro-lateral, nearer to vent than snout tip; anal tube median. Tail moderately convex, tapering gradually to rounded tip, TL slightly longer than HBL; caudal musculature heavy, deeper than fins in proximal half; fin margins sub-parallel, dorsal fin originating just behind root of tail; TL 1.37-1.65 of HBL.

Colour/Markings. - (In life) Head-body and tail uniform purplish-brown; venters a lighter shade, translucent; dorsal and ventral fins lighter than caudal muscle; lateral line pores conspicuous on dorsum, venter and along caudal muscle.

Oral Disc. - Mouth ventral, subterminal; width less than half of HBW; upper lip with crowded papillae at lateral corners only; lower lip with staggered, double row of slender, short papillae; jaw sheaths with fine, long serrations, black in marginal half.

LTRF. - 5(3-5)/3.

Feeding Strategy. - In captivity, the tadpole was supplied with small pieces of banana and commercial pellet fish food. These food items were gnawed upon in a calm, unhurried manner.

Development. - The tadpole acquired fully developed hind limbs (Stage 40) after eight weeks and eruption of fore-limbs (Stage 42) was at the end of 10 weeks. Metamorphosis was complete within two days. Throughout its development, the maximum size attained was about 4 cm TTL. At Stage 42, the characteristic white spots on the limbs have become distinct and in the new emergent, the white dorsal quarter of the eye, white upper eye-lid, spots on

the canthus and dorsum are conspicuous. The belly remained translucent but was striated with chalk-white markings. The emergent froglet had a snout-vent length (SVL) of 20.0 mm with tail fully resorbed.

Material examined. - (n = 5); ZRC.1.3295, ZRC.1.3476.

***Polypedates leucomystax* (Boie, in Gravenhorst)
(Fig. 15; Table 15)**

Vernacular Names. - Common Tree Frog, Four-lined Tree Frog (Lim & Lim, 1992); Malayan House Frog, Malay- Katak Kampung (Kiew, 1984b); Brown Tree Frog (Karsen et al., 1986); Asian Tree Frog (Mattison, 1993).

Geographical Distribution. - Eastern Himalayas, India, China, Taiwan, Hong Kong, Northern Indochina to Borneo, Sulawesi, Philippines, Sumatra, Java, Peninsular Malaysia, Singapore (Kampen, 1923; Karsen et al., 1986, Brown & Alcala, 1994).

Typical Habitats. - Disturbed forest, agricultural areas, gardens (Lim & Lim, 1992).

Reproductive Strategy. - Oviposition is within foam nests that are churned up by the amplexing pair as the unpigmented eggs (150-900) are released. Such nests are known to be attached to low lying shrubs or high up in the branches of trees overhanging semi-permanent water bodies. In the absence of such vegetation, eggs may be placed at the edges of pools or directly above water. Soon, the ball of foam (5-10 cm diameter) dries on its outer surface, forming a crust which prevents dessication. Eventually, the young hatch as the foam liquidates within the nest, breaks through the outer crust and plunges into the water below, to continue the usual aquatic development. This process is usually hastened by rains.

Larval Microhabitats. - Tadpoles are normally found in temporary pools that do not contain fish (Taylor, 1962). Waters may be clear or turbid. Larvae are tolerable of high temperatures (38-40°C) in such exposed areas as observed by Inger and Tan (1996).

Larval Morphology. - Head-body ovoid in plan view, HBW 0.44-0.49 of HBL; dorsal surface flattened, rounded below; snout broadly rounded; nostrils dorsal; eyes dorso-lateral, visible from below, positioned at anterior third of head-body; inter-narial much less than inter-orbital; spiracle slit-like, low on the left side, in line with mouth and ventral edge of caudal muscle midway between snout tip and vent; vent dextral, opening at mid-length of ventral fin. Tail higher than head-body, sharply pointed; deepest position nearer head-body than tip of tail; caudal muscle weak, higher than fins at anterior third of tail only; both fins convex, dorsal fin originating anterior to base of tail, ventral fin slightly shallower than dorsal; TL 2.02-2.34 of HBL.

Colour/Markings. - (In life) Head-body and tail muscle brown to dirty buff, irregularly mottled with darker; venters lighter buff or white; fins clear, occasionally scattered with brown to black pigments; snout tip with distinct, iridescent white spot; a dark streak from eye towards snout.

Oral Disc. - Mouth antero-ventral in position; marginal papillae at lateral corners of upper lip except for median gap; jaw sheaths serrated, edged with black.

Table 15. Developmental changes in HBL and TTL of larval *Polypedates leucomystax*. Stages 26-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
26	10	4.0-5.3	13.2-20.2
28	4	5.1-7.7	19.9-24.3
30	2	8.9-10.5	25.8-27.4
32	2	10.3-13.2	27.3-30.2
35	4	11.9-16.8	32.4-36.1
37	5	12.6-17.5	38.6-44.6
40	3	11.8-15.8	36.8-42.1
41	3	12.7-16.9	35.3-41.9
42	4	11.5-20.1	31.2-47.4
43	1	13.2	26.7
45	1	12.6	14.2
46	8		SVL=10.8-21.2mm

LTRF. - 4(2-4)/3 or 4(2-4)/3(1); second to fourth rows on upper lip widely separated by upper mandible; first row on lower lip occasionally separated by narrow, indistinct median gap.

Feeding Strategy. - In captivity, the tadpoles were voracious feeders and devoured all forms of food provided, from commercial fish flake or pellet food to water plants. Necrophagy and cannibalism were also observed in this species, especially in crowded conditions. A highly versatile, non-specialised feeder, the tadpoles are able to scrape algae off the substratum, shred the leaves off aquatic plants, nibble at the water surface for edible, floating debris and also tear apart conspecific tadpoles.

Development. - The pre-larval, or embryonic development of this species has been thoroughly documented (eg. Alcala, 1962; Ting, 1970; Khoo, 1971). Seven to eight days after oviposition, the larvae are at Stage 25 and very soon, they begin feeding. The iridescent spot on the snout tip becomes more prominent as the larvae matures. Under natural conditions or in captivity, about $2\frac{1}{2}$ months are required for developing tadpoles to complete metamorphosis. A few individuals, however, have been observed to complete development in half that time and other stragglers may not emerge even after $3\frac{1}{2}$ months. York (1979) noted that as little as 3% of the original clutch survive to metamorphose in natural conditions. Such a high mortality is probably due to starvation. Hence, the tendency towards cannibalism, which pushes a few individuals closer to metamorphosis at the expense of the weaker conspecifics within the same batch. In the later stages (Stage 40 onwards), the characteristic 'four-lines' on the dorsum begin to appear and darken. Once tail resorption is complete, the young emergent is already a miniature replica of the adult in every aspect.

