THE FEMALE ANURAN REPRODUCTIVE SYSTEM IN RELATION TO REPRODUCTIVE MODE

by

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III. RESULTS

SUMMARY

Anurans display considerable morphological diversity in the female reproductive system, and a great variety of reproductive modes. In this study I defined the relationships between interspecific morphological variation and reproductive modes among 108 species.

Associations between reproductive mode and morphology must be related to the nature of the spawn, therefore I constructed a classification of modes based on egg diameter and the degree of embryonic dependence on stored yolk, to facilitate comparison with morphology:

Mode I - eggs with little yolk, larvae aquatic and feeding

Mode II - eggs containing moderate yolk reserve, only late larval stages feeding

Mode III - eggs containing large yolk reserve which nourishes embryo or larva throughout development

Mode IV - viviparity (not considered here, because the eggs contain little yolk, therefore reproductive morphology is not influenced by the same parameters as in species of Modes I - III).

In defining egg characteristics for each mode, I observed the following features:

1) unpigmented eggs in species which oviposit away from sunlight, and a significant trend towards loss of pigmentation from Mode I to III;

2) egg diameter (a) is positively correlated with snout-vent length in species of Modes II and III but not I, and (b) increases significantly from Mode I to III;

3) ovarian complement (a) is positively correlated with snout-vent length within a mode, and (b) decreases significantly from Mode I to III;

4) a negative correlation between egg diameter and ovarian complement;

5) for a given snout-vent length, ovarian complement volume remains similar regardless of mode.

I investigated the nature of morphological variation and the ontogeny of the reproductive system. Those features which exhibited significant interspecific variation, together with correlations with reproductive mode, were as follows:

1) the number of ovarian lobes is positively correlated with snout-vent length and decreases from Mode I to III. These correlations reflect changes in surface area of ovarian epithelium (larger in larger species, smaller for a smaller number of larger eggs), which is achieved by changes in the number of lobes;

2) ovarian asymmetry, which occurs in *Rheobatrachus silus*, was not observed in other species, and therefore appears to be unrelated to reproductive mode as defined here;

3) the number of convolutions of the *pars convoluta* of the oviduct is proportional to the length of that region, and is positively correlated with snout-vent length in Modes I and III but not in Mode II. It is negatively correlated with egg diameter, and significantly smaller in Modes II and III than in Mode I. These correlations probably reflect changes in surface area of secretory oviduct wall, achieved by altering oviduct length, in species with different

egg diameters and/or ovarian complements, which therefore require different quantities of oviduct secretions;

4) oviduct width (an indicator of lumen diameter) is positively correlated with egg diameter, and is significantly larger in Modes II and III than in Mode I, thus enabling the large eggs of Modes II and III species to traverse the oviduct;

5) in foam-nesting species the posterior-most convolutions are greatly enlarged and therefore probably secrete mucus for foam production;

6) the ovisacs remain separate, or unite posteriorly, or are completely united. Separate ovisacs are present only in species with small eggs, and there is a significant trend towards fusion from Mode I to III; fusion may reduce the risk of large eggs impacting during oviposition.

There is no apparent correlation of any pattern of reproductive morphology with taxonomic status. Similar morphological modifications have evolved in unrelated species which share the same reproductive mode, presumably in response to similar physiological and environmental pressures.

DECLARATION

This thesis contains no material accepted for the award of any other degree or diploma in this or any other university.

To the best of my knowledge this thesis contains no material previously published or written by another person, except when due reference is made in the text.

Should this thesis be accepted for the award of a higher degree, I consent to it being made available for photocopying and loan.

PHILIPPA HORTON

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I

INTRODUCTION

(a) BACKGROUND AND AIMS

(i) Reproductive Diversity in the Anura

The traditional view of the reproductive cycle of a frog is that it involves the deposition of large numbers of small eggs in a pond or similar water body, the hatching of these eggs into tadpoles which then feed and grow, and the metamorphosis of the tadpoles into juvenile frogs. But more recently there has been an increasingly widespread recognition that this breeding pattern is atypical of a large proportion of anuran species. This growing recognition has culminated with the discovery of gastric brooding in *Rheobatrachus silus* (Corben *et al.*, 1974). Lamotte and Lescure (1977) have reviewed most of the literature concerning species with reproductive patterns, or modes, which diverge from the totally aquatic mode described above; they include more than 90 genera in their account. Not only are there many species with divergent reproductive modes, but anurans also display perhaps the most diverse array of reproductive modes of any vertebrate group. Anuran reproductive modes range from completely aquatic to completely independent of free-standing water, with varying degrees of parental care involved, including gastric brooding in *Rheobatrachus*, ovoviviparity, and viviparity in *Nectophrynoides occidentalis*.

Many of the features which characterize reproductive mode in frogs are behavioural, but many are related to the nature of the eggs and their protective coatings, and therefore directly involve the female reproductive system. Thus the female reproductive system may be a structure which displays distinctive morphological variation among frogs. Surprisingly, in view of the diversity of reproductive modes, few herpetologists have considered the reproductive system, but the limited evidence gathered to date indicates that the system does exhibit morphological diversity. What is the precise nature of this morphological variation in the female anuran reproductive system, and how is it related to reproductive mode? These questions are as yet unanswered, and are the ones which I address in this study.

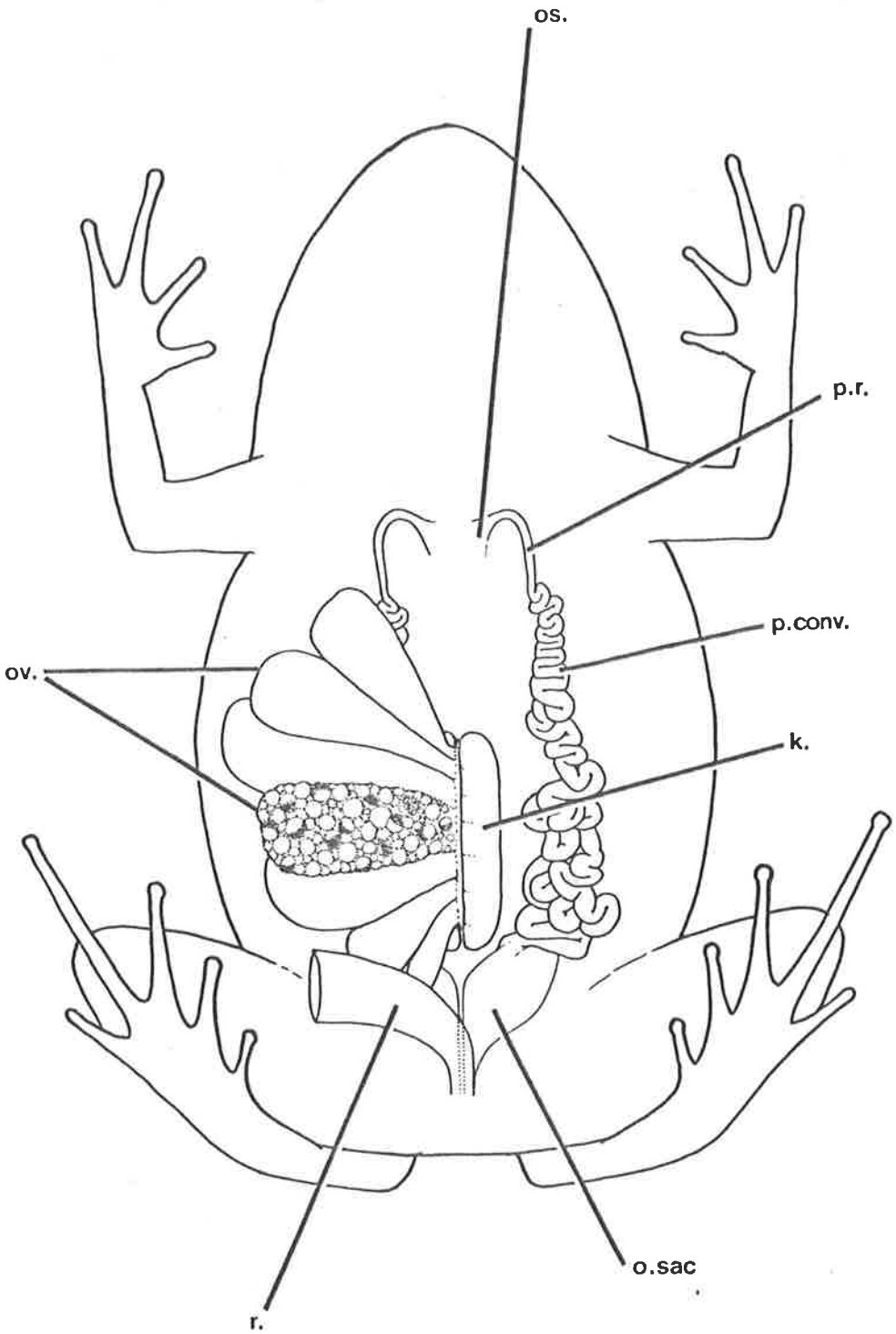
(ii) Published Data on the Female Anuran Reproductive System

The anuran reproductive system as a whole has received only fragmentary attention, other than in part of the work of J.L. Bhaduri and his colleagues, who examined the urinogenital systems of a large number of species, as detailed later. A number of accounts, such as those of Noble (1931), Lofts (1974), Kluge (1977), Romer and Parsons (1977), and Wake (1979), deal with the form and development of the gonads and reproductive tract of anurans in general. They note that the ovaries generally are lobed, sac-like structures, and that the oviducts usually are highly convoluted tubes terminating in thin-walled sacs which empty into the cloaca, as shown in Fig. 1, but they do not consider any species in particular, nor make comparisons between species.

Individual species of diverse families have been studied for their particular interest either as laboratory frogs or because of their taxonomic status or divergent reproductive mode. Among other features, the morphology of the female reproductive system of such species has been

FIG. 1 Generalized female anuran reproductive system, ventral view.

k. = kidney; os. = ostium; o.sac = ovisac;
ov. = ovary; p.conv. = *pars convoluta*;
p.r. = *pars recta*; r. = rectum.


os.
p.r.
p.conv.
ov.
k.
o.sac
r.

examined; these observations are summarized in Table 1.

The first comparative account of female anuran reproductive morphology was that of Spengel (1876). He noted that the ovaries consist of longitudinal rows of thin-walled pouches, or lobes, and that the number of lobes is different in different species but reasonably consistent within a species. He found that *Pelodytes punctatus* possesses unlobed ovaries, *Alytes obstetricans* possesses 3-4 lobes per ovary, *Discoglossus pictus* 5, *"Ixalus"* sp. and *Polypedatus "quadrilineatus"* 6-8, *Pelobates fuscus* 9-12, *Hyla* sp. 9, *Rana* spp. 15, and *Bufo* spp. up to 30 lobes. He recorded that the oviducts are highly convoluted, and that the nature of their termination in the cloaca varies. In *Hyla* sp., *Polypedates "quadrilineatus"*, *"Ixalus"* sp., *Discoglossus pictus*, *Rana* spp., and *Pelobates fuscus*, the oviducts remain separate. But in all of the *Bufo* species which he examined they unite shortly before the single opening into the cloaca, and are united even further in *Alytes obstetricans*. He reported a variable condition in *Bombina bombina* (as *Bombinator igneus*): in one individual the oviducts entered the cloaca separately, but in the remaining seven the oviducts united so that there was only a single opening into the cloaca.

Bhaduri and associates published a series of papers on the morphology of the anuran urinogenital system (Bhaduri, 1932, 1946, 1953; Bhaduri and Banerjee, 1939; Bhaduri and Rudra, 1944; Bhaduri and Basu, 1957; Bhaduri and Mondal, 1962, 1965). These contributions constitute the most important and detailed published study on female anuran reproductive morphology. Those of their data relevant to my study are summarized in Table 2.

Bhaduri noted that the number of ovarian lobes may differ between

TABLE 1: Morphological data on the female reproductive system, from published accounts of individual anuran species. Familial classification follows Duellman (1975) except for Australian leptodactyloids which are retained in the Leptodactylidae, following Tyler (1979).

Family, Species, and Source of Data	Features of Reproductive Morphology
Bufonidae	
Nectophrynoides malcolmi (Wake, 1980, and *in litt.*)	ovaries - sacciform, unlobed oviducts - with 5 or 6 pronounced curves; ovisacs united
N. occidentalis (Angel and Lamotte, 1944; Xavier, 1973)	ovaries - simple sacs oviducts - narrow, unconvoluted; terminal portions are extremely distensible sacs which are united posteriorly and function as uteri
Hylidae	
Litoria aurea (Briggs, 1940)	ovaries - greatly folded sacs with large internal cavity divided by partitions oviducts - highly convoluted; ovisacs remain separate
Leiopelmatidae	
Leiopelma archeyi (Stephenson and Stephenson, 1957)	ovisacs united
Leptodactylidae	
Eleutherodactylus jasperi (Wake, 1978)	ovaries - sacciform oviducts - narrow and convoluted anteriorly, posteriorly in the form of dilated sacs; terminal portions united to form a common chamber which contains developing young
Heleophryne purcelli (Hoffman, 1931)	oviducts - much coiled, unite posteriorly
Myobatrachus gouldi (Watson and Saunders, 1959)	oviducts - broad and convoluted; ovisacs unite
Rheobatrachus silus (Horton and Tyler, 1982; Horton, 1983)	ovaries - with few lobes oviducts - broad with few convolutions; ovisacs united basally
Sminthillus limbatus (Griffiths, 1959)	oviducts - only the right one, which is dilated and coiled, present anterior to the ovisacs; ovisacs united

Family, Species, and Source of Data	Features of Reproductive Morphology
Microhylidae	
Breviceps verrucosus (Beddard, 1908a)	oviducts - poorly convoluted; ovisacs united
Pipidae	
Xenopus (Deuchar, 1975)	ovaries - appear many-lobed in illustration oviducts - appear highly convoluted in illustration
Ranidae	
Rana catesbeiana (Minkoff, 1975)	ovaries - many-lobed oviducts - narrow, highly convoluted; ovisacs remain separate
R. esculenta (Ecker, 1864)	
R. pipiens (Rugh, 1951; Minkoff, 1975)	
R. temporaria (Ecker, 1864; Marshall, 1912; Borradaile, 1945)	
Rhacophoridae	
Chiromantis rufescens (Coe, 1974)	oviducts - convoluted, posteriorly with a large pad of tissue (the "foam gland") on the ventral surface, consisting of three large, swollen oviducal folds held together by connective tissue
Rhinodermatidae	
Rhinoderma darwini (Beddard, 1908b)	oviducts - much coiled; ovisacs united

TABLE 2: Published data of Bhaduri and associates[1] on the female anuran reproductive system. Familial classification follows that of Duellman (1975).

Family and Species (reproductive mode in parentheses[2])	SVL (mm) of Mature Specimens	No. Lobes Per Ovary	Fusion of Ovisacs[3]	Other Features
Ascaphidae				
Ascaphus truei (II)	-	1	1	urinogenital sinus present
Discoglossidae				
Barbourula busuangensis (II)	75.7	1-2	2	
Pelobatidae				
Megophrys monticola (I)	62.0	7-8	2	
M. parva (I)	49.0	4-5	1 or 2 ?	
Scaphiopus couchi (I)	66.0	11-12	2	
S. holbrooki (I)	57.0	9	2	
Leptodacylidae				
Eleutherodactylus alticola (III)	22.3	1	2	
E. nubicola (III)	35.0	1	2	
E. orcutti (III)	-	1	2	
Heleophryne purcelli (II)	49.0	4-5	1	
Leptodactylus melanonotus (I)	37.0	4-5	0	posterior region of *pars convoluta* greatly enlarged
L. pentadactylus (II)	136.0	ca 6	0	" "
L. podicipinus (I)	36.0	4-5	0	" "
Pleurodema cinerea (I)	-	8-10	0	posterior region of *pars convoluta* enlarged
Bufonidae				
Ansonia muelleri (II)	31.4	2	2	
Bufo melanostictus (I)	-	-	1	

Family and Species (reproductive mode in parentheses[2])	SVL (mm) of Mature Specimens	No. Lobes Per Ovary	Fusion of Ovisacs[3]	Other Features
Rhinodermatidae				
Rhinoderma darwini (III)	26.0	1	1	
Dendrobatidae				
Dendrobates auratus (II)	-	1	2	
D. tinctorius (II)	42.0	1	2	
Phyllobates nubicola (II)	15.5	1	2	
Hylidae				
Gastrotheca boliviana (II or III?)	38.0	1	1	
Hyla gratiosa (I)	60.0	9-11	0	
Pachymedusa dacnicolor[4] (II)	95.0	8-9	1	posterior region of *pars convoluta* enlarged
Microhylidae				
Breviceps poweri (III)	-	-	2	
Kalophrynus pleurostigma (I)	45.0	6-7	0	
Kaloula picta (I)	46.0	6-7	0	
Microhyla ornata (I)	22.3	-	0	urinogenital sinus present
Oreophryne annulata (III)	-	1	2	
Ranidae				
Arthroleptis sylvaticus (III)	-	1	1?	urinogenital sinus present
Cacosternum boettgeri (I)	21.0	5	2	
Hemisus marmoratum (II)	-	ca 4	1	
Ooeidozyga laevis (I)	49.1	3-4	0	
Phrynobatrachus keniensis (I)	21.5	3-4	0	
P. natalensis (I)	31.0	4	0	
P. versicolor (I)	30.0	5-6	0	
Platymantis corrugatus[4] (III)	43.7	1	1	

Family and Species (reproductive mode in parentheses[2])	SVL (mm) of Mature Specimens	No. Lobes Per Ovary	Fusion of Ovisacs[3]	Other Features
Platymantis meyeri[4] (III)	34.2	1	1	
P. novae-britannae[4] (III)	-	1	1	
Rana crassipes (I)	59.8	5-6	0	
R. mascareniensis (I)	52.5	ca 12	0	
R. subsigillata (I)	67.3	6-7	1	
Staurois natator (II)	44.0	4-5	1	
Hyperoliidae				
Afrixalus fulvovittatus (I)	23.0	4-5	1	
Chrysobatrachus cupreonitens (?)	29.0	ca 3	2	
Hyperolius marmoratus (I)	29.5	5-6	2	
Kassina senegalensis[4] (I)	45.0	4-5	2	
Leptopelis karissimbensis (II?)	48.8	-	0	
L. viridis (II?)	-	-	0	
Rhacophoridae				
Chiromantis rufescens (II)	66.0	ca 5	0	posterior region of *pars convoluta* greatly enlarged
Rhacophorus maximus (?)	-	-	0	

[1] Data from: Bhaduri and Rudra (1944), Bhaduri (1953), Bhaduri and Basu (1957), Bhaduri and Mondal (1965).

[2] Following my classification of reproductive modes detailed in section (b). Mode I = eggs with little yolk reserve; early stage tadpoles hatch and develop aquatically. Mode II = eggs with moderate yolk reserve; only well developed or later stage larvae motile and feed and develop aquatically. Mode III = eggs with large yolk reserve sufficient for entire development up to the end of metamorphosis.

[3] 0 = Bhaduri's (1953) *uterus separatus* group, 1 = *uterus septatus* group, 2 = *uterus communis* group.

[4] Current name; considered under synonymous genus or species by Bhaduri.

species, and that in some the ovaries are unlobed. He observed that the oviducts are narrow, straight tubes in juveniles, but are highly convoluted in adult individuals. He found no significant morphological variation in the *pars convoluta*, except that in a few species the posterior region of the *pars convoluta* is enormously enlarged (Table 2). It was to the ovisac, which he termed "uterus", that he paid the greatest attention. His investigations showed that the ovisacs may remain separate or may unite and that the extent of union may differ. He proposed three categories (Bhaduri, 1953): (i) the *uterus separatus* group, in which the ovisacs remain separate and enter the cloaca separately; (ii) the *uterus septatus* group, in which the ovisacs are separated to a greater or lesser extent anteriorly but unite posteriorly; and (iii) the *uterus communis* group, in which the ovisacs are completely united to form a common chamber, with a single opening into the cloaca. Finally, he observed the presence of a urinogenital sinus in three species (Table 2).

Apart from Bhaduri's work, few of these investigations are detailed enough to allow the comparison of reproductive morphology between species and they do not permit correlation with reproductive mode. Bhaduri's contributions are the most valuable for detecting variation in reproductive morphology because he examined several particular features in a relatively large number of species. From Bhaduri's work it is apparent that the gross morphology of the female reproductive system follows a similar pattern in all of the species which he investigated; this pattern is illustrated in Fig. 1. Since the basic function of the system is the same for almost all species, i.e. to produce ova capable of being fertilized and of surviving in the external environment, it is not surprising that the system should remain relatively uniform in gross morphology. However, Bhaduri's descriptions and illustrations also indicate that there is considerable variation in particular details of reproductive

morphology, for example in the number of lobes of the ovary. Unfortunately Bhaduri examined only one specimen of almost all species he considered, so the existence of intraspecific variation is not apparent from his work. Therefore it is impossible to define the nature of interspecific variation in reproductive morphology from his studies, or to ascertain correlations with reproductive mode. Nonetheless, Bhaduri believed that some of the variation might be related to differences in reproductive modes. In discussing three species of *Platymantis* (as *"Cornufer"*), Bhaduri and Mondal (1965) commented that saclike (i.e. unlobed) ovaries containing few large eggs are an adaptive feature of terrestrial breeding habits. Bhaduri (1953) and Bhaduri and Basu (1957) considered that the greatly enlarged posterior region of the *pars convoluta*, which they found in five species of foam-nesting frogs, is probably the site of formation of the mucus for foam production. Bhaduri (1953) noted that the oviducts of *Dendrobates* and *Phyllobates* are relatively broad in transverse section, and suggested that this feature may be associated with their large egg size. Bhaduri and Mondal (1965) considered that partially or completely united ovisacs are correlated with the large size of the eggs of the species in which such fusion is found. However, none of these suggestions was substantiated with firm evidence.

(iii) Aims of This Study

My principal aims in this study are to establish and define the nature of morphological variation in the female anuran reproductive system, and to estimate the extent of intraspecific and interspecific variation amongst a wide range of species. In the main part of my study I describe those features or parameters of reproductive morphology which exhibit significant interspecific variation, and I also consider the ontogeny of some of these features in order to detect possible intra-

specific variation between different developmental stages. I then consider the interspecific variation in conjunction with the reproductive modes of the species concerned in order to detect and describe relationships between reproductive mode and morphology. I discuss anuran reproductive modes in detail in section (b) in order to devise a system of classification of modes which will facilitate correlation with reproductive morphology of the species I consider. I also consider the possible functional constraints associated with reproductive mode which necessitate morphological change in the reproductive system. To do so, I investigate parameters which may affect reproductive morphology: body size, egg diameter, number of eggs per ovary, and egg capsule thickness, and correlate these parameters with features of reproductive morphology.

Predictions have been made regarding the reproductive mode of species for which the mode is unknown, based on ovarian egg complement and egg diameter and pigmentation, for example by Tyler (1976a) for *Arenophryne rotunda*, and by Clarke (1983) for *Nannophrys* species. The work of Salthe and Duellman (1973) on factors associated with reproductive mode (none of which concerned reproductive morphology) substantiated the relationships of egg and clutch size with reproductive mode. The results of my study may substantiate predictions about unknown reproductive modes based upon the nature of the reproductive system, such as that of Watson and Saunders (1959) who inferred from the female reproductive system and eggs of *Myobatrachus gouldi* that this species undergoes terrestrial and direct development (habits verified by Roberts, 1981). It may also be possible to make such predictions from the reproductive morphology of juvenile individuals, unlike those predictions based on number and size of eggs, which must be made from mature or almost mature individuals. A secondary aim of my study is thus to determine the suitability of female reproductive morphology for inferring reproductive

mode if the latter is unknown.

The gastric brooding frog *Rheobatrachus silus* possesses probably the most bizarre of all anuran reproductive modes, in which the young are reared in the stomach of the female (Corben *et al.*, 1974; Tyler and Carter, 1981). A further aim of my study is to examine the female reproductive system of *R. silus* in detail, and in the light of the nature of variation in anuran reproductive morphology observed in the main part of my study, to determine any features peculiar to *R. silus* reproductive morphology which may be related to the gastric brooding habit. The data published in Horton and Tyler (1982) and Horton (1983) (Appendices IV and III, respectively) are those which I gathered during this investigation of the reproductive system of *R. silus*.

(b) ANURAN REPRODUCTIVE MODES

An extremely diverse array of reproductive strategies is displayed amongst the Anura, in terms of site of egg deposition, of parental behaviour following oviposition, and of embryonic development. The combination of environmental, behavioural and developmental characteristics of reproduction constitutes the reproductive mode of the species. To facilitate the comparison of reproductive modes of frogs, as in this study, it is convenient to assign these modes to categories. I will outline some of the reproductive modes that have been described by other authors in order to illustrate the range of modes, and their allocation to categories. Published classifications of reproductive modes will then be discussed, followed by my own classification and reasons for its choice. In referring to the young of frogs, for convenience I consider

"embryos" to be those prior to hatching from the egg capsules, "larvae" to be those which have hatched but not completed metamorphosis, and "tadpoles" to be motile, feeding larvae.

The majority of frog species are totally aquatic in their breeding strategies. The eggs are small and are laid in pools, ponds, lentic streams, or similar bodies of water. They hatch within a few days, releasing tadpoles which metamorphose into juvenile frogs. Such an entirely aquatic reproductive mode is found in members of almost all frog families, and is the least specialized. While retaining a pattern of totally aquatic development, other species provide a greater degree of protection for their young. For example, species of the *Hyla boans* group lay their eggs in basins constructed in mud on banks of rivers or lakes (Lutz, 1960; Lamotte and Lescure, 1977). A number of diverse and predominantly rainforest-dwelling species from several families make use of small pools of water which have collected in bamboos, tree trunks or the bases of bromeliad leaves (Lamotte and Lescure, 1977). Many members of the Leptodactylidae and Rhacophoridae lay their eggs in nests of foam, constructed from mucus secreted from the oviducts. This mucus is filled with air bubbles created by the female beating her hands, or it is beaten to foam by the feet of one or both parents. Such foamy nests are laid floating on the water surface in some Australian limnodynastine leptodactylids (Tyler and Davies, 1979), in cavities adjacent to water in some species of *Leptodactylus* (Heyer, 1969), or in trees overhanging water (*Chiromantis*; Coe, 1974).

A lotic environment presents difficulties to aquatic breeding frogs because of the likelihood of eggs and tadpoles being swept downstream to less favourable habitats. Some species have overcome such difficulties by attaching their relatively large, yolky eggs to the underside of

submerged rocks. The eggs hatch into relatively large tadpoles of streamlined, muscular form, with well developed suctorial mouthparts. Such torrent-breeding species include *Ascaphus truei* in which the eggs develop very slowly and the large tadpoles hatch after one month (Noble and Putnam, 1931).

Whether or not the aquatic breeding site is lotic, the eggs and early larval stages of anurans are particularly vulnerable to environmental depredations. The aquatic site may also be ephemeral and unable to support larvae for their entire development. Many anurans are not confronted with these problems as their eggs are laid away from bodies of water and early larval stages are non-motile and non-feeding, or else embryonic development may be extended, so that only later stages adopt an aquatic, feeding lifestyle. The energy requirements of early developmental stages of these species are provided entirely by extra yolk stored within the egg, thus the ova are somewhat larger than those of species in which development occurs almost entirely as tadpoles. The eggs may be deposited on the ground under stones, moss, logs, or buried in soil, for example in *Pseudophryne bibroni*, in which the embryos develop to stage 27 of Gosner (1960) (Woodruff, 1976) and then, following heavy rains which flood the site, hatch, whereupon well-developed, feeding tadpoles are released (Tyler, 1978). Other species deposit their eggs in vegetation, for example *Centrolenella* species oviposit on leaves overhanging streams; advanced tadpoles hatch and fall to the water below to feed and complete development (Lamotte and Lescure, 1977). A male adult in *Pseudophryne bibroni* and *Centrolenella* species is often found with the eggs and possibly remains with them until they hatch. Other species exhibit a greater degree of parental care. For example, dendrobatids lay their eggs on the ground or in vegetation; these hatch and the larvae wriggle onto the back of an attendant parent and are carried for one to many days

until they are released into water to feed and develop there (Silverstone, 1975, 1976). Females of some species of *Gastrotheca* carry their eggs and young in a dorsal marsupium until the young reach an advanced stage of development whereupon they are released and complete development as free-swimming tadpoles (Duellman and Fritts, 1972). A number of other species protect their developing eggs by laying them in nests constructed in folded leaves of vegetation overhanging water, for example species of *Phyllomedusa*, in which the egg mass may be protected at each end of the leaf nest by eggless jelly capsules (Cannatella, 1982). Pyburn (1980) has demonstrated that in *P. hypochondrialis* the enclosing leaf and eggless capsules prevent drying and death of embryos during the 8-9 days prior to hatching.