Material examined. - (n = 47); ZRC.1.1490-1497, ZRC.1.2053-2097, ZRC.1.2227-2250, ZRC.1.3436, ZRC.1.3437, ZRC.1.3438, ZRC.1.3439, ZRC.1.3440, ZRC.1.3441, ZRC.1.3442.

Additional Remarks. - Accounts of parasitism by an invertebrate on this species were discussed by York, 1979. The calliphorid fly, *Lucilia* sp., is known to insert its eggs within

the freshly deposited foam nests of *P. leucomystax*. The fly larvae often hatch before the frog eggs do and may consume or destroy 40-100% of a single clutch. In the field, a foam nest at the water's surface suffered a same fate just two days after deposition. At least 10 maggots were counted as they crawled through the foam nest, devouring all the embryos and disintegrating the nest prematurely.

Theloderma horridum (Boulenger)

Vernacular Names. - Thorny Tree Frog, Malay- Katak Pokok Duri (Kiew, 1984b).

Geographical Distribution. - Borneo, Southern Thailand, West Malaysia, Mentawai Islands, Singapore (Leong et al., 1996).

Typical Habitats. - Primary forest inhabitant; typically arboreal, usually sighted on tree trunks (A.T.C. Wong, T.S. Tan pers. comm.; Inger et al., 1995; Leong et al., 1996). Known from single location at BTNR in Singapore.

Reproductive Strategy. - Based on Boulenger's (1903) description, the spawn is deposited on the trunk in frothy masses 'about the size of a cricket ball, a foot or two above the surface of the water' in buttress tanks. Boulenger (1903) reported that the egg masses resembled those produced by *Polypedates leucomystax*, but are smaller and paler in colour.

Larval Microhabitats. - Tree holes and tank buttresses formed by the coalescence of adjacent tree buttresses, which form cavities containing 'several gallons of rain water and dead leaves' (Boulenger, 1903). The 'deep brown colour' of such waters suggest a relatively high tannin content and acidity. Boulenger (1903) reported predation of spawn by the snake *Rhabdophis chrysargus* at these sites.

Larval Morphology. - (After Boulenger, 1903) Head-body much depressed, almost circular from dorsal view, HBL 0.57-0.63 of TL; eyes superior, inter-orbital distance 2.5-3.0 times eye diameter; spiracle sinistral, in posterior third of head-body, directed straight backwards; anus dextral, close to lower edge of tail. Tail 2.67-3.0 times as long as deep, rounded at the end; depth of muscular portion (at middle of the length) about 0.5 of total depth; upper caudal crest not extending onto head-body; TTL between 15-50 mm.

Colour/Markings. - (In life) Uniform dark brown or blackish, with distinct, whitish lines of sensory organs.

Oral Disc. - Mouth ranid in type, elliptical, width slightly greater than inter-ocular distance; sides and lower edge of lip fringed with papillae, lower lip with infra-marginal row; both jaw sheaths black.

LTRF. - From Boulenger's (1903) illustration, the correct formula is 4(2-4)/3 and not 3(1-3)/3 as reported in Bourret (1942) and subsequently by Liem (1970). Wassersug et al. (1981) pointed out a possible misprint in Boulenger's written description of the three rows of denticles on the lower lip. Boulenger described the labial tooth rows as being 'interrupted', which is contradictory to his own figure and the results of specimen examination by Wassersug et al. (1981), which proved to be uninterrupted.

Feeding Strategy. - Boulenger (1903) did not mention any aspect of feeding behaviour or dietary preferences. Wassersug et al. (1981), however, in describing the larvae of *Theloderma stellatum*, observed that they 'very closely resembled larval *Theloderma horridum* from Jalor, Malaysia'. It was initially suggested that the larvae of *T. stellatum* feeds on microscopic plankton, which was deduced from the presence of many rows of dense gill filters in the buccal chamber. Further examination of other buccal characteristics (eg. musculature) revealed that this larva is a mosaic of unusual features that does not give clear indications as to its feeding ecology. Hence, that of *T. horridum* possibly remains unknown as well.

Development. - Boulenger (1903) recorded the ova to be unpigmented or 'quite devoid of colour', but the larvae soon became a uniform velvet black. The characteristic blue-grey hue on the ventral side of the adult only began to appear once the hind limbs were well developed. This colour was not as intense when compared to older specimens, being a mere greyish-white in very young individuals.

Material examined. - None.

FAMILY MICROHYLIDAE

In Singapore, this family of narrow-mouthed frogs is represented by confirmed records of five species, belonging to three genera. One of the more interesting species is *Kalophrynus pleurostigma* with its unique breeding behaviour. This species has consistently utilised the ground pitchers of *Nepenthes ampullaria* as receptacles for oviposition and subsequent larval development. Unlike *K. pleurostigma*, the larvae of *Kaloula pulchra*, *Microhyla butleri* and *Microhyla heymonsi* thrive in much larger water bodies of open grassland, cultivated areas, roadsides and are rarely to be found within the forest. However, larvae of *Microhyla borneensis* have been found at BTNR and CCNR. The larval descriptions for all five species are provided.

Kalophrynus pleurostigma Tschudi (Fig.16; Table 16)

Vernacular Names. - Black-spotted Sticky Frog, Red-sided Sticky Frog (Lim & Lim, 1992); Black-spotted Sticky Toad, Malay- Kodok Bulu (Kiew, 1984b).

Geographical Distribution. - Brunei, Sabah, Sarawak, Kalimantan, Philippines, Sumatra, Malay Peninsula, Singapore (Inger, 1966; Lim & Lim, 1992; Das, 1995).

Typical Habitats. - Mainly a primary forest inhabitant, but also adaptable to secondary forest (Lim & Ng, 1991). Usually found on forest floor. Known from both BTNR and CCNR in Singapore.

Reproductive Strategy. - Breeding has been reported to occur in shallow, temporary pools of rain water, rain-filled road ruts, water-filled holes in logs, decaying bamboo internodes, burrows in stream banks, pitcher plant cups (Inger, 1954, 1956, 1966, 1985; Berry, 1972; Lim & Ng, 1991). The eggs are spherical, unpigmented and laid in clusters. Average size of eggs are 2.9 mm including membranes and 2.3 mm without membranes (Berry, 1972).