Many frogs lay large eggs which contain sufficient yolk to enable the developing embryos or larvae to be totally independent of external food sources and usually also of free-standing water. The young may hatch before the end of metamorphosis but do not swim or feed, or else the embryos may remain within the egg capsule throughout development and hatch as juvenile frogs; there are no motile, feeding larval stages. Young which hatch before the end of metamorphosis are found in members of several families; such species include *Kyarranus* species in which the eggs are laid in burrows in wet or flooded earth or moss where the larvae remain (Moore, 1961; Ingram and Corben, 1975; Anstis, 1981), and *Leiopelma* (Bell, 1978). Complete intracapsular embryonic development with no larval stages at all has also evolved, apparently independently, in several families. Members of the genus *Eleutherodactylus* follow this pattern; they lay their eggs concealed beneath moss, leaf litter or similar, and juvenile frogs hatch rapidly from them (Lamotte and Lescure, 1977). The microhylid frogs of New Guinea also oviposit in leaf litter or similar concealed sites, and an adult male is often found with the

eggs and may remain with them until they hatch as juvenile frogs (Tyler, 1963; Menzies, 1975).

Parental brooding of the young, often striking in form, is exhibited by a number of species either with non-feeding larvae or lacking larvae, as detailed by Lamotte and Lescure (1977). For example, several species of *Gastrotheca* retain their young within the dorsal marsupium throughout their development, and the juveniles finally emerge through the posterior aperture of the pouch (Duellman and Fritts, 1972). *Assa darlingtoni* also broods its young, but in inguinal pouches of the male only (Straughan and Main, 1966; Ingram *et al.*, 1975). In *Rheobatrachus silus*, the female swallows her eggs or larvae and retains them in her stomach throughout their development, during which time her digestive functions cease, and she gives birth to them via the mouth (Tyler and Carter, 1981). One species of *Eleutherodactylus* (*E. jasperi*), and two species of *Nectophrynoides* (*N. tornieri* and *N. viviparus*) are ovoviviparous and retain their young in the oviducts of the female (Barbour and Loveridge, 1928; Orton, 1949; Lamotte and Xavier, 1972; Wake, 1978). *Nectophrynoides occidentalis*, which also retains its eggs in the oviducts, has been demonstrated to provide nutrients, secreted from the oviduct walls, for its developing young and is therefore viviparous (Xavier, 1973).

Among the Anura there is almost a continuum of patterns of development of the young from aquatic, motile and feeding larvae, to those with early embryos or larvae nourished by yolk and only advanced larvae aquatic and feeding, to those in which the embryos or larvae rely on stored yolk and are completely independent of external energy sources. There are also many combinations of developmental pattern with site of oviposition and form of parental care. Nonetheless, a feature which is also apparent is the extent to which parallelism in reproductive modes

has occurred, apparently in response to similar environmental pressures. For example, among montane species, representatives of several unrelated groups have overcome the problems of breeding in fast-flowing water. Similarly, the construction of foam nests to contain eggs has evolved apparently independently in members of two families. Martin (1970) has discussed parallel evolution in breeding ecologies of the foam-nesting *Leptodactylus* and Australian limnodynastine leptodactylids, both of which show trends from aquatic to terrestrial development in accordance with changes in habitat characteristics. Many species inhabiting humid and frequently montane areas, where terrestrial eggs can survive without desiccation, have evolved similar developmental patterns which reduce or avoid dependence on free-standing water, and in these frogs the eggs are relatively large due to increased yolk reserves to supply the developing embryos or non-feeding larvae (Goin and Goin, 1962).

Because of such parallelism it is possible to allocate the majority of reproductive modes to particular categories. Jameson (1957) made the first detailed attempt to classify reproductive modes and listed the following categories:

I. Aquatic development: (a) without nests
(b) aquatic nests
(c) terrestrial nests
(d) tadpoles carried to water.

II. Direct development: (a) terrestrial nests
(b) embryo carried until birth.

Salthe and Mecham (1974) followed much the same categorization, but noted that the situation is highly complex and that there are intermediate patterns falling between the subcategories. For example, a few species lay eggs terrestrially but early-stage tadpoles hatch and development is

almost entirely in water, so they lie between I(b) and I(c) (in the latter Salthe and Mecham (1974) include only species in which considerable development takes place before hatching and subsequent aquatic development). There are also species in which there is a tadpole-like larva, but it is entirely non-feeding, and therefore intermediate between I(c) and II(a) (in the latter Salthe and Mecham (1974) include only species in which only vestiges of tadpole form are apparent during development). Crump (1974) considered 10 different reproductive modes in three categories to cover the breeding patterns of 78 species at her study site in Ecuador:

I. Eggs and larvae in water
   - A. Mode 1 - unconstrained body of water
   - B. Mode 2 - tree cavity above ground
   - C. Mode 3 - constructed basin;

II. Eggs out of water, larvae develop in water
   - A. Mode 4 - eggs on vegetation above water
   - B. Mode 5 - eggs in foam nest, tadpoles in water
   - C. Mode 6 - eggs on land and larvae carried to water;

III. Neither eggs nor larvae unprotected in water
   - A. Mode 7 - eggs and tadpoles in terrestrial nest
   - B. Mode 8 - non-aquatic eggs, and direct development
   - C. Mode 9 - eggs and young buried in pits of dorsum - aquatic
   - D. Mode 10 - eggs and young attached to dorsum - terrestrial.

McDiarmid (1978) considered one aspect of anuran reproduction: parental care, and constructed a classification with 12 different forms of parental care grouped in two broad categories: 1) investment (of eggs) at fixed site, and 2) investment at mobile site (i.e. parent). But

McDiarmid's (1978) classification does not consider the reproductive modes of the numerous species which exhibit no apparent parental care.

Considering the diversity of breeding strategies in the Anura, a classification such as that of Crump (1974), which covers every combination of egg deposition site and pattern of development among the species investigated, is probably the most satisfactory. Further categories could be added to accomodate other species if their reproductive modes differed from those already listed. It is probably impossible to construct a simple classification of only a few categories unless one particular factor is to be considered, such as degree of parental care, or extent of aquatic and feeding larval development.

Unlike the studies of Jameson (1957), Crump (1974) and Salthe and Mecham (1974), who examined frog reproductive modes from a general point of view, I consider reproductive mode here only as it affects the morphology of the female reproductive system. Its bearing on the reproductive system must stem largely from the nature of the eggs such as their size and number, i.e. from the form of embryonic and larval development and its energy source. The nature of the jelly surrounding each egg may also affect the reproductive system, but largely in its histochemical properties rather than its morphology. Therefore, for convenience, the classification of reproductive modes employed here will be a simplified one based principally on the nature of the maternal investment in the young, and thus on the type of development prior to the end of metamorphosis. Little emphasis on parental care or environmental factors is given, except where required to highlight relevant peculiarities in reproductive modes of particular species considered in this thesis. The following classification therefore does not necessarily accommodate the reproductive modes of all anuran species.

MODE I - small eggs with little yolk reserve (mean mature egg diameters of species considered in this study: 0.8 - 1.9mm, Fig.3); small early-stage tadpoles hatch and develop aquatically.

(a) eggs laid in water without foam nest

(b) eggs laid in foam nest.

MODE II - eggs with moderate yolk reserve (mean mature egg diameters of species considered in this study: 1.7 - 4.0mm, Fig.3); only well developed or later stage larvae motile and feed and develop aquatically.

(a) eggs laid and young develop in lotic environment

(b) eggs laid in lentic environment, or on land not in foam nest

(c) eggs laid in foam nest

(d) eggs and/or early larval stages carried by parent.

MODE III - eggs with large yolk reserve sufficient for entire development up to the end of metamorphosis (mean mature egg diameters of species considered in this study: 1.9 - 5.0mm, Fig.3); larval stages may or may not be present.

(a) eggs, and larvae if present, terrestrial

(b) eggs and larvae, or larvae only, carried by parent

(c) ovoviviparous.

MODE IV - viviparous (*Nectophrynoides occidentalis*) - eggs containing scarcely any yolk (Angel and Lamotte, 1944).

Modes I and II are equivalent to the aquatic development and Mode III to the direct development of Jameson (1957) and Salthe and Mecham (1974). These authors, and Wake (1980), used the term "direct development" in this broad sense, to include both species in which non-feeding larvae

hatch from the eggs and those in which development is entirely intracapsular and juvenile froglets hatch. Other authors, however, such as Lamotte and Lescure (1977), and apparently Noble (1931) and Crump (1974), consider "direct development" in a narrower sense, restricted to those species in which the eggs hatch into fully metamorphosed juveniles, with no larval stages. The latter usage is correct in that the egg hatches "directly" into a froglet, but since the ecological larva, i.e. the tadpole, is lost in species in which the non-feeding young hatch before the end of metamorphosis, and at least some tadpole features may be present in the embryos of species with post-metamorphic hatching, it is more satisfactory to use the term in a broad sense.

The reproductive modes of some species considered in this thesis cannot be confidently assigned to any of the categories given above, either because their breeding biology is not or poorly known, or because of the simplified nature of the classification. These species are as follows. *Crinia georgiana* lays moderately large eggs in shallow water, and in the field they hatch after about seven days (Main, 1957), which is slightly delayed in comparison with species with totally aquatic and unspecialized development. Thus this species falls between Mode I(a) and Mode II(b). Since there is this slight modification of reproductive mode and enlargement of eggs, *C. georgiana* is assigned here to Mode II(b). The reproductive biology of *Taudactylus* spp. is not known in great detail. Their eggs are attached to rocks in flowing creeks (Liem and Hosmer, 1973) and are of significantly larger diameter than those of similarly sized species of Mode I. Species of *Taudactylus* may therefore be torrent-adapted frogs with larvae which are well-developed at hatching, so I place them in Mode II(a). For *Afrixalus* species (Schiøtz, 1975) and *Chiromantis petersi* and *C. xerampelina* (Coe, 1974) there might be a slight delay in hatching, or after hatching a delay before the larvae

become free-swimming, but since the delay is short and there is no obvious increase in egg diameter, these species are assigned here to Mode I. (The third *Chiromantis* species, *C. rufescens*, would be classed as a Mode II species because there is a significant delay before tadpoles are released (Coe, 1974)). The reproductive mode of *Callixalus pictus* is not known, but it is a bamboo-dwelling species and may lay its eggs in the internodes of bamboo stems (R.F. Laurent, *in litt.*). Since many other hyperoliids are Mode II(b) species and since the nature of the ovaries of the one immature specimen of *C. pictus* I examined suggests that the eggs are relatively large, this species is tentatively allotted to Mode II(b). The breeding biology of most New Guinean microhylids and of many *Eleutherodactylus* species has never been observed, but those few species for which it is known are all of Mode III(a) (Tyler, 1963; Menzies, 1975; Lamotte and Lescure, 1977). Therefore I allocate all New Guinean microhylids and *Eleutherodactylus* spp. which I dissected to Mode III(a).

II

MATERIALS, METHODS AND TERMINOLOGY

(a) SPECIMENS

For this study, representatives of as great a diversity of reproductive modes as possible were obtained. However, the choice of species was influenced by availability, so the material was predominantly Australian and particularly of Mode I. In all, females of 108 species, representing 51 genera and 11 families, were examined. They are listed with any details of collection in Appendix I.

Recent concepts of anuran families, such as those of Duellman (1975), Laurent (1979) and Dubois (1983), are conflicting in some details. The most conservative classification (Duellman, 1975) is followed here with the exception that the Myobatrachidae is not recognized as separate from the Leptodactylidae, following the argument of Tyler (1979).

Specimens were dissected with the aid of a low-power binocular dissecting microscope. Measurements were made with dial calipers and taken to the nearest 0.1 mm.

(b) SIZE OF SPECIMENS

Measurements of reproductive organs may alter with size of the

species, and therefore for comparative purposes need to be related in some way to body size. Because the reproductive organs are three-dimensional, a measure of body mass or volume for each species would be desirable. However, there are numerous problems associated with expressing measurements against body mass or volume because of the variability of the latter: 1) gut content and fat-body accumulation may vary dramatically; 2) whilst abdominal volume may remain similar, the head and limbs may differ between species, rendering body volume variable; 3) reproductive condition may alter mass or volume considerably. Ovarian volumes in two mature female *Notaden melanoscaphus* dissected for this study were 0.6 ml in one which had recently oviposited, and 3.6 ml (about 20% of the total body volume) in the other in which the ovaries were mature. Kluge (1981) calculated that the average clutch of eggs accounts for 22.7% of the female's weight in *Hyla rosenbergi*; 4) the state of preservation and the degree of lung distension at the time of preservation may alter volume; 5) preserved specimens may already have been dissected for other purposes, as was usually the case in this study, so volume measurements cannot be taken. Salthe and Duellman (1973) encountered similar problems and remarked:

> *"It would have been desirable to estimate body volume of female frogs, as was done for salamanders by Salthe (1969); however, the body shapes of frogs are far less uniform than are those of salamanders. There is no mathematically simple shape that can be used to generalize the body shape of all frogs, nor in most cases is there any means of assigning to a given species any one of a series of mathematically simple, idealized body shapes. Therefore, volumetric data on adult frogs have not been utilized."*

Because of the inherent variability of body volume measurements, snout to vent length (SVL) was used as a size index in this study,

measured only in reproductively mature specimens. An unavoidable error associated with SVL measurements of preserved specimens is due to the degree of flexure of the body, but there are no other significant errors as there are for body mass or volume. Relationships of some reproductive variables may be geometric with body mass or volume but allometric with SVL, but since correlations or trends were the primary consideration here and not the mathematical form of such relationships, SVL was an adequate measure.

(c) EGGS

The stage at which secondary oocytes complete their meiotic divisions and become ova probably takes place shortly after ovulation (Lofts, 1974; Frye, 1977). For convenience, the term "oocyte" was applied here to ovarian eggs prior to ovulation, and "ovum" to all eggs which have been ovulated but not fertilized. In species with pigmented eggs, mature, postvitellogenic oocytes were considered to be those with pigmented animal hemispheres clearly defined from the vegetal hemispheres. In species with unpigmented eggs, judgement of oocyte maturity was more difficult and was based on either measurements of any ova present, or published data on egg diameters, or previous observation of the appearance of an ovary with mature oocytes.

(d) SIZE OF EGGS

For reasons similar to those discussed above for the measurement of body size, egg volume would be a desirable expression of egg size. However, it would have been necessary to estimate egg volume from egg diameter, thus rendering volumes very inaccurate, since errors in

diameter measurements would be greatly magnified. In addition, diameter is the measure used most frequently in the literature as a measurement of egg size. Therefore, egg diameter was employed as a measure of egg size.

Egg diameter was calculated as the mean of 20 ova or mature oocytes (dissected from the ovaries) per individual, or of fewer if numbers of eggs were small. Kaplan (1979) has noted disadvantages of diameter measurements of oocytes: oocytes not all at the same stage of vitellogenesis; irregularities of oocyte shape; shrinkage in preservation; swelling of freshly dissected oocytes. If ova or mature oocytes were not present in specimens dissected, measurements of egg diameter were quoted from the literature. These values are mostly of fertilized eggs and may not correspond with measurements of preserved oocytes, particularly as developing embryos are subject to size changes (Kaplan, 1979). Such inaccuracies may be significant in detailed comparisons between populations or species, but since only correlations and gross trends between groups of species were analysed here, these inaccuracies in egg diameter were considered to be of relatively minor significance.