Table 16. Developmental changes in HBL and TTL of larval *Kalophrynxus pleurostigma*. Stages 25-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
25	5	2.3-2.6	6.5-7.1
28	5	3.0-3.2	8.3-9.1
36	5	3.7-4.1	10.9-11.1
41	5	3.8-4.3	9.8-10.2
43	5	3.9-4.3	5.8-8.3
45	5	3.8-4.4	3.9-4.6
46	5	SVL=4.3-4.7mm	

Larval Microhabitats. - The small, semi-permanent bodies as mentioned above are inhabited by the larvae for only very short spans of time (2 weeks). In Singapore, the ground pitchers of *Nepenthes ampullaria* have been successfully utilised as a receptacle for oviposition and subsequent larval development (Lim & Ng, 1991). On the 24th of August, 1996, a batch of at least 80 unpigmented larvae (Stages 20-23) was observed within the ground pitcher of *N. ampullaria* at the same vicinity where Lim & Ng (1991) first discovered this breeding strategy. The early larvae were suspended in viscous, mucilaginous mass. 20 larvae were collected to be reared in captivity. This site was regularly visited for the subsequent two weeks for comparison of developmental rates *ex situ* and *in situ*.

Larval Morphology. - Head-body subspherical, slightly flattened above, snout truncate; eyes lateral, visible from above and below; nostrils dorsal, not opened until Stage 40; spiracle median, without free flap, equidistant between eye and vent; ventral margin concave; vent median, in form of long tube, not open; gut in form of two, fat loops visible ventrally. Tail lanceolate, without terminal filament, tip bluntly rounded; fins with sub-parallel margins, deeper than tail muscle after proximal third; dorsal fin originating at end of head-body, thick at origin; ventral twice depth of dorsal in anterior quarter of tail; TL 1.3-1.9 of HBL.

Colour/Markings. - (In life) Early stages grey, immaculate, venters translucent; later stages brownish-black on dorsum and laterally, belly grey, head and back with fine, green-gold flecks.

Oral Disc. - Mouth terminal, directed anteriorly; lips not expanded; oral papillae, labial teeth and jaw sheaths entirely absent.

LTRF. - N.A.

Feeding Strategy. - It has been thought that the larvae subsist entirely on yolk throughout its developmental period (Inger, 1966). This is deduced from the fact that the tadpoles possess a weakly-developed mouth, a yolk-filled gut and exhibits rapid development. Such a feeding strategy was verified by dissections performed on tadpoles at various stages (Lim & Ng, 1991). Extensive lipid deposits were discovered within their short, clear guts at the hind limb bud stages. These deposits decrease as hind limbs and fore limbs develop further. At the emergence of all four limbs and beginning of tail resorption, dark coloured detritus was visible within the gut (Lim & Ng, 1991; pers. obs.). It is highly likely that the advanced stages derive some form of nutrition from this detritus, as indicated by Lim & Ng (1991).

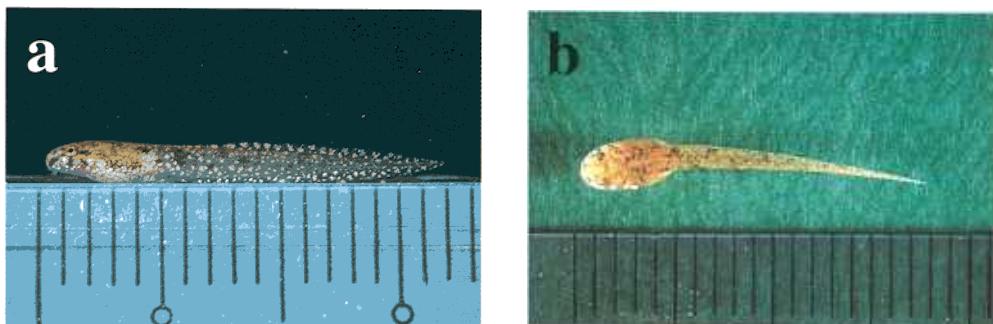


Fig. 13. Lateral (a) and dorsal (b) aspects of *Rana plicatella* larva (Stage 26).

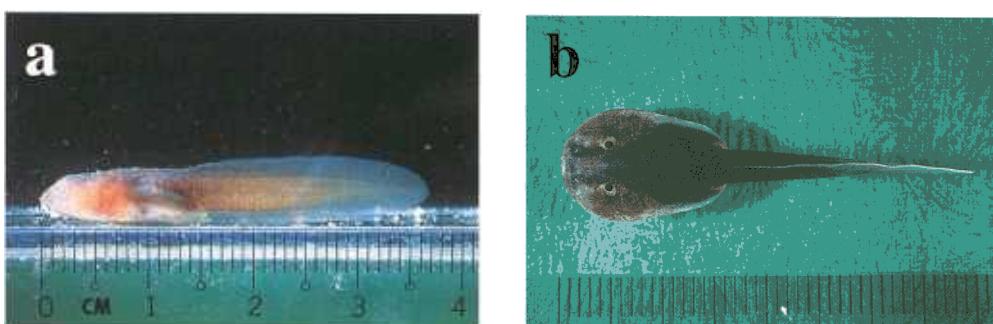


Fig. 14. Lateral (a) and dorsal (b) aspects of *Nyctixalus pictus* larva (Stage 28).

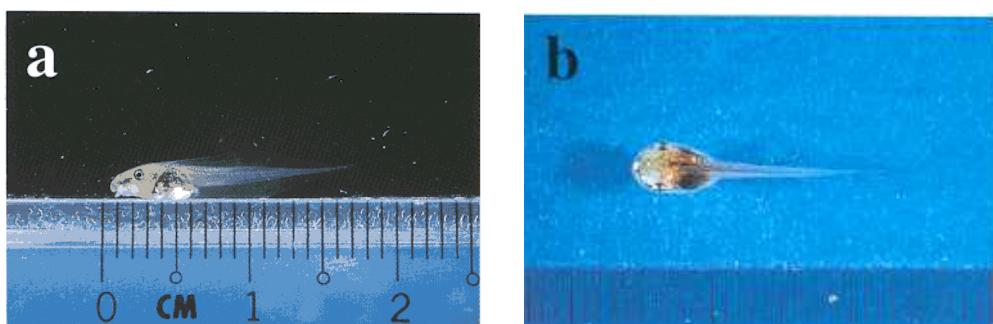


Fig. 15. Lateral (a) and dorsal (b) aspects of *Polypedates leucomystax* larva (Stage 27).