(e) NUMBER OF EGGS

Ovarian complements were calculated as the number of mature oocytes per ovary, thus they are not the complement per individual, i.e. of both ovaries, and therefore are not comparable with the clutch size values used by some authors (e.g. Salthe and Duellman, 1973). If oocytes were immature, ovarian complement was taken as the number of vitellogenic or maturing oocytes; these were readily distinguishable in species with pigmented eggs. For species with unpigmented eggs, those oocytes judged to be of the largest size (generally somewhat yellower than the smaller,

immature oocytes) were counted. For ovaries with a small complement, all mature/maturing oocytes were counted under the dissecting microscope. In the case of ovaries with a large complement, a small portion of ovary was excised, blotted to remove excess alcohol, weighed (weight a), and its contained mature/maturing oocytes (x) counted under the microscope. The remainder of the ovary was then blotted and weighed (weight b), and its number of oocytes estimated: $y = bx/a$. Approximate ovarian complement was then: $x+y$.

(f) VOLUME OF EGGS PER OVARY

The approximate volume of an ovum or mature oocyte was calculated for each species from values of egg diameter (thus volume values may be highly inaccurate, since inaccuracies in diameter values were cubed), and the total volume of mature eggs per ovary estimated by calculating ovarian complement x egg volume. This total volume, termed complement volume, is not equivalent to ovarian volume because it does not include the volumes of oogonia and immature oocytes, interstitial spaces between eggs, or ovarian tissue. But complement volume closely approximates ovarian volume, since the mature oocytes constitute the bulk of the ovary. Complement volume is an adequate measurement since the factor considered here is the total amount of energy, in terms of mass or volume of yolk, invested into each reproductive effort (i.e. the mature eggs in an ovary).

(g) OVIDUCTS, AND OVIDUCT LENGTH AND CONVOLUTIONS

Anuran oviducts are termed "Müllerian ducts" by some authors (for example Bhaduri, 1953; Griffiths, 1959; Potemkina, 1963), but a recent

trend is towards use of the term "oviducts". The latter term is applied here.

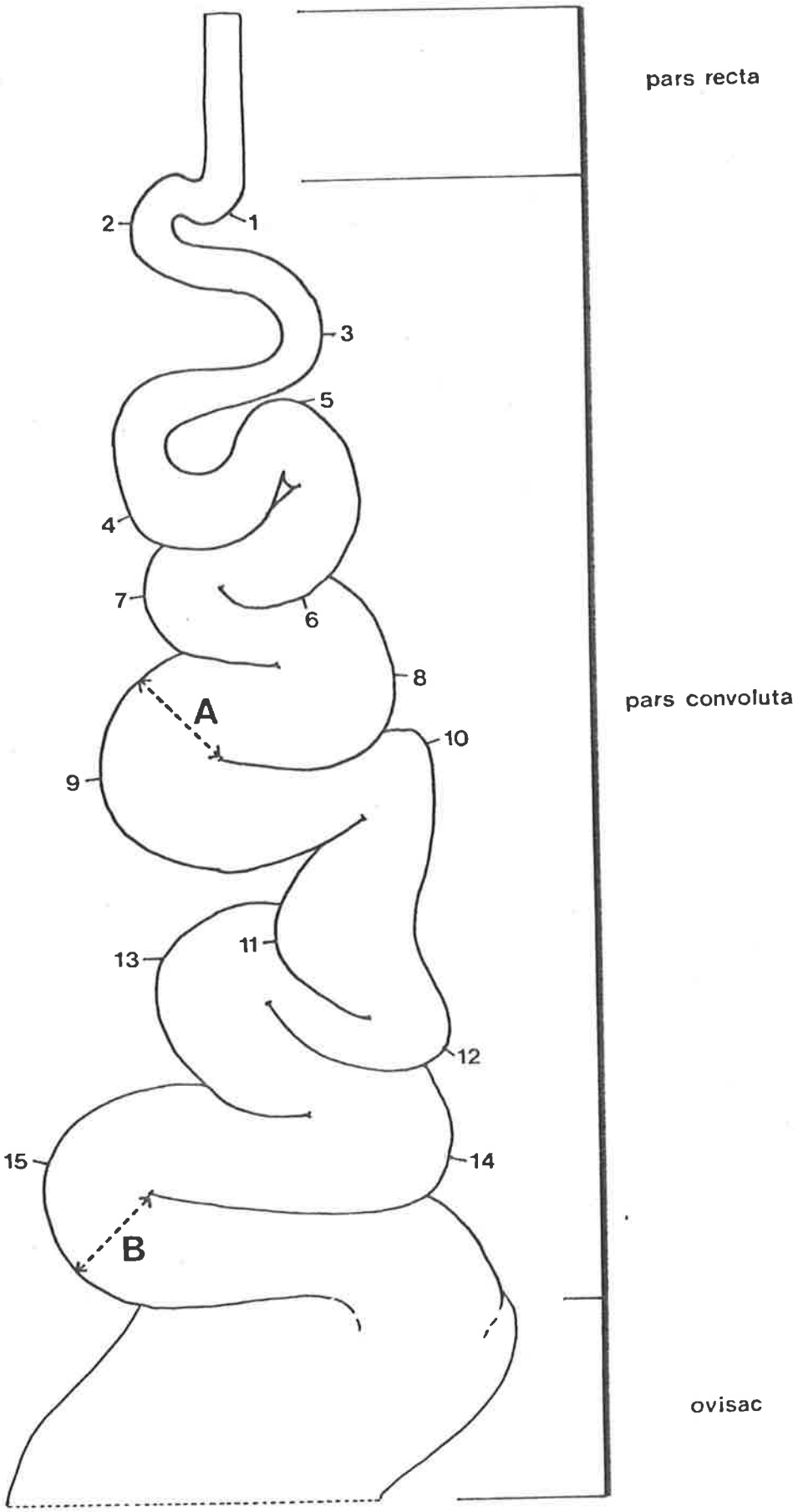
The length of an oviduct was measured by removing it from the specimen, freeing it of attendant connective tissue, and floating it in 65% ethanol in a petri dish under which was attached 1mm gauge graph paper. The longitudinal midline of the oviduct was then projected by eye against the grid and its length estimated.

In specimens with convoluted oviducts, the numbers of convolutions per oviduct were counted; successive convolutions were considered to constitute each crest of a fold in the oviduct (Fig. 2). In some specimens the histological structure of the convoluted portion of the oviduct was examined, by removing portions of the tissue, sectioning them at 7-8μm and staining the sections with Mayer's haematoxylin and eosin.

(h) OVIDUCT WIDTH

Oviduct widths were measured at two points on each oviduct, the first approximately half way along the length of the *pars convoluta*, and the second at the posterior end of the *pars convoluta* (Fig. 2); the mean of these two values was then calculated for each oviduct. In foam-nesting species, in which the posterior region of the oviduct is enlarged, each oviduct was measured at one point only: at approximately the mid-point of the *pars convoluta*. Oviduct width was used as an index of the diameter of the oviduct lumen, but as such it may be unduly variable because it includes the oviduct wall which may not be the same thickness in all species. Width was measured only in specimens with mature or almost mature oocytes in the ovaries so that the oviduct walls could be expected to have been at their maximum thickness, prior to the release

FIG. 2 Generalized anuran oviduct with 15 convolutions. Numerals represent apices of convolutions. A and B represent the points at which oviduct width was measured.


pars recta
1
2
3
4
5
6
7
8
A
9
10
11
12
13
14
15
B
pars convoluta
ovisac

of mucopolysaccharide jelly during ovulation. However, the assumption that repletion of oviducal glands is synchronous with oocyte maturation may not be valid; repletion may follow some time after the end of vitellogenesis. In addition, oviduct wall thickness may be affected by the length of time between ovulations; if there are several ovulations per breeding season the glands may not return to maximum storage capacity between each one. Thus the width measurements should be considered with caution.

(i) OVISACS

Two terms are commonly applied to the distensible chamber at the posterior end of the oviduct: "uterus" (for example by Christensen, 1930; Rugh, 1951; Bhaduri, 1953), and "ovisac" (for example by Marshall, 1912; Briggs, 1940; Griffiths, 1959; Watson and Saunders, 1959; Horton and Tyler, 1982). Bhaduri (1953) argued that the chamber should be described from a point of view of anatomical relationships or homology, rather than function, and that although it is difficult to homologize this structure with the mammalian uterus, the term "uterus" is to be preferred. Holmes (1979) gives a generalized definition of "uterus" as "an enlarged portion of oviduct modified to serve as a place for development of young or of eggs." However, in only four anuran species (*Nectophrynoides occidentalis*, *N. tornieri*, *N. viviparus* and *Eleutherodactylus jasperi*) is the terminal portion of the oviduct known to function as a protective chamber for the developing young until birth of the fully-formed juveniles. In all other species it serves merely to store the eggs for a short period between ovulation and oviposition. For this reason the term "ovisac" is applied here.

(j) DISPOSITION OF OVISACS: HISTOLOGICAL PROCEDURES

To determine the course and fate of the ovisacs as they approach the cloaca, if indeterminable under the dissecting microscope, the ovisacs, rectum and cloaca were excised from the specimen. The tissue was then processed through ethenol and xylene, embedded in paraffin wax, sectioned at 8 or 9μm, and the sections stained with Mayer's haematoxylin and eosin.

(k) ONTOGENETIC MATERIAL

Developmental series of tadpoles of four South Australian species of frogs were reared for ontogenetic studies. *Limnodynastes tasmaniensis* spawn was obtained from a breeding colony of adults collected from various localities near Adelaide and maintained at room temperature in a large tank in the laboratory. Details of spawn collection for other species are: *Limnodynastes dumerili* 1) Uraidla, Sth Aust., 13.x.1981, J. Moller; 2) laid by adults coll. R. Torrens, St Peters, Sth Aust., 13.x.1981, M. Thompson. *Pseudophryne bibroni*: 1) Mitcham, Sth Aust., 27.v.1981, P. Horton; 2) laid by adults coll. Fifth Ck, Montacute, Sth Aust., May 1981, J. Moller; 3) Greenhill, Sth Aust., 14.viii.1981, C. Miller. *Litoria ewingi*: 1) Mitcham, Sth Aust., 27.v.1981, P. Horton; 2) Brownhill Ck, Sth Aust., 19.ix.1980, D. Towns.

Tadpoles were reared in glass tanks with aerated, filtered and dechlorinated water, in a 30°C controlled temperature room with daylength set from 0600 to 2000 hrs, and were fed thawed, deep-frozen lettuce (not previously boiled). Small numbers of individuals were killed at intervals from early stages until metamorphic climax, preserved in Tyler's tadpole fluid (Tyler, 1962), and staged according to Gosner (1960). Some individuals were reared beyond metamorphosis, maintained

in glass tanks and fed adult *Drosophila melanogaster* and small larvae of *Tenebrio molitor*, and killed at intervals in 3% chloral hydrate solution and preserved in 65% ethanol.

(l) PROCESSING OF ONTOGENETIC MATERIAL

Initially specimens were dissected under the microscope. To determine the stage of gonad differentiation, progressively earlier stage individuals were sectioned for histological examination. Gonads of tadpoles were excised together with the kidneys and dorsal musculature, with the cartilaginous spinal column removed. Gonads and oviducts of juveniles were excised together with kidneys, dorsal musculature, and vertebral and pelvic skeletons, and decalcified in Perenyi's fluid for four to six hours. These tissues were processed through ethanol and xylene, embedded in paraffin wax, sectioned at 7 or 8µm, and the sections stained with Mayer's haematoxylin and eosin.

(m) URINARY DUCTS

Various terms are applied to the ducts carrying urine from the anuran kidneys: Wolffian ducts (Bhaduri, 1953), ureters (Ecker, 1864), archinephric ducts (Minkoff, 1975), opisthonephric ducts (Kluge, 1977). According to species, the archinephric duct may drain the kidneys and testes, or an accessory duct (opisthonephric) may be formed to drain the more posterior part of the kidneys, or in some, such as *Alytes* (Romer and Parsons, 1977), the entire kidney may be drained by this extra duct, leaving the archinephric duct to carry sperm only. In female anurans there is a similar but more retarded development of an accessory duct, despite the lack of other use of the archinephric duct (Romer and Parsons, 1977). In no species, however, is this accessory duct equiva-

lent to the mammalian ureter, which is metanephric in origin. The origins, archinephric or opisthonephric, of urinary ducts were not determined in this study, so the general term "urinary duct" was applied throughout.

(n) STATISTICAL ANALYSES

Numerical data were subjected to analyses following the methods of Sokal and Rohlf (1969) and Campbell (1974), in conjunction with the critical values given by Rohlf and Sokal (1969) and Campbell (1974). Variables were checked for normality (Kolmogorov-Smirnov one-sample test) and homogeneity of variances (F max test) before all statistical analyses involving parametric tests. If necessary, the variables were transformed to their natural logarithmic values in order to produce normal distribution of data points and to reduce heterogeneity of variances, so that parametric tests could be employed. Some values of egg diameter were less than 1.0mm, therefore egg diameters were transformed to the logarithms of 10 times their value. Regression lines were required in a number of instances, but Model I regression could not be used because in no case did the data meet the requirement of the independent variable being measured without error and under the control of the investigator (Sokal and Rohlf, 1969, pp.408-409,410). Analysis of covariance therefore was not employed either. Regression lines were calculated with Bartlett's three-group method for Model II regression, as detailed by Sokal and Rohlf (1969).

III

RESULTS

(a) REPRODUCTIVE MODES

Each of the 108 species considered in this study (listed in Appendix I) was allocated to one of the categories of reproductive mode detailed in the Introduction (under Anuran Reproductive Modes). Allocations of some species were only tentative, as also discussed in the Introduction, due to a lack of information about their breeding ecologies. The main categories of reproductive mode considered are: Mode I (eggs small with little yolk reserve; small, early stage tadpoles hatch and develop aquatically), Mode II (eggs with moderate yolk reserve; only well developed or later stage larvae motile and feed and develop aquatically), and Mode III (eggs with large yolk reserve sufficient for entire development up to the end of metamorphosis; larval stages may or may not be present). Fifty-nine species were classed in Mode I, 16 in Mode II, and 33 in Mode III. The mode of each species is given in Table 3.

(b) SNOUT-VENT LENGTH

Measurements of snout-vent length (SVL) of adult individuals are presented in Table 3. In some instances only juveniles of a species were available for study, so published values of SVL of mature individuals are quoted. Ranges of SVL are:

TABLE 3: Reproductive mode, snout-to-vent length (SVL), and presence (+) or absence (o) of egg pigmentation, in all species investigated. Number of specimens seen of each species is in parentheses. SVL values are mean values for each species except for those of which only one specimen was seen.