Fig. 16. Lateral (a) and dorsal (b) aspects of *Kalophryneus pleurostigma* larva (Stage 35).

Whether this ingestion of the detritus is intentional or accidental remains to be confirmed. Despite the abundance of microorganisms and insect larvae within the pitcher fluid, the larvae were not observed to actively graze or consume such potential food sources.

Development. - At the time of collection, larvae were between the Stages 21-23, with external gills still present. The dark-grey, antero-ventral cement glands were also present. Five days from collection date, hind limb buds were already visible (Stages 27-30) and the ventral gut coils were distinct. Another five days later, the hind feet were well formed and the elbows of the fore limbs were beginning to protrude at the sides (Stages 37-40). Simultaneously, pigmentation was gradually increased. Finally, fifteen days from its collection date, the well-formed fore limbs erupt and tail resorption is complete within one day.

Simultaneously, the undisturbed larvae at the original site had also begun emerging from the pitchers. This was observed at night and new emergents were crawling along the slanted walls of the pitcher. As noted by Lim & Ng (1991), the froglets were 'excellent jumpers' despite their diminutive size (SVL 4-5 mm) and disappeared among the surrounding leaf litter as soon as they leapt away. As to what the young emergents feed on at this period remains to be determined. The characteristic inguinal ocellus is not yet developed at this stage.

Material examined. - (n = 35); ZRC.I.2938-2957, ZRC.I.2958-2967, ZRC.I.2968-2983, ZRC.I.3425, ZRC.I.3426.

Additional Remarks. - Berry (1972) apparently discovered two distinguishable larval forms of *K. pleurostigma* in Peninsular Malaysia. She believed that the larger form (TTL 13 mm) belonged to that of *K. pleurostigma pleurostigma*. These larvae can be differentiated by an 'acutely pointed' tail and a 'ventrolateral' mouth. The smaller form, which has a rounded tail and a terminal mouth, was thought to belong to an 'unknown subspecies of *K. pleurostigma*'. The larvae observed in Singapore agree with descriptions of the 'smaller form', as no larvae have been found bearing an 'acutely pointed' tail. However, Inger (1985) reported that a variation in tail shape comparable to that observed by Berry between samples occurred within a Bornean sample reared from a single egg clutch. Thus, the possibility of two taxa being involved remains to be verified.

Kaloula pulchra Gray

(Fig. 17; Table 17)

Vernacular Names. - Banded Bullfrog (Lim & Lim, 1992); Painted Toad, Malay-Kodok Betong Sisa (Kiew, 1984b); Asian Bullfrog, Painted Frog (Mattison, 1993); Malaysian Painted Toad (Walls, 1995); Asiatic Painted Frog (Karsen et al., 1986).

Geographical Distribution. - India, South China, Hong Kong, Burma, Bengal, Thailand, Malay Peninsula, Sumatra, Borneo, Sulawesi (Kampen, 1923; Parker, 1934; Inger, 1966). Supposedly introduced to Singapore (Parker, 1934; Lim & Chou, 1990).

Typical Habitats. - Normally associated with human habitations; abundant in towns, cities and villages. Though largely unknown from natural, undisturbed forests, this species has been found intruding into local nature reserves.

Table 17. Developmental changes in HBL and TTL of larval *Kaloula pulchra*. Stages 26-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
26	15	3.3-3.8	9.2-10.1
28	6	4.2-5.6	11.3-13.8
31	5	5.5-6.8	14.1-17.1
34	4	6.1-7.9	14.9-16.8
36	3	6.9-8.2	16.4-17.8
38	3	7.7-9.1	15.8-17.7
40	5	7.9-8.7	16.1-18.5
42	3	8.6-9.3	17.5-19.3
44	4	9.9-10.2	12.2-14.1
46	6	SVL=10.1-11.3mm	

Reproductive Strategy. - Often found breeding in temporarily flooded bodies of water formed after heavy downpours. Amplexus is axillary and the eggs are deposited in small clumps of between two to three dozen within a sticky mucus. Up to a hundred eggs may be laid by a female. The eggs (1.5-2.0 mm diameter) float in mats and the portions exposed to the surface are considerably flattened from above.

Larval Microhabitats. - Larvae have been encountered in flooded, stagnant drains, lawns, roadside ditches. Leaf litter may or may not be present at these sites.

Larval Morphology. - Head-body oval, HBW 0.67-0.83 of HBL; dorsum flattened; snout broad and truncate; nostrils dorsal, inter-narial much narrower than inter-orbital; eyes lateral, inter-orbital six to eight times inter-narial; spiracle median, prolonged posteriorly as a transparent tube, attached to belly dorsally, opening at level of mid-thigh; vent median, anal tube curving downwards and backwards, projecting just below the lower caudal membrane. Tail pointed, without terminal filament; fin margins subequal, convex. TL 1.69-2.12 of HBL.

Colour/Markings. - (In life) Head-body from olive-brown to black above, occasionally with golden speckles; venters lighter, marbled with white; at head region, a dark line connecting nostril with anterior corner of eye. Caudal fins usually colourless, except for isolated dark blotches.

Oral Disc. - Mouth terminal, very small, consisting of a straight upper lip and a contractile lower one; oral papillae, labial tooth rows and jaw sheaths absent.

LTRF. - N.A.

Feeding Strategy. - Larvae are very active and constantly on the move to search for food sources. In captivity, tadpoles were fed with commercial fish food and aquatic plants. Smith (1916a) reported that they 'devour both animal and plant matter, and the more putrid it is, the more they seemed to like it'. The larvae apparently tackled any piece of meat or fruit in a manner similar to ranid-type tadpoles with jaw sheaths and teeth, rather than the toothless

microhylid group. Heyer (1973), while examining the gut contents of tadpoles, found the exoskeletons of larval mosquitoes within the guts of this species.

Development. - In captivity, the larvae developed rather rapidly and the earliest emergents were completing their metamorphosis after three weeks. By the fourth week, more than half of the batch would have emerged. At the late two-limb stage (Stages 37-41), the distinct bands on the hind-limbs are already noticeable. After eruption of fore-limbs, the tail is fully resorbed by the second day and young emergents can vary from black to bronze brown, with white to golden brown patches on the limbs. The light flank mark may or may not be present. Provided with small, live foods (eg. fruit flies and young crickets) and a moist substrate for burrowing, the young can grow rather rapidly in captivity (Smith, 1916a; Walls, 1995).

Material examined. - (n = 54); ZRC.1.3443, ZRC.1.3444, ZRC.1.3445, ZRC.1.3446, ZRC.1.3447, ZRC.1.3448.

Microhyla borneensis Parker

(Fig. 18)

Vernacular Names. - Rufous Froglet, Malay- Katak Anai (Kiew, 1984b); Bornean Narrow-Mouthed Frog (Inger & Stuebing, 1997).

Geographical Distribution. - Borneo, Southern Thailand, Peninsular Malaysia, Singapore (Leong & Chou, 1997).

Typical Habitats. - Inhabitant of forest floor in primary rainforest (Berry, 1975). Isolated populations in BTNR and CCNR.

Reproductive Strategy. - Unknown.

Larval Microhabitats. - Seven to eight larvae at the limb-bud stage (Stages 27-28) were discovered in a clear forest pool formed as a result of heavy showers. The pool measured approximately 80 by 50 cm and not more than 5 cm deep. The bottom was laden with silt and leaf litter. The larvae were seen hovering just beneath the water surface, with their tail tips beating rapidly, not unlike larvae of *Microhyla heymonsi*.

Larval Morphology. - Head-body ovoid, flattened above, spherical below; HBW 0.51-0.53 of HBL; snout truncate; nostrils dorsal, nearer to snout tip than eye, inter-narial 0.25-0.27 of inter-orbital; eyes lateral, visible from above and below; spiracle median, fused with venter; spiracular opening with smooth, convex margin, position of spiracle 0.69 HBL from snout tip; vent median, opening into a short, thick tube in line with margin of ventral fin. Tail tapering gradually towards a short, terminal filament; fins sub-parallel, tapering abruptly at posterior fifth towards a narrow point; dorsal fin originating from root of tail, shallower than tail muscle for anterior half; ventral fin deeper than or equal to height of caudal muscle at anterior half; TL 1.85-2.13 of HBL.

Colour/Markings. - (In life) Head-body and tail muscle orange- to reddish-brown; distinct dark patch in between and at the rear of eyes, dorso-lateral patch beginning from mid-body straight towards root of tail; a dark lateral band running from the snout, through the eyes, towards the hind limbs; head speckled with orange-gold iridocytes; lateral corners of lips

reddish; venters light, speckled with dark pigments especially around the throat; anterior half of tail pigmented black, followed by an unpigmented zone, after which is a characteristic dark band extending onto dorsal and ventral fins; posterior to this is another orange band, ending in a dark terminal filament.

Oral Disc. - Mouth dorso-terminal, lower lip only slightly expanded, lateral corners of lip with knob-like protruberance; papillae, labial teeth and jaw sheaths absent.

LTRF. - N.A.

Feeding Strategy. - In captivity, larvae were reared on a diet of crushed/powdered pellet fish food. The presence of such finely ground particles would be quickly detected by the larvae and increased gulping actions at the water surface would follow. The floating particles would gradually be drawn towards the mouth. Finer particles would be ingested and larger ones 'spat' away forcefully. The feeding habit consists of the alternate drawing of food towards the mouth and forcing away of the larger food sizes.

Development. - Of the larvae collected, only one individual successfully completed metamorphosis. All larvae were obtained at Stage 31 of development (HBL 3.5 mm, TTL 10.5 mm). Hind limb development proceeded steadily over the following month. By the fifth week from collection, the larva had well developed hind limbs (Stage 39, HBL 5.9 mm, TTL 17.5 mm). Within the next few days, the fore-limb emerged and tail resorption was complete in another day (Stage 42, HBL 6.2 mm, TTL 11.5 mm). The emergent (Stage 46, SVL 5.0 mm) was kept for three more weeks to allow for development of colouration. Its dorsum was a reddish-brown with a dark brown marking at the pectoral region. Cross-bars were faintly visible on the limbs. Ventrally, its belly was pale and translucent but the throat region was heavily mottled with dark pigments.

Material examined. - (n = 8); ZRC.1.2221, ZRC.1.3427, ZRC.1.3428, ZRC.1.3492.

Additional Remarks. - An excellently preserved specimen collected by C.F. Lim (27.10.1974) in 'leaf litter' at a swamp forest and catalogued in the ZRC as 'undetermined' was encountered (ZRC.1.2221). This Stage 37 larva was examined and found to be comparable to the ones collected in the field, in terms of size (TTL 17.7 mm), external morphology and pigmentation patterns. The characteristic dark band at the posterior third of the tail was still distinguishable.

***Microhyla butleri* Boulenger**
(Fig. 19; Table 18)

Vernacular Names. - Painted Chorus Frog (Lim & Lim, 1992); Noisy Froglet, Malay-Katak Bising (Kiew, 1984b); Butler's Pigmy Frog (Karsen et al., 1986).

Geographical Distribution. - South China, Burma, Thailand, Annam, Peninsular Malaysia, Singapore (Parker, 1934; Lim & Lim, 1992).

Typical Habitats. - Inhabitant of both cleared areas (eg. gardens, grassy roadside banks) and disturbed forest. Either found on low bushes or on the ground hidden among grasses, shrubs and other vegetation.

Table 18. Developmental changes in HBL and TTL of larval *Microhyla butleri*. Stages 26-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
26	2	6.3-6.6	11.9-12.3
28	4	7.1-8.4	12.5-14.0
30	2	8.8-9.4	13.9-14.8
34	3	9.3-9.8	15.1-16.2
36	3	9.1-10.2	16.3-16.9
40	3	9.3-11.1	17.1-18.9
44	2	9.4-9.8	18.5-19.6
46	5	SVL=9.3-10.1 mm	

Reproductive Strategy. - Median to large areas of rain-filled pools are often used as breeding sites. Berry (1964) found this species to breed throughout the year. In the mating adults, amplexus is axillary. Information on the size of egg clutch was unavailable.

Larval Microhabitats. - As noted by Pope (1931) and Parker (1934), larvae of this species are often found in relatively permanent pools. In the field, larvae were obtained from similar water bodies and observed to be relatively gregarious.

Larval Morphology. - Head-body with 'tear-drop' shape from dorsal perspective, flattened above and arched at junction with tail; HBW 0.72-0.85 HBL; highest part of head-body sloping from root of tail muscle towards snout tip; snout broadly rounded; nostrils dorsal, nearer to snout tip than eyes; eyes lateral, located at widest part of head-body, inter-orbital six to seven times inter-narial; spiracle median, opening under a transparent sheath just anterior of anus; anus median, an oval slit opening just beneath margin of ventral fin. Tail terminating in a filament; ventral fin usually deeper than dorsal and muscular portion; TL 1.59-1.82 of HBL.