Taxa	n	Reproductive Mode	SVL (mm)	Egg Pigmentation
Leiopelmatidae				
Ascaphus truei	1	IIa	43.7	o
Leiopelma hochstetteri	1	IIIa	40.7	o
Pipidae				
Xenopus laevis	1	Ia	88.9	+
X. muelleri	1	Ia	55.5	+
Pelobatidae				
Pelobates fuscus	1	Ia	80.0[1]	+
Bufonidae				
Bufo marinus	1	Ia	130.0	+
Nectophrynoides malcolmi	2	IIIa	24.2	+
N. tornieri	2	IIIc	25.4	o
Leptodactylidae				
Limnodynastinae				
Adelotus brevis	2	Ib	35.8	o
Heleioporus eyrei	2	IIc	53.8	o
Lechriodus melanopyga	1	Ib	44.9	+
Limnodynastes dorsalis	5	Ib	56.5	+
L. dumerili	3	Ib	61.9	+
L. ornatus	2	Ib	40.2	+
L. peroni	1	Ib	49.8	+
L. tasmaniensis	numerous	Ib	36.6	+
Megistolotis lignarius	1	Ib	46.3	+
Neobatrachus ?centralis	3	Ia	47.8	+
N. sp.	3	Ia	43.6	+
Notaden melanoscaphus	4	Ia	46.0	+
N. nichollsi	1	Ia	53.2	+
Myobatrachinae				
Assa darlingtoni	1	IIIb	19.6	o
Crinia georgiana	1	IIb	29.8	+
Myobatrachus gouldi	5	IIIa	55.5	o
Pseudophryne bibroni	2	IIb	30.3	+
Ranidella bilingua	1	Ia	17.4 - 20.0[2]	+
R. riparia	5	Ia	24.1	+
R. signifera	12	Ia	23.9	+
Taudactylus acutirostris	1	IIa	32.5	+
T. diurnus	1	IIa	26.7	+
Uperoleia inundata	1	Ia	27.4	+

1 From Mertens (1960)
2 From Martin *et al.* (1980)

Taxa	n	Reproductive Mode	SVL (mm)	Egg Pigmentation
Rheobatrachinae				
Rheobatrachus silus	21	IIIb	50.6	o
Eleutherodactylinae				
Eleutherodactylus achatinus	5	IIIa	-	o
E. chloronotus	5	IIIa	40.3	o
E. curtipes	6	IIIa	36.0	o
E. devillei	5	IIIa	39.0	o
E. walkeri	3	IIIa	21.0	o
Dendrobatidae				
Phyllobates aurotaenia	3	IId	30.6	+
Hylidae				
Cyclorana australis	8	Ia	79.9	+
C. brevipes	1	Ia	45.0	+
C. longipes	1	Ia	42.2	+
C. maini	2	Ia	46.4	+
Litoria alboguttata	2	Ia	66.7	+
L. bicolor	4	Ia	27.6	+
L. caerulea	2	Ia	72.3	+
L. chloris	2	Ia	55.6	+
L. coplandi	1	Ia	35.0	+
L. dahli	numerous	Ia	73.6	+
L. eucnemis	1	Ia	67.0	+
L. ewingi	2	Ia	35.4	+
L. inermis	4	Ia	34.4	+
L. iris	4	IIb	37.8	+
L. lesueuri	1	Ia	65.3	+
L. microbelos	1	Ia	14.4	+
L. modica	2	IIa	33.7	o
L. nannotis	2	IIa	63.0	o
L. nasuta	2	Ia	49.6	+
L. pallida	5	Ia	37.2	+
L. peroni	2	Ia	60.4	+
L. pratti	2	IIa	34.0	o
L. raniformis	1	Ia	72.2	+
L. rheocola	2	IIa	37.5	o
L. rothi	7	Ia	48.8	+
L. rubella	6	Ia	32.4	+
L. tornieri	1	Ia	36.3	+
L. wotjulumensis	1	Ia	54.1	+
Nyctimystes papua	4	IIa	71.5	o
Phrynohyas venulosa	1	Ia	76.3	+
Ranidae				
Arthroleptella lightfooti	1	IIIa	22.0[1]	o
Arthroleptis poecilonotus	1	IIIa	29.1	o
Cacosternum boettgeri	1	Ia	21.0	+
Rana cascadea	1	Ia	55.0	+
R. grisea	1	Ia	87.5	+
R. papua	1	Ia	84.3	+

[1] From Poynton (1964)

Taxa	n	Reproductive Mode	SVL (mm)	Egg Pigmentation
Hyperoliidae				
Afrixalus dorsalis	1	Ia	25.9	o
A. fornasini	1	Ia	35.9	o
A. quadrivittatus	1	Ia	26.2	o
Callixalus pictus	1	IIb	41.0[1]	-
Cryptothylax greshoffi	1	Ia	51.9	+
Hyperolius marmoratus	1	Ia	30.4	+
Leptopelis bocagei	1	IIb	48.6	o
L. macrotis	1	IIb	-	o
Rhacophoridae				
Chiromantis petersi	1	Ib	77.7	o
C. xerampelina	1	Ib	64.3	o
Microhylidae				
Asterophryinae				
Asterophrys turpicula	1	IIIa	42.0	o
Barygenys nana	1	IIIa	26.4	o
Hylophorbus rufescens	1	IIIa	37.4	o
Phrynomantis humicola compta	1	IIIa	53.9	o
P. h. humicola	1	IIIa	46.6	o
P. lateralis	4	IIIa	48.4	o
P. louisiadensis	1	IIIa	-	o
P. robusta	1	IIIa	57.8	o
P. stictogaster	3	IIIa	79.3	o
P. wilhelmana	3	IIIa	49.0	o
Xenobatrachus rostratus	2	IIIa	37.0	o
Xenorhina bouwensi	1	IIIa	21.6	o
Sphenophryninae				
Cophixalus darlingtoni	1	IIIa	23.4	o
C. neglectus	1	IIIa	25.7	o
C. ornatus	1	IIIa	27.4	o
C. parkeri	1	IIIa	29.6	o
C. riparius	1	IIIa	50.5	o
Copiula fistulans	2	IIIa	33.9	o
Oreophryne biroi	1	IIIa	28.5	o
Sphenophryne schlaginhaufeni	1	IIIa	-	o
Dyscophinae				
Calluella guttulata	1	Ia	37.9	+
Microhylinae				
Chaperina fusca	1	Ia	23.1	+
Kaloula pulchra	1	Ia	54.3	+
Microhyla heymonsi	1	Ia	23.6	+

[1] From Laurent (*in litt.*)

Mode I species: 14.4 - 130 mm (mean 49.8 ± 21.8 mm)

Mode II species: 26.7 - 71.5mm (mean 41.0 ± 13.1 mm)

Mode III species: 19.6 - 79.3mm (mean 37.4 ± 14.0 mm)

Values of SVL are from a population with normal distribution (Kolmogorov-Smirnov one-sample test) and their variances are not significantly heterogeneous (F max test). The mean for Mode I species does not differ significantly from that for Mode II, nor Mode II from Mode III (Student's t-test), but the mean for Mode I is significantly greater than that for Mode III ($0.001 < P < 0.01$).

(c) EGGS

(i) Egg Diameter

Values of egg diameter (mm) are given in Table 4 for species for which ova or mature oocytes could be measured or for which published values were available.

Comparison of egg diameters between modes

A histogram of egg diameters for species of Modes I, II and III is given in Fig. 3. Ranges of egg diameters are:

Mode I species: 0.8 - 1.9 mm (mean 1.32 ± 0.23 mm)

Mode II species: 1.7 - 4.0 mm (mean 2.44 ± 0.72 mm)

Mode III species: 1.9 - 5.0 mm (mean 3.38 ± 0.96 mm)

Values of egg diameter are from a population with normal distribution (Kolmogorov-Smirnov one-sample test) but the variances are significantly heterogeneous (F max test, $P < 0.01$). Values of log (10 x egg diameter) are also normally distributed and the variances are not significantly heterogeneous. Thus log (10 x egg diameter) values were employed for parametric tests. (Diameters were multiplied by 10 before log transformation since some values were less than 1.0). Results of these and

TABLE 4: Egg diameter, egg volume, ovarian complement, and complement volume, for all species investigated. Egg diameters are mean values for each species. Ovarian complements are mean values for left and right ovaries for all specimens for that species.

Taxa	Egg Diameter (mm)	Egg Volume (cu.mm)	Ovarian Complement	Complement Volume (cu.mm)
Leiopelmatidae				
Ascaphus truei	4.0[1]	33.5	27	905
Leiopelma hochstetteri	-	-	18	-
Pipidae				
Xenopus laevis	1.1	0.7	690	483
X. muelleri	1.1	0.7	360	252
Pelobatidae				
Pelobates fuscus	-	-	-	-
Bufonidae				
Bufo marinus	1.5	1.8	4,366	7,728
Nectophrynoides malcolmi	2.7-3.0[2]	12.1	17	206
N. tornieri	3.0-4.0[2]	22.5	16	359
Leptodactylidae				
Limnodynastinae				
Adelotus brevis	1.5	1.8	267	473
Heleioporus eyrei	3.3[3]	18.8	136	2,560
Lechriodus melanopyga	1.3	1.2	508	584
Limnodynastes dorsalis	1.2	0.9	1,132	1,030
L. dumerili	1.7[4]	2.6	1,107	2,845
L. ornatus	1.2	0.9	424	386
L. peroni	1.3	1.2	707	813
L. tasmaniensis	1.2	0.9	141	128
Megistolotis lignarius	1.2	0.9	187	170
Neobatrachus ?centralis	1.4	1.4	176	253
N. sp.	1.5	1.8	335	593
Notaden melanoscaphus	1.4	1.4	444	639
N. nichollsi	1.5	1.8	-	-
Myobatrachinae				
Assa darlingtoni	2.8	11.5	6	69
Crinia georgiana	1.8	3.1	88	268
Myobatrachus gouldi	4.3	41.6	39	1,623
Pseudophryne bibroni	2.5	8.2	36	294
Ranidella bilingua	1.2[5]	0.9	28	25
R. riparia	1.5	1.8	24	42
R. signifera	1.4	1.4	59	85
Taudactylus acutirostris	1.8	3.1	29	88
T. diurnus	1.7	2.6	24	62
Uperoleia inundata	1.3	1.2	30	35

1 From Noble and Putnam (1931)
2 From Wake (1980)
3 From Lee (1967)
4 From Martin (1967)
5 From Martin *et al.* (1980)

Taxa	Egg Diameter (mm)	Egg Volume (cu.mm)	Ovarian Complement	Complement Volume (cu.mm)
Rheobatrachinae				
Rheobatrachus silus	4.6	51.0	12	611
Eleutherodactylinae				
Eleutherodactylus achatinus	-	-	-	-
E. chloronotus	2.8	11.5	16	184
E. curtipes	2.2	5.6	19	105
E. devillei	2.5	8.2	27	221
E. walkeri	1.9	3.6	5	18
Dendrobatidae				
Phyllobates aurotaenia	1.9	3.6	12	43
Hylidae				
Cyclorana australis	1.4	1.4	2,610	3,758
C. brevipes	1.4	1.4	-	-
C. longipes	1.2	0.9	410	373
C. maini	1.2[1]	0.9	-	-
Litoria alboguttata	1.1	0.7	2,130	1,491
L. bicolor	1.0	0.5	322	167
L. caerulea	1.1	0.7	729	510
L. chloris	1.4	1.4	588	847
L. coplandi	1.4	1.4	171	246
L. dahli	1.2	0.9	-	-
L. eucnemis	-	-	-	-
L. ewingi	1.6	2.2	181	389
L. inermis	1.2	0.9	175	159
L. iris	2.1	4.9	25	121
L. lesueuri	1.1	0.7	1,366	956
L. microbelos	0.8	0.3	104	28
L. modica	2.1	4.9	37	179
L. nannotis	3.5	22.5	74	1,661
L. nasuta	1.3	1.2	1,080	1,242
L. pallida	1.2	0.9	192	175
L. peroni	1.3	1.2	374	430
L. pratti	2.1	4.9	42	204
L. raniformis	1.4	1.4	1,231	1,773
L. rheocola	3.0	14.1	50	707
L. rothi	1.3	1.2	505	581
L. rubella	1.1	0.7	287	201
L. tornieri	1.2	0.9	168	153
L. wotjulumensis	1.7	2.6	868	2,231
Nyctimystes papua	2.2	5.6	327	1,825
Phrynohyas venulosa	-	-	-	-
Ranidae				
Arthroleptella lightfooti	-	-	-	-
Arthroleptis poecilonotus	2.3	6.4	16	102
Cacosternum boettgeri	0.9[2]	0.4	-	-
Rana cascadea	1.8	3.1	224	683
R. grisea	1.8	3.1	-	-
R. papua	1.4	1.4	1,981	2,853

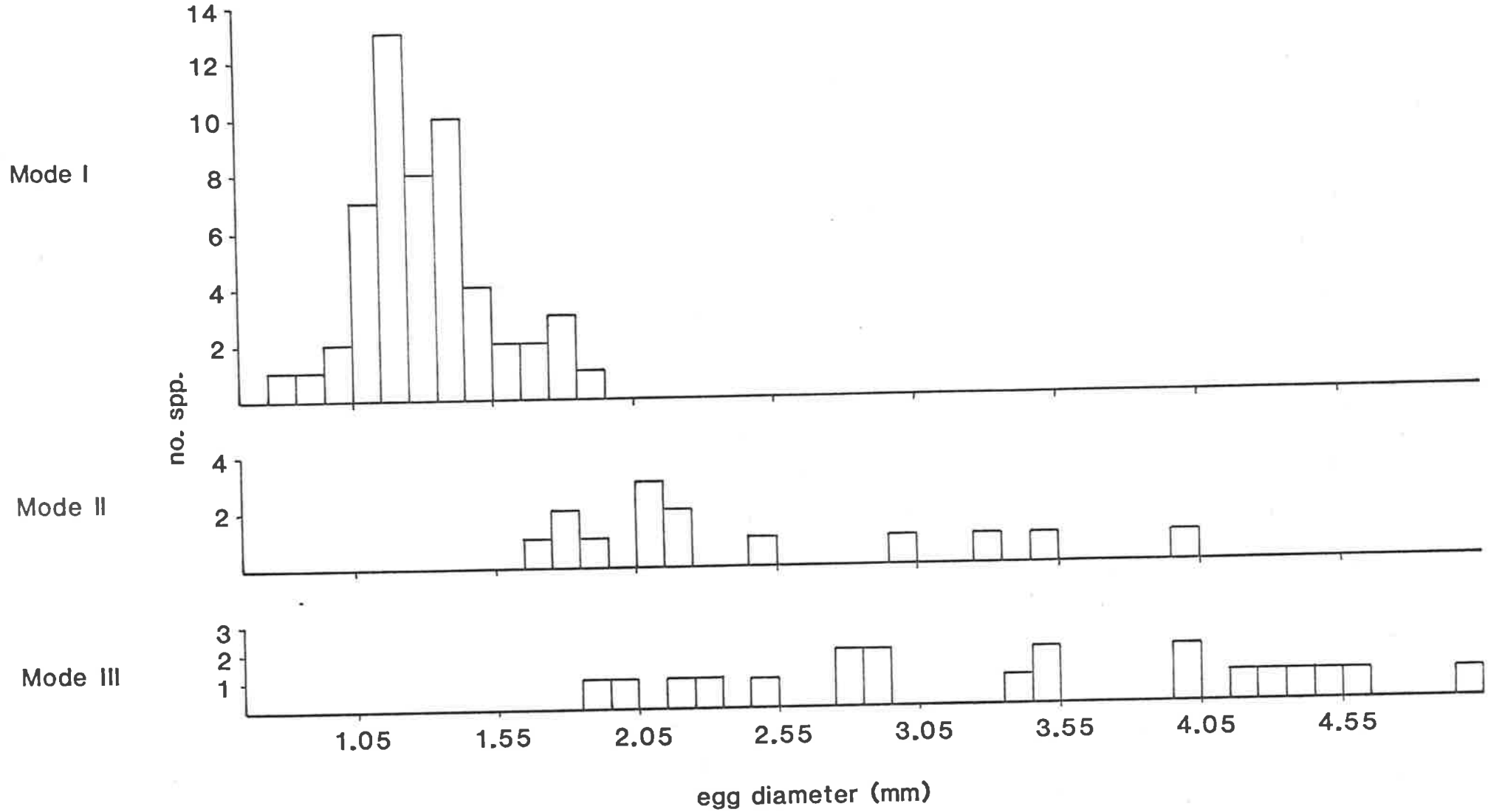
[1] From Tyler and Martin (1977)