Colour/Markings. - (In life) Head-body and tail a translucent-white to golden-yellow; anal tube pigmented with gold specks; fins either clear or mottled with iridescence and scarlet. As noted by Smith (1917), tadpoles kept in captivity demonstrated a 'distinct diminution in the brilliance of their colouration.'

Oral Disc. - Mouth terminal, width 0.26-0.33 of HBW; oral papillae, labial teeth and jaw sheaths absent; lower lip about equal to upper, not produced into a funnel.

LTRF. - N.A.

Feeding Strategy. - Usually suspended in mid-water to greater depths in the pool, these tadpoles hover with an inclined, head-lowered posture. A stationary position in the water column is achieved through the constant beating of the whip-like flagellum at the tail end, in perfect synchrony with the gulps of water regularly taken. The force generated by this backward propulsion apparently counteracts the potential forward movement caused by continuous gulping of water and its expulsion through the spiracle (Parker, 1928). The large volumes of water filtered through the buccal cavity ultimately contain food items, such as plankton, algae or protozoans, which are effectively sorted out and passed to the gut.

Development. - In captivity, larvae were observed to complete metamorphosis within five to six weeks. A drastic transformation occurs at metamorphosis. The original, spheroidal head-body form is abruptly reduced to an elongate, compressed form at Stage 40. As soon as the fore-limbs emerge, the tail begins resorption (Stage 42 onwards). At this point, the four-limbed larva becomes positively buoyant and can only remain just beneath the surface of the water. By the following day, the tail would have disappeared and the young froglet would display the symmetrical, iridescent wavy bands over a dark brown dorsum. Cross-bars on the limbs are also noticeable at this stage.

Material examined. - (n = 24); ZRC.1.1542, ZRC.1.3429, ZRC.1.3430.

Microhyla heymonsi Vogt

(Fig. 20; Table 19)

Vernacular Names. - Dark-sided Chorus Frog (Lim & Lim, 1992); Answering Froglet, Malay-Katak Tanya-Jawab (Kiew, 1984b).

Geographical Distribution. - Taiwan, South China, Thailand, Sumatra, Peninsular Malaysia, Singapore (Pope, 1931; Lim & Lim, 1992).

Typical Habitats. - Similar preferences as *M. butleri*, known to inhabit clearings and disturbed forests (Berry, 1975).

Reproductive Strategy. - Berry (1964) found this species to breed throughout the year in Singapore. She also noted that aggregations of the adults at breeding sites increased on wet nights. Amplexus is axillary. Eggs are deposited in small, loose clumps of between 30 to 80 (up to 100 eggs may be released at one mating). The entire clump may be attached to an adjacent bank or submerged vegetation.

Larval Microhabitats. - All larvae of this species were collected from still, clear to turbid waters found along trail-side ditches, road ruts or flooded grassland. Pope (1931) suggested that the larvae are adapted to life in swift-flowing water. This remains to be verified as tadpoles of this species were never found in fast-flowing waters but in lentic conditions only.

Larval Morphology. - Head-body ovoid, rounded ventrally and moderately flattened dorsally at the head region; HBW 0.56-0.58 of HBL; snout bluntly rounded; nostrils dorsal, nearer snout tip than eyes; eyes lateral, inter-orbital width four to seven times inter-narial distance; spiracle median, opening in a transparent sheath below centre of gut, anterior to anus; vent median, a short tube from body-tail junction leading vertically towards margin of ventral fin. Tail possessing a terminal filament; fin margins sub-parallel, tapering at posterior third, uniting in a fine point, lower fin slightly deeper than upper fin, but not as deep as anterior half of caudal muscle; TL 1.94-2.17 of HBL.

Colour/Markings. - (In life) Head-body and tail muscle pale buff to yellow brown; dorsally a distinct iridescent patch between the eyes (especially conspicuous in the early stages); anterior half of tail distributed with fine, dark pigments; an iridescent streak along mid-dorsal ridge of caudal muscle; both fins usually clear

Table 19. Developmental changes in HBL and TTL of larval *Microhyla heymonsi*. Stages 26-46 reared.

STAGE	NO.	HBL (mm)	TTL (mm)
26	8	4.1-5.3	12.9-14.4
28	3	5.4-6.1	14.1-14.8
30	5	5.8-6.5	14.7-15.3
32	2	5.6-6.8	15.2-16.8
34	2	6.2-6.6	15.9-17.5
36	4	5.8-6.5	16.6-19.0
40	8	6.1-7.8	18.2-23.1
42	4	6.5-7.5	19.5-22.3
44	5	6.9-7.2	11.5-18.3
46	7	SVL=4.5-6.8mm	

Oral Disc. - Mouth dorso-terminal, lower lip expanded into a broad funnel surrounding the mouth, upper lip horse-shoe shaped; a knob-like protrusion on both sides of the mouth within the oral disc; oral papillae, labial tooth rows and jaw sheaths absent.

LTRF. - N.A.

Feeding Strategy. - Usually frequenting the upper levels of the water column, where its feeding position is with the tail inclined to a level below the head region. As already mentioned, the lower lip is furnished with a large, cutaneous flap which can be erected or depressed at will. When the tadpole is at rest below the surface of the water, this flap is lowered and curved backwards upon itself. During feeding, this expanded structure is raised and spread out, forming a very shallow, saucer-like arrangement. This acts as a funnel and serves to furnish as large an area as possible for trapping any minute particles floating on the water, which are drawn towards it by the rapid, sucking action of the tadpole.

In captivity, the larvae of this species responded just as well as those of *M. borneensis* to powdered fish food lightly dusted over the water surface. Their techniques of attracting and rejecting the various sized food particles were very similar, if not identical to each other. Larvae of *M. heymonsi* however, were capable of ingesting larger sized particles than the larvae of *M. borneensis*.

Development. - In captivity, larvae of this series required from four to six weeks before emergents appeared. As the tadpole matured, the inter-orbital iridescence began to fade. By the four-limbed stage (Stage 41 onwards), the dorsum has increasingly darkened and a thin, pale vertebral line becomes noticeable. The dark, lateral bands running from snout tip to groin also becomes prominent. Cross-bars on the limbs also begin to appear at this stage. Tail resorption is complete within a day and the emergents are already able to leap considerable distances onto land. In the young froglets, a ()-shaped marking is sometimes seen flanking the vertebral stripe mid-dorsally.