[2] From Jurgens (1979)

Taxa	Egg Diameter (mm)	Egg Volume (cu.mm)	Ovarian Complement	Complement Volume (cu.mm)
Hyperoliidae				
Afrixalus dorsalis	1.3	1.2	-	-
A. fornasini	1.6[1]	2.2	67	144
A. quadrivittatus	-	-	-	-
Callixalus pictus	-	-	-	-
Cryptothylax greshoffi	1.9	3.6	-	-
Hyperolius marmoratus	1.3	1.2	-	-
Leptopelis bocagei	2.2	5.6	144	804
L. macrotis	-	-	-	-
Rhacophoridae				
Chiromantis petersi	1.4	1.4	448	645
C. xerampelina	1.8	3.1	193	589
Microhylidae				
Asterophryinae				
Asterophrys turpicula	-	-	8	-
Barygenys nana	3.4	20.6	4	82
Hylophorbus rufescens	4.0[2]	33.5	8	268
Phrynomantis humicola compta	-	-	9	-
P. h. humicola	4.5	47.7	11	525
P. lateralis	3.5	22.5	13	292
P. louisiadensis	-	-	-	-
P. robusta	4.2	38.8	12	465
P. stictogaster	5.0[2]	65.4	20	1,309
P. wilhelmana	4.4	44.6	13	580
Xenobatrachus rostratus	-	-	19	-
Xenorhina bouwensi	2.0[2]	4.2	5	21
Sphenophryninae				
Cophixalus darlingtoni	-	-	8	-
C. neglectus	-	-	18	-
C. ornatus	-	-	8	-
C. parkeri	-	-	13	-
C. riparius	-	-	12	-
Copiula fistulans	2.9	12.8	11	140
Oreophryne biroi	4.0[3]	33.5	6	201
Sphenophryne schlaginhaufeni	-	-	12	-
Dyscophinae				
Calluella guttulata	1.2	0.9	692	630
Microhylinae				
Chaperina fusca	1.2	0.9	-	-
Kaloula pulchra	1.1	0.7	378	265
Microhyla heymonsi	1.0	0.5	270	140

1 From Schiøtz (1975)
2 From Zweifel (1972)
3 From Parker (1934)

FIG. 3 Numbers of species with egg diameters in given size classes, for species of Mode I, Mode II, and Mode III.


Mode I
Mode II
Mode III
no. spp.
14
12
10
8
6
4
2
4
2
3
2
1
1.05
1.55
2.05
2.55
3.05
3.55
4.05
4.55
egg diameter (mm)

subsequent statistical analyses are summarized in Table 12.

The mean of Mode I log (10 x egg diameter) values is significantly less than those of Modes II and III (Student's t-test, $P < 0.001$) and the mean of Mode II is significantly less than that of Mode III ($0.001 < P < 0.01$).

Correlation of egg diameter with SVL

Log (10 x egg diameter) is plotted against SVL for specimens of each mode, in Fig. 4. There is a significant positive correlation between egg diameter and SVL for Modes II and III (Kendall's coefficient of rank correlation, $0.001 < P < 0.01$), but there is no significant correlation for Mode I. For a given SVL, log (10 x egg diameter) is always greater in Modes II and III species than in Mode I species, and is generally greater in Mode III than in Mode II.

(ii) Ovarian Complement

Values of the number of mature or vitellogenic oocytes per ovary (ovarian complement) are given in Table 4 for each species examined for which this could be estimated; these figures are for one ovary only.

Comparison of ovarian complements between modes

Ranges of ovarian complements are:

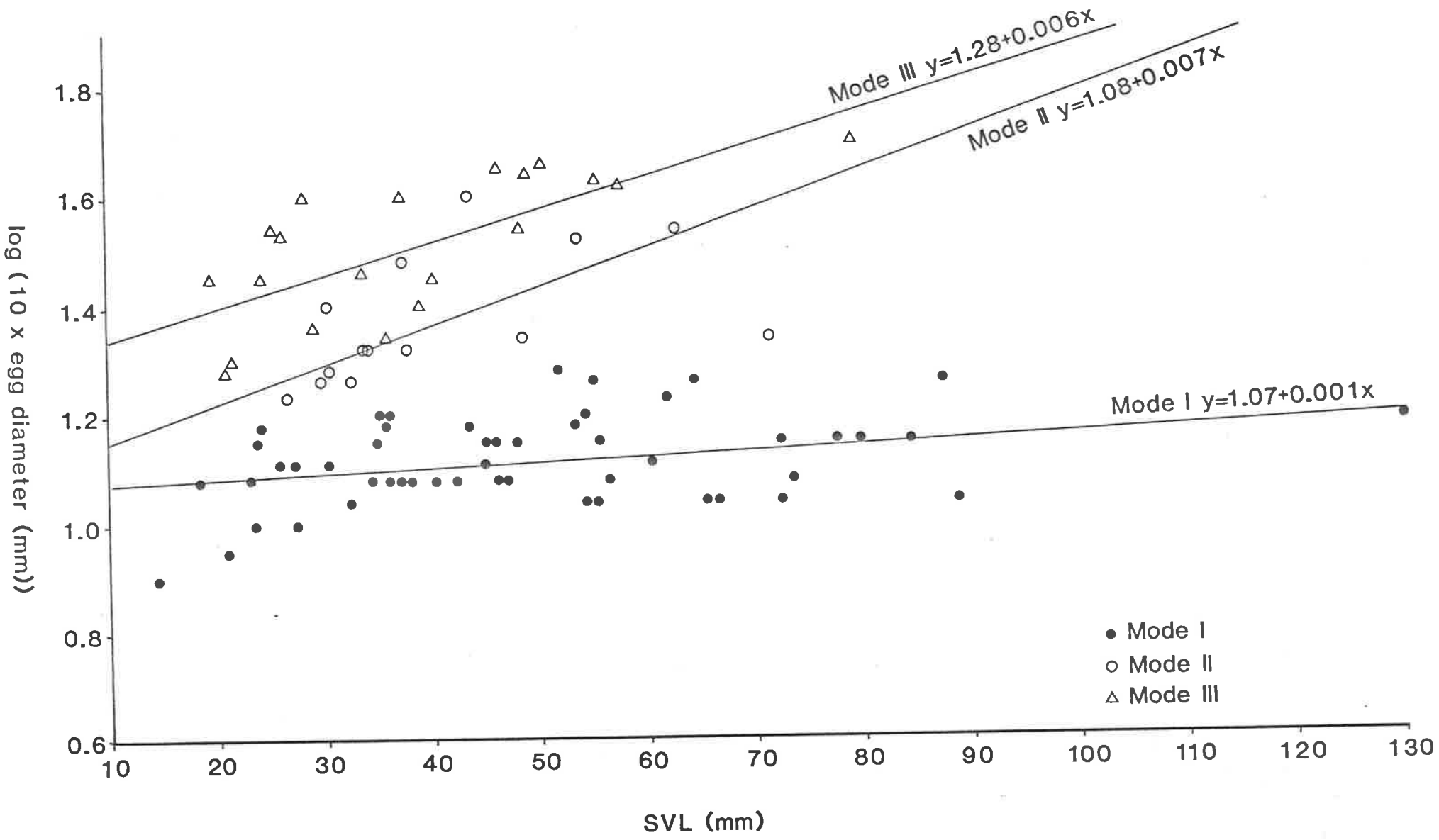
Mode I species: 24 - 4366 (mean 638.4 ± 806.2)

Mode II species: 12 - 327 (mean 75.1 ± 83.4)

Mode III species: 4 - 39 (mean 13.4 ± 7.2)

Values of ovarian complement are from a population which deviates significantly from normal (Kolmogorov-Smirnov one-sample test, $P < 0.01$), but log (ovarian complement) values form a normal distribution.

FIG. 4 Log (10 x egg diameter) vs SVL for species of Modes I, II and III.


Mode III y=1.28+0.006x
Mode II y=1.08+0.007x
Mode I y=1.07+0.001x
Mode I
Mode II
Mode III
log (10 x egg diameter (mm))
SVL (mm)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
10
20
30
40
50
60
70
80
90
100
110
120
130

Variances of ovarian complement values are significantly heterogeneous (F max test, $P < 0.01$) and those of log (ovarian complement) are also significantly heterogeneous, but for convenience log (ovarian complement) data were subjected to parametric tests despite the slightly heterogeneous variances. Results of these and subsequent statistical analyses are summarized in Table 12.

The mean of Mode I log (ovarian complement) values is significantly greater than those of Modes II and III, and that of Mode II is significantly greater than that of Mode III (Student's t-test, all $P < 0.001$).

Correlation of ovarian complement with SVL

Log (ovarian complement) is plotted against SVL for species of each mode, in Fig. 5. For a given SVL, log (ovarian complement) is generally greater in Mode I species than Mode II, and generally greater in Mode II species than in Mode III. There is a significant positive correlation between ovarian complement and SVL for each of Modes I, II and III (Kendall's coefficient of rank correlation, $P < 0.001$ for Mode I, and $0.01 < P < 0.05$ for Modes II and III).

Correlation of ovarian complement with egg diameter

Values of log (ovarian complement) are plotted against log (10 x egg diameter) for each species of Modes I, II and III, in Fig. 6. There is a trend towards a decreasing ovarian complement with increasing egg diameter, and application of the Kendall's coefficient of rank correlation test indicates a significant negative correlation ($P < 0.001$). Within each mode there is considerable scatter of points (Fig. 6) and no significant correlation between egg diameter and ovarian complement (Kendall's coefficient of rank correlation).

FIG. 5 Log (ovarian complement) vs SVL for species of Modes I, II and III.

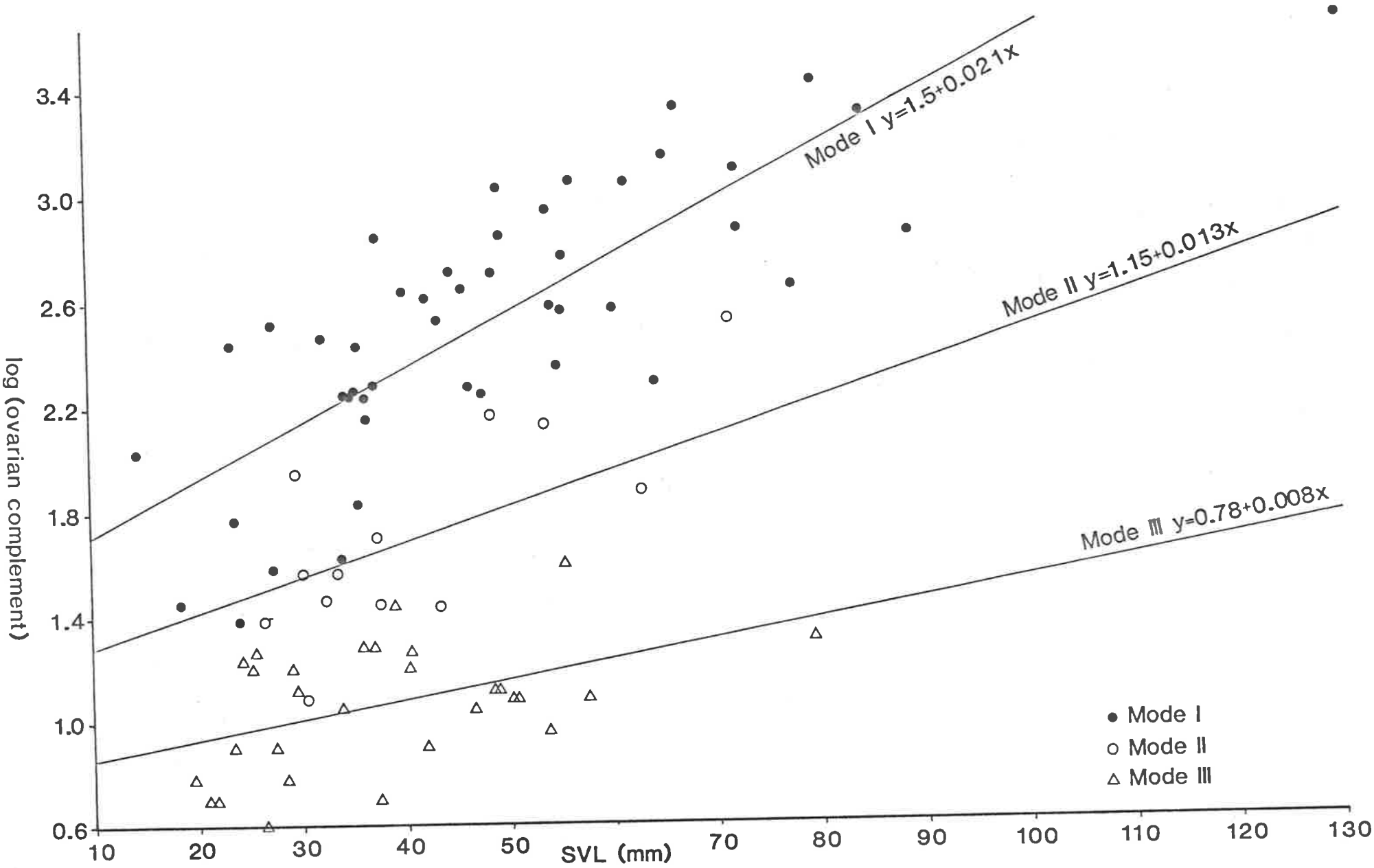
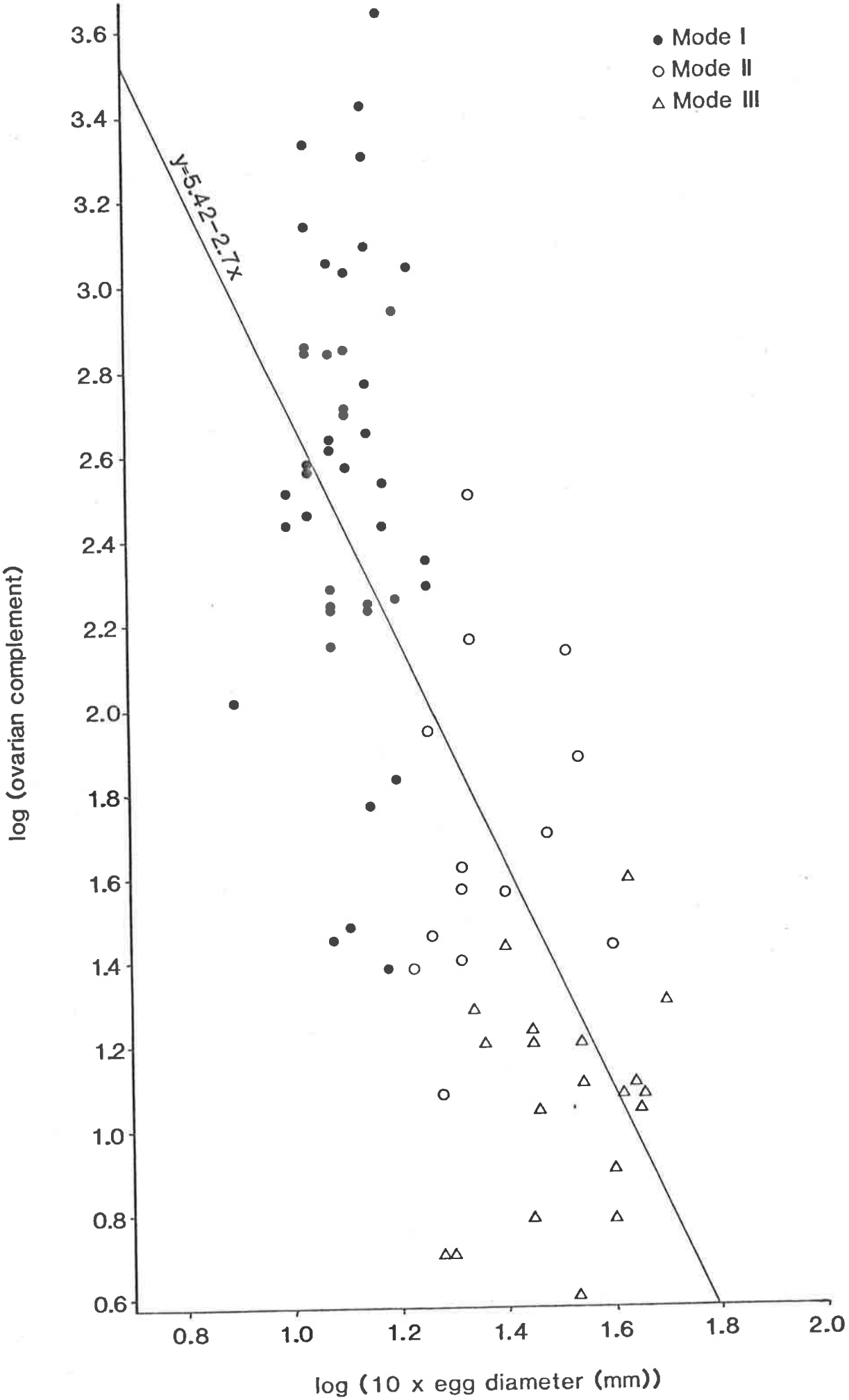

Mode I y=1.5+0.021x
Mode II y=1.15+0.013x
Mode III y=0.78+0.008x
Mode I
Mode II
Mode III
log (ovarian complement)
SVL (mm)
3.4
3.0
2.6
2.2
1.8
1.4
1.0
0.6
10
20
30
40
50
70
80
90
100
110
120
130

FIG. 6 Log (ovarian complement) vs log (10 x egg diameter) for species of Modes I, II and III combined.


Mode I
Mode II
Mode III
y=5.42−2.7x
log (ovarian complement)
log (10 x egg diameter (mm))
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0

(iii) Complement Volume

Complement volume, calculated from ovarian complement x egg volume (the latter calculated from egg diameter), is given for most species in Table 4. Complement volumes are plotted against SVL for each species in Fig. 7, from which it can be seen that for a given SVL ovarian volume falls over a relatively narrow range, regardless of reproductive mode. Complement volume therefore remains similar in species of similar size, despite differences in egg sizes and ovarian complements.

(iv) Egg Pigmentation

In many species, the animal hemisphere of each mature egg is invested with melanin, giving it a dark brown to almost black appearance. Presence or absence of egg pigmentation in each species is given in Table 3. Of the Mode I species examined, 53 possess eggs with pigmented animal hemispheres, and six possess unpigmented eggs (*Adelotus brevis*, three *Afrixalus* spp. and two *Chiromantis* spp.). Six of the Mode II species possess pigmented eggs, and seven species unpigmented eggs. All but one (*Nectophrynoides malcolmi*, in which the animal hemispheres are pigmented) of the Mode III species lack egg pigmentation.

(v) Egg Jelly Capsules

Measurements of the thickness of jelly capsules surrounding ova were obtained for a few species. These few measurements, together with published values for other species, are given in Table 5. These values are not of capsule diameters but of the thickness of mucopolysaccharide jelly material covering the egg at one point. Most values taken from the literature were calculated thus: ½ x (capsule diameter - egg diameter).

FIG. 7 Complement volume (= ovarian complement x egg volume) vs SVL for species of Modes I, II and III combined.

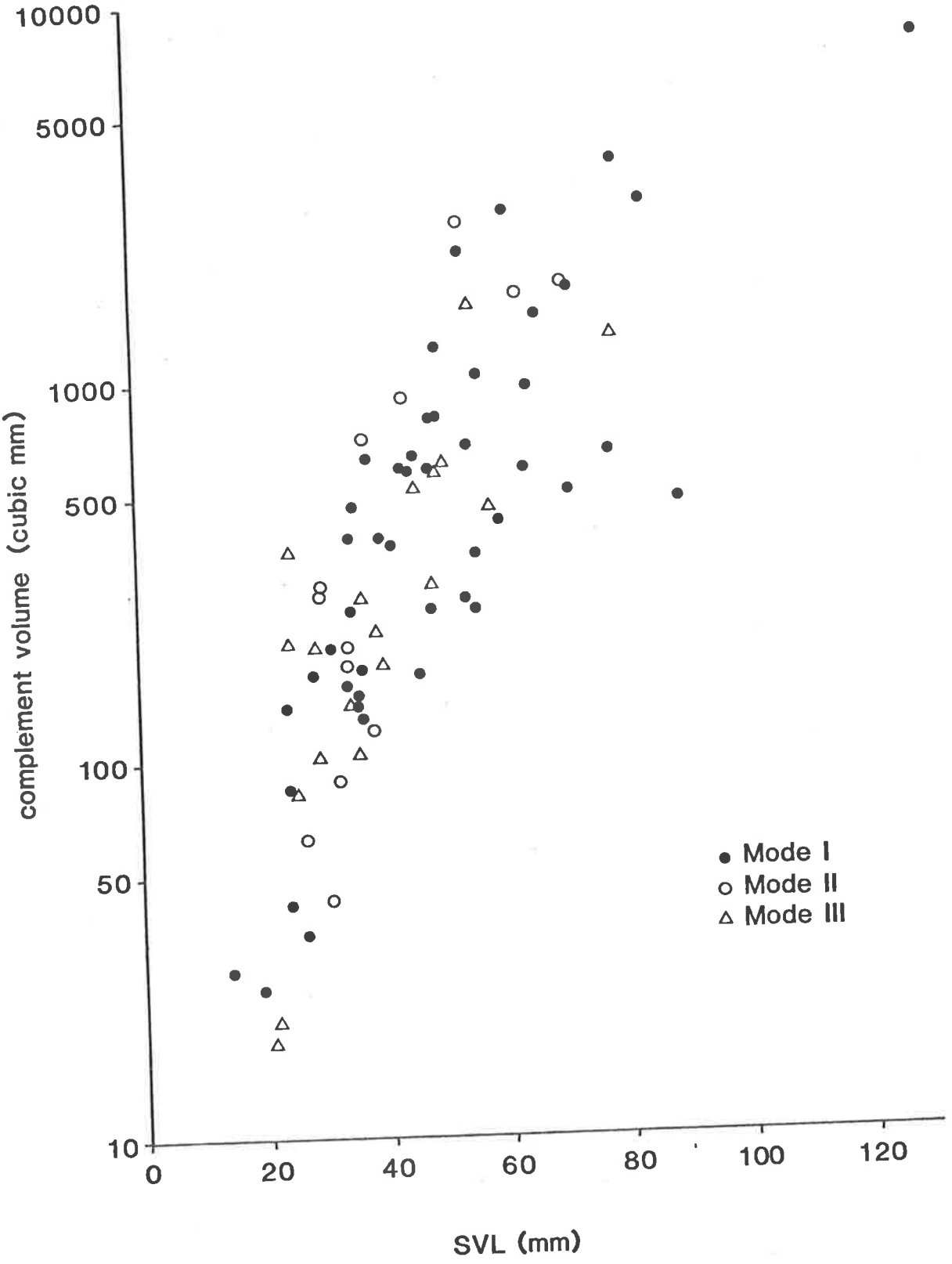

10000
5000
1000
500
100
50
10
complement volume (cubic mm)
0
20
40
60
80
100
120
SVL (mm)
Mode I
Mode II
Mode III

TABLE 5: Thickness of egg jelly capsules

Taxa	Thickness (mm) (* - measurements from ova in ovisac)
Leiopelmatidae	
Ascaphus truei	0.25 (from Noble and Putnam, 1931)
Pipidae	
Xenopus laevis	approx. 0.3 (from Freeman, 1968)
Leptodactylidae	
Limnodynastinae	
Limnodynastes tasmaniensis	0.5
Notaden melanoscaphus	0.7*
Myobatrachinae	
Assa darlingtoni	approx. 1.0 (from Ingram *et al.*, 1975)
Crinia georgiana	" 0.6 (from Main, 1957)
Myobatrachus gouldi	" 1.2 (from Roberts, 1981)
Pseudophryne bibroni	1.7*
Ranidella bilingua	approx. 0.3 (from Martin *et al.*, 1980)
R. signifera	1.4 (from Harrison, 1922)
Hylidae	
Cyclorana australis	0.7*
Litoria caerulea	approx. 0.4 (from Harrison, 1922)
L. ewingi	" 1.2 (from " ")
Hyperoliidae	
Hyperolius marmoratus	approx. 1.8 (from Wager, 1926)
Microhylidae	
Copiula fistulans	0.8*
Sphenophryne schlaginhaufeni	0.35

Thicknesses for the Mode I species range from 0.3 to 1.4 mm, and values for the three Mode II species and for the four Mode III species cover similar ranges. No statistical analysis of the data was made since numbers of species were too small for Modes II and III, but there are no apparent trends with reproductive mode.

(d) OVARIES

(i) The Anuran Ovary, General Description

The bilaterally paired ovaries are situated ventro-medial to the kidneys, suspended from the body wall by a pair of mesenteries, the mesovaria, through which enter blood vessels and nerves supplying the ovary. When enlarged with mature oocytes, the ovaries occupy much of the body cavity and may envelop other abdominal organs. Each ovary is saccular and is covered with a thin germinal epithelium which is continuous with the peritoneum. Oocytes lie embedded in cortical tissue under the germinal epithelium, and, as they develop, bulge into the ovarian cavity, which is lined by a thin layer of medullary tissue (Lofts, 1974). The ovary may be a single sac, but frequently is divided into a number of sacs or lobes (Fig. 1) between which usually lie major divisions of ovarian blood vessels. The lobes may be separated from one another only at their extremities so that they are indistinct, or they may be divided almost completely. Several ovaries, from unlobed to many-lobed, are illustrated in a variety of species of Modes I, II and III, in Figs. 20-27.

(ii) Number of Lobes of the Ovary

The number of lobes of each ovary was counted for most specimens examined. In some individuals it was not possible to determine the

number due either to poor preservation of the ovaries or else to compaction and hardening after preservation of large, ripe ovaries, the lobes of which were then impossible to separate. The results of all statistical analyses concerning ovarian lobe numbers are summarized in Table 12.

Intraspecific variability in lobe number

For those species of which several specimens were examined, it is apparent that lobe number remains relatively consistent within the species. For example in 28 specimens of *Limnodynastes tasmaniensis* reared from eggs in the laboratory and in seven others collected from field localities, there were 3 - 5 lobes, with one ovary in one individual bilobed. In 20 individuals of *Rheobatrachus silus* there were 2-4 lobes per ovary, one unlobed ovary, and one with five lobes (Horton and Tyler, 1982 - Appendix IV). There is no apparent correlation of lobe number with time of year of collection, as illustrated in 18 individuals of *Rheobatrachus silus* (Horton and Tyler, 1982), indicating no seasonal variation. Within a species there appears to be no appreciable increase in lobe number with an increase in size of the individuals, as is illustrated in Fig. 8 for 35 individuals of *Litoria dahli* which were all at a similar stage of reproductive maturity with the oviducts beginning to convolute (no significant correlation between SVL and lobe number; Kendall's coefficient of rank correlation).

Comparison of lobe numbers between modes

Means and standard deviations of lobe numbers were calculated for each species and are given in Table 6. A histogram of lobe numbers for species of Modes I, II and III is given in Fig. 9. Ranges of lobe numbers are: Mode I species: 1 - 24.5 (mean 8.71 ± 5.69)

Mode II species: 1 - 8.8 (mean 3.58 ± 2.97)

FIG. 8 Number of ovarian lobes (mean of left and right ovaries) vs SVL in 35 individuals of *Litoria dahli*, coll. near Nankeen Billabong, N.T., 27.iii.1981, M. Cappo.