Material examined. - (n = 48); ZRC.1.1541, ZRC.1.3431, ZRC.1.3432, ZRC.1.3433, ZRC.1.3434.



Fig. 17. Lateral (a) and dorsal (b) aspects of *Kaloula pulchra* larva (Stage 39).



Fig. 18. Lateral (a) and dorsal (b) aspects of *Microhyla borneensis* larva (Stage 31).



Fig. 19. Lateral (a) and dorsal (b) aspects of *Microhyla butleri* larva (Stage 33).



Fig. 20. Lateral (a) and dorsal (b) aspects of *Microhyla heymonsi* larva (Stage 39).

DISCUSSION

Predation and injury

Besides the adults, the larval stages of anurans are also preyed upon by many species of vertebrates as well as aquatic invertebrates (Duellman & Trueb, 1994). In the field, an account of predation on anuran larvae was observed when an arachnid *Thalassius albocinctus* (Doleschall) (F. Pisauridae) captured a tadpole of *Rana chalconota*. Both were found within a tray net while sampling for larvae in a forest stream. The spider was approximately 6 cm across and did not release its grip on the tail base of the two-limbed (Stage 40) tadpole even when caught out of the water. On a separate occasion, a spider of the same species, but smaller in size (4 cm across) was also spotted feeding on the tadpoles of *Microhyla butleri*. It was observed to feed only on the tail muscle portion and disregarded the head portion. Three to four 'tailless' tadpoles were found just beneath the water surface, adjacent to a leaf platform from which it was hunting. A similar predator-prey relationship was also reported by Johnson (1996) between the larvae of *Hyla femoratus* and the spider *Dolomedes* sp. (F. Pisauridae).

Throughout the sampling period, other potential predators encountered were dragonfly nymphs and diving beetles. Vertebrate predators most likely to feed on the larvae were the carnivorous fishes found in the freshwater habitats of Singapore (Lim & Ng, 1990). Examples of such fishes include *Channa lucius*, *Channa gachua*, *Channa striata*, *Luciocephalus pulcher*, *Nandus nebulosus*, *Clarias batrachus* and *Clarias teijsmanni*, all of which were encountered on various occasions in the field during larval surveys. In the smaller, quiet pools, other species such as *Monopterus albus* are likely to feed on the larvae present, as has been recorded by Heyer (1973). The water-snake *Homalopsis buccata* (Linnaeus) was encountered in the field at the same microhabitats where larvae were to be found and this species is a likely larval-predator.

Naturally incurred injuries of tadpoles were observed during field sampling. A large proportion of the injured larvae had either bruised or bitten tail ends, which possibly indicates attempts by potential predators to feed on them. Such injuries were observed in some individuals of *Leptobrachium nigrops*, *Limnonectes malesiana*, *Rana chalconota*, *Rana erythraea*, *Microhyla butleri* and *Microhyla heymonsi*. In captivity, a group of *M. heymonsi* larvae was regularly harassed by the mosquito fish, *Gambusia holbrookii*, which blended very well amongst the microhylid larvae. The fish would sneak up from the rear of the tadpoles and make a quick dash to bite off a portion of their terminal filaments, leaving a number of tadpoles without this locomotory apparatus. Regeneration and healing of injured tail parts was observed in captivity for those species previously mentioned, although the tails never attained their original lengths.

Developmental anomalies

Although its incidence was low, certain abnormalities of development were observed in various specimens sampled. One-legged individuals possessing only either left or right hind limbs but without the opposite limb were seen in larvae of *Bufo quadriporcatus* and *Rana plicatella*. For *Bufo melanostictus*, a bizarre anomaly was observed in an individual with fully erupted fore limbs but without any hint of hind limbs at all.

In an undersized Stage 42 larva of *Rana limnocharis*, the fingers and toes on the left limbs were not fully formed while those on the right were normally developed. A similar reduction in phalangeal formation was noted in a group of metamorphosing *Microhyla heymonsi*. In

a batch of *Polypedates leucomystax*, a few individuals were observed to have buoyancy problems and were constantly afloat near the water surface. Such tadpoles also appeared to be more dorso-ventrally depressed than their conspecifics and were not feeding regularly. These abnormalities are most likely to be genetic in origin as no potential sources of mutagenic substances were detected at the sampling sites.

Interspecific comparisons

From observations of the feeding behaviour of the larval anurans already described, three species share similarities in terms of the structure and function of their mouths. *Megophrys nasuta*, *Microhyla borneensis* and *Microhyla heymonsi* are all surface feeders and have similarly designed mouths. The oral discs of these three tadpoles are orientated antero-dorsally and their lower lips are expanded to form a 'funnel'-shaped structure. This extensible portion of the mouth disrupts the surface tension while acting as a sieve for food particles. A similar comparison between the surface feeding larvae from two different families (Megophryidae and Microhylidae) has also been made by Smith (1926).

During larval development, the nutritional mode of two species from different families bear a striking resemblance to each other. The larvae of both *Pelophryne brevipes* (F. Bufonidae) and *Kalophrynx pleurostigma* (F. Microhylidae) have (i) diminutive sizes (TTL up to 11 mm), (ii) poorly developed mouthparts, (iii) are weak swimmers, (iv) possess only a few gut coils laden with yolk and (v) have one of the shortest developmental stages among the larvae (16-30 days). This strategy appears to be an example of the convergent adaptation of two larval species from vastly different families towards an optimum utilisation of small, temporary bodies of water within such forest habitats.

Future studies

Detailed examination of internal buccopharyngeal structures using electron microscopy (eg. Wassersug et al., 1981; Inger, 1985) may help in determining the possible diets of these tadpoles, while serving as reliable taxonomic characteristics at the same time. Ecological studies considering intra-specific and inter-specific interactions between individual or co-habiting populations of tadpoles would shed light on the selection pressures involved in such situations. These studies would also provide more clues to the population dynamics of larval anurans in tropical situations. Examples of such studies are those reported by Heyer (1973) and Inger et al. (1986).

Locally, the larvae of six anuran species has not been encountered yet. The tadpoles for three of these species, namely *Rana baramica*, *Limnonectes paramacrodon* and *Rhacophorus cyanopunctatus*, still remain unknown. Additional field surveys around the known adult habitats may eventually reveal their actual larval identities. Future encounters of larval *Pelophryne brevipes*, *Rana glandulosa* or *Theloderma horridum* can be verified by comparison with the descriptions of their tadpole stages already provided.

Even among the commonly encountered species, questions still remain with regards to certain aspects of the larval stage. The tadpole of *Rana chalconota*, for example, possesses a set of glandular patches on its body which have been thought to act as poison glands (Liem, 1961). The exact purpose and function of these sub-dermal structures still remains to be verified. In another ranid species, *Rana cancrivora*, the tadpoles which occur at the hot springs of the island, Pulau Tekong, present interesting case studies as to how successful or well adapted the population might be to the above-average temperatures and salinities.

CONCLUSION

In small, urbanised Singapore, habitats still remain for the continued survival of anuran populations. Among these populations, it has been demonstrated that a large variety of larval forms exist. Each of these larval types has been equipped with a particular set of characteristics that enables it to survive the larval period, complete metamorphosis and proceed to further challenges in its respective habitat. However, certain larval forms are better equipped than others at surviving under various conditions. This apparent segregation of niche enables the local anuran fauna to be categorised into two broad groups: 'true forest-species' and 'non forest-species'.

It is the first group that is of prime importance, if conservation of natural habitats is to be a priority. Species belonging to this group serve as reliable indicators of the relative health of such nature areas (Lim, 1994). Population declines of certain anuran species may point towards the possible degradation of a particular microhabitat or ecosystem which is increasingly unable to support these species together with their larval stages. Already, examples of the decline and disappearance of amphibian populations have been witnessed around the globe. The need to monitor and maintain anuran populations, even in Singapore, could never be greater.

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APPENDIX I

The characteristic call/s of 20 anuran species from Singapore are briefly described.

No.	Species	Description of Call/s
1.	<i>Leptobrachium nigrops</i>	A 'rattling gurgle' (Lim & Lim, 1992).
2.	<i>Megophrys nasuta</i>	An 'anvil-clinking "kang-kang"' (Yong, 1976); a 'loud, short honk' (Dring, 1979); a 'metallic honk' (Lim & Lim, 1992).
3.	<i>Bufo melanostictus</i>	'Long trills of from 4-30 seconds' (Heyer, 1971).
4.	<i>Ocidozyga laevis</i>	An 'unobtrusive and not unmusical "chink, chink" often repeated' (Smith, 1916c). Alcala (1962) noted that its call 'resembles the syllables "ek-ek-ek" repeated softly and at a slow pace'.
5.	<i>Rana baramica</i>	A 'long call consisting of a series of rapidly repeated notes that sounds like "wit-wit-wit-wit-wit-wit"' (Arak, 1984); a 'loud, continuously repeating "yip-yip-yip"' (Lim & Lim, 1992). As noted by Dring (1979), males usually call from among thick tangles of vegetation, roots or leaf litter. Calls are heard at dusk and continue into the night.
6.	<i>Limnonectes blythii</i>	Although the Bornean population has been regarded as being "voiceless" (Inger, 1966; Inger & Stuebing, 1989), Hendrickson (1966) identified the call of Singapore <i>R. blythii</i> as a 'muffled, fairly musical grunt'. He also observed individuals in the act of calling at Pulau Tioman and described the call as sounding 'remarkably like the imitation of flatulence which can be made by expressing air in a short burst through tightly compressed lips'. Matsui (1995) described calling males from Peninsular Malaysia producing a 'short, single note of low frequency consisting of many pulses.' Emerson (1995) noted that females made a 'low, soft tonal call'. Males responded by uttering 'the same low, soft call.'
7.	<i>Rana cancrivora</i>	A 'rattling croak . . . heard at night in marshy areas along the coast' (Lim & Lim, 1992).
8.	<i>Rana chalconota</i>	A 'soft "pink pink" like dripping water' (Dring, 1979); a 'staccato series of clicking notes' (Inger & Stuebing, 1989); a 'series of soft clicking chirps' (Lim & Lim, 1992). Males form calling groups along side pools of streams and the edges of ponds (Inger & Stuebing, 1989).
9.	<i>Rana erythraea</i>	A 'squeaky warble' (Inger & Stuebing, 1989). This species is reported to call while sitting in water and does not start calling until after 10 p.m. (Arak, 1984). In captivity, a gravid, adult female was heard 'squeaking' at irregular occasions during both day and night.
10.	<i>Rana glandulosa</i>	A 'loud, resonant WAHK! in rapid sequence' (Inger & Stuebing, 1989).
11.	<i>Rana limnocharis</i>	The call is 'powerful and resembles the clatter of castanettes in the distance' (Kirtisinghe, 1957); a 'raspy chirp, rapidly repeated' (Inger & Stuebing, 1989).

No.	Species	Description of Call/s
12.	<i>Rana plicatella</i>	A series of deep, long-drawn, crescendo croaks by males calling beside small streams, usually from under dead leaves (pers. obs.).
13.	<i>Nyctixalus pictus</i>	Single, short, soft whistles (Lee, K. L., pers. comm.).
14.	<i>Polypedates leucomystax</i>	A 'low-pitched, nasal quack' (Inger & Stuebing, 1989).
15.	<i>Theloderma horridum</i>	'Low grunts or croaks, uttered singly at intervals' (Boulenger, 1903).
16.	<i>Kalophrynus pleurostigma</i>	A series of staccato chirps accelerating towards the end (pers. obs.); a 'long series of unpulsed notes, . . . emitted very irregularly both in length and interval' (Matsui et al., 1996).
17.	<i>Kaloula pulchra</i>	A 'very loud low-pitched voice that can be heard from a considerable distance', created by filling the subgular vocal sac while afloat and spread-eagled on the water surface (Taylor, 1962); their calls resemble 'the bellows of cattle' (Lim & Lim, 1992).
18.	<i>Microhyla borneensis</i>	Males utter a single, short 'krick' note at intervals of around five minutes (pers. obs., Leong & Chou, 1997)
19.	<i>Microhyla butleri</i>	The cry of calling males sounds like 'the gritting of human teeth' (Taylor, 1962); a 'series of partially pulsed notes, each note lasting 0.16-0.21 seconds' (Heyer, 1971).
20.	<i>Microhyla heymonsi</i>	The call is likened to 'k-r-r-i-c-k, k-r-r-i-c-k repeated at regular intervals' (Grandison, 1972); a 'series of long-drawn "kriiick"' (Lim & Lim, 1992).