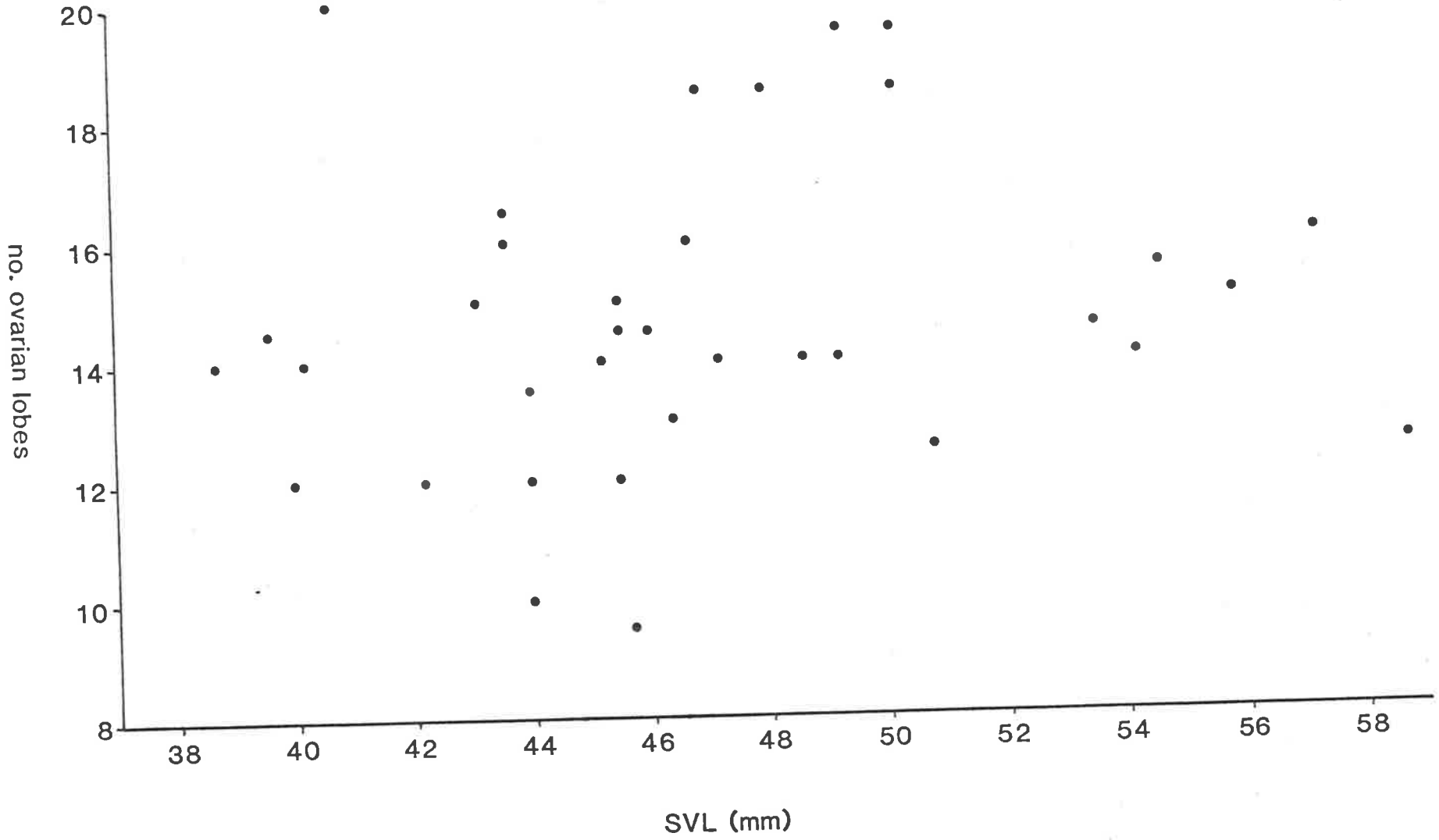

20
18
16
14
12
10
8
no. ovarian lobes
38
40
42
44
46
48
50
52
54
56
58
SVL (mm)

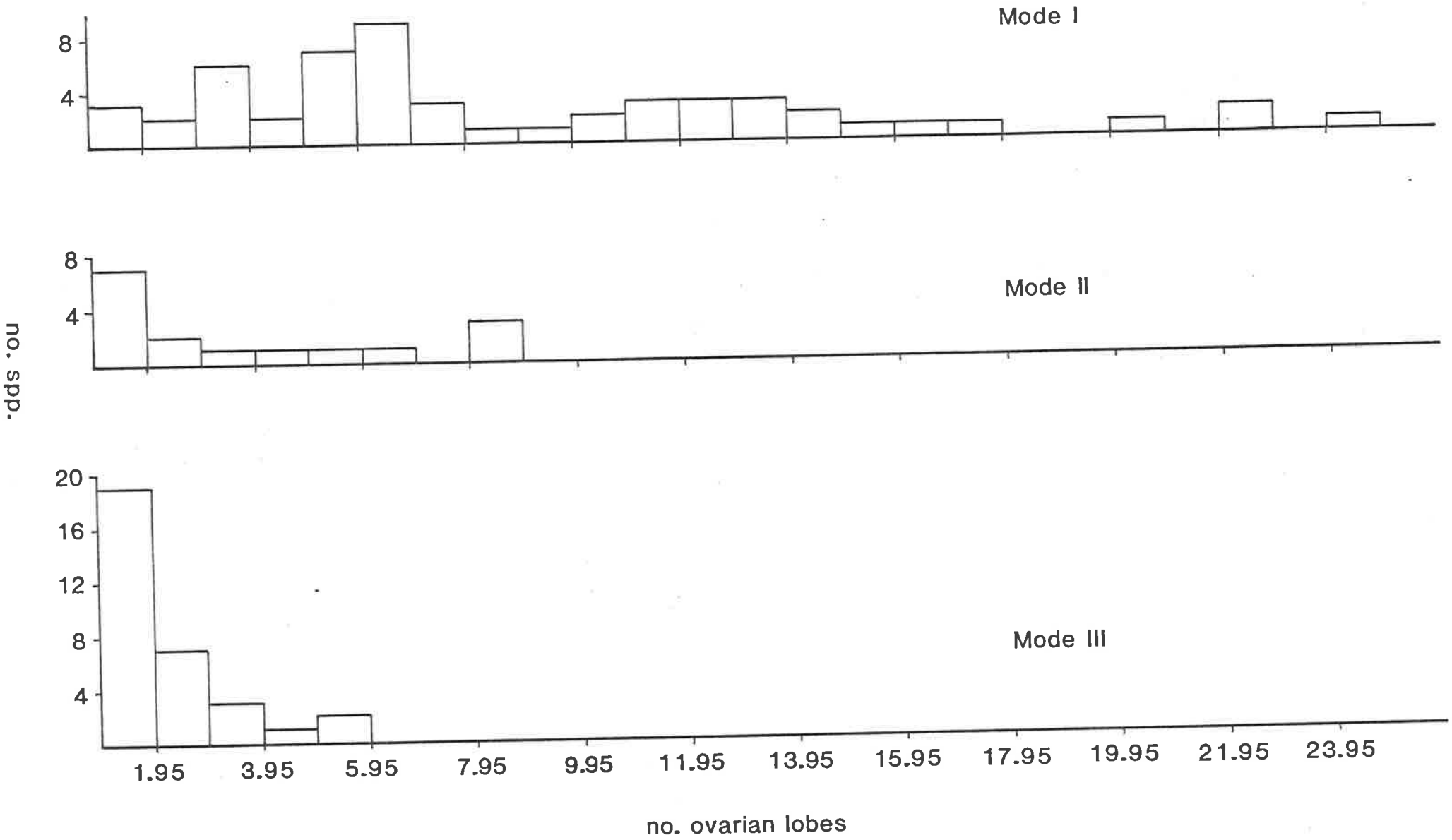
TABLE 6: Number of lobes per ovary for all species investigated. The number of lobes is the mean for left and right ovaries of all specimens of that species. Standard deviations are in parentheses.

Taxa	Number of Lobes
Leiopelmatidae	
Ascaphus truei	1.0
Leiopelma hochstetteri	1.0
Pipidae	
Xenopus laevis	24.5 (± 0.7)
X. muelleri	17.5 (± 0.7)
Pelobatidae	
Pelobates fuscus	6.5 (± 0.7)
Bufonidae	
Bufo marinus	20 (± 1.4)
Nectophrynoides malcolmi	1.0
N. tornieri	1.0
Leptodactylidae	
Limnodynastinae	
Adelotus brevis	-
Heleioporus eyrei	6.3 (± 2.5)
Lechriodus melanopyga	6.0
Limnodynastes dorsalis	6.1 (± 1.6)
L. dumerili	7.7 (± 1.0)
L. ornatus	6.8 (± 1.3)
L. peroni	-
L. tasmaniensis	3.6 (± 0.8)
Megistolotis lignarius	3.5 (± 0.7)
Neobatrachus ?centralis	7.7 (± 1.0)
N. sp.	6.8 (± 1.2)
Notaden melanoscaphus	9.9 (± 1.3)
N. nichollsi	11.5 (± 0.7)
Myobatrachinae	
Assa darlingtoni	1.5 (± 0.7)
Crinia georgiana	1.0
Myobatrachus gouldi	1.0
Pseudophryne bibroni	1.0
Ranidella bilingua	1.0
R. riparia	1.0
R. signifera	1.3 (± 0.4)
Taudactylus acutirostris	1.0
T. diurnus	1.0
Uperoleia inundata	3.0
Rheobatrachinae	
Rheobatrachus silus	2.8 (± 0.8)

Taxa	Number of Lobes
Eleutherodactylinae	
Eleutherodactylus achatinus	2.2 (± 0.8)
E. chloronotus	1.0
E. curtipes	1.3 (± 0.5)
E. devillei	1.5 (± 0.6)
E. walkeri	1.0
Dendrobatidae	
Phyllobates aurotaenia	1.0
Hylidae	
Cyclorana australis	22.1 (± 2.9)
C. brevipes	11.5 (± 0.7)
C. longipes	11.5 (± 0.7)
C. maini	13.5 (± 1.0)
Litoria alboguttata	22.3 (± 1.5)
L. bicolor	4.6 (± 0.5)
L. caerulea	14.8 (± 4.2)
L. chloris	12.8 (± 1.0)
L. coplandi	6.5 (± 2.1)
L. dahli	14.6 (± 2.6)
L. eucnemis	12.0
L. ewingi	5.5 (± 0.7)
L. inermis	5.0 (± 1.4)
L. iris	1.3 (± 0.5)
L. lesueuri	15.5 (± 0.7)
L. microbelos	3.0
L. modica	3.3 (± 1.7)
L. nannotis	5.8 (± 1.3)
L. nasuta	5.8 (± 1.3)
L. pallida	5.7 (± 0.8)
L. peroni	7.5 (± 1.3)
L. pratti	2.8 (± 0.5)
L. raniformis	13.0
L. rheocola	4.5 (± 0.6)
L. rothi	8.1 (± 1.5)
L. rubella	6.3 (± 1.2)
L. tornieri	4.5 (± 0.7)
L. wotjulumensis	5.5 (± 0.7)
Nyctimystes papua	8.8 (± 1.3)
Phrynohyas venulosa	16.0
Ranidae	
Arthroleptella lightfooti	2.5 (± 0.7)
Arthroleptis poecilonotus	1.0
Cacosternum boettgeri	5.0
Rana cascadea	6.0 (± 1.4)
R. grisea	-
R. papua	12.0

Taxa	Number of Lobes
Hyperoliidae	
Afrixalus dorsalis	6.0
A. fornasini	2.5 (± 0.7)
A. quadrivittatus	3.5 (± 0.7)
Callixalus pictus	2.0 (± 1.4)
Cryptothylax greshoffi	5.5 (± 0.7)
Hyperolius marmoratus	3.0
Leptopelis bocagei	8.0
L. macrotis	8.5 (± 0.7)
Rhacophoridae	
Chiromantis petersi	13.0
C. xerampelina	10.0
Microhylidae	
Asterophryinae	
Asterophrys turpicula	1.0
Barygenys nana	1.0
Hylophorbus rufescens	3.0
Phrynomantis humicola compta	2.5 (± 0.7)
P. h. humicola	2.0
P. lateralis	3.0
P. louisiadensis	5.0
P. robusta	3.0
P. stictogaster	5.0
P. wilhelmana	2.8 (± 1.2)
Xenobatrachus rostratus	4.5 (± 0.7)
Xenorhina bouwensi	1.0
Sphenophryninae	
Cophixalus darlingtoni	1.0
C. neglectus	1.0
C. ornatus	1.0
C. parkeri	1.0
C. riparius	2.0
Copiula fistulans	1.0
Oreophryne biroi	1.0
Sphenophryne schlaginhaufeni	-
Dyscophinae	
Calluella guttulata	-
Microhylinae	
Chaperina fusca	2.0
Kaloula pulchra	10.0
Microhyla heymonsi	-

FIG. 9 Numbers of species with ovarian lobe numbers in given size classes, for species of Mode I, Mode II, and Mode III.


Mode I
Mode II
Mode III
8
4
8
4
20
16
12
8
4
no. spp.
1.95
3.95
5.95
7.95
9.95
11.95
13.95
15.95
17.95
19.95
21.95
23.95
no. ovarian lobes

Mode III species: 1 - 5 (mean 1.89 ± 1.21)

Values of lobe numbers are from a population with normal distribution (Kolmogorov-Smirnov one-sample test), but the variances are significantly heterogeneous (F max test, $P < 0.01$). Values of log (lobe number) are also normally distributed and the variances are not significantly heterogeneous, therefore these transformed values were employed for parametric tests.

The mean of Mode I log (lobe number) values is significantly greater than those of Modes II and III (Student's t-test, $P < 0.001$), and the mean for Mode II is significantly greater than that for Mode III ($0.01 < P < 0.05$).

Correlation of lobe numbers with SVL

Log (lobe number) is plotted against SVL for species of each mode, in Fig. 10. For a given SVL, log (lobe number) is almost always greater in Mode I species than in Mode III species. Values of log (lobe number) for Mode II species are scattered but tend to be intermediate between those of Modes I and III. There is a significant positive correlation between lobe number and SVL for each of Modes I, II and III (Kendall's coefficient of rank correlation; $P < 0.001$ for Mode I, $0.001 < P < 0.01$ for Mode II, $0.01 < P < 0.05$ for Mode III). Trends in lobe number are clearer among larger species because in many of the smaller species, particularly of Modes II and III, the ovaries are unlobed.

Correlation of lobe numbers with egg diameter

Values of log (lobe number) are plotted against log (10 x egg diameter) for each species of Modes I, II and III, in Fig. 11. There is a trend towards a smaller number of lobes with increasing egg diameter, and application of Kendall's coefficient of rank correlation indicates a

FIG. 10 Log (ovarian lobe number) vs SVL for species of Modes I, II and III.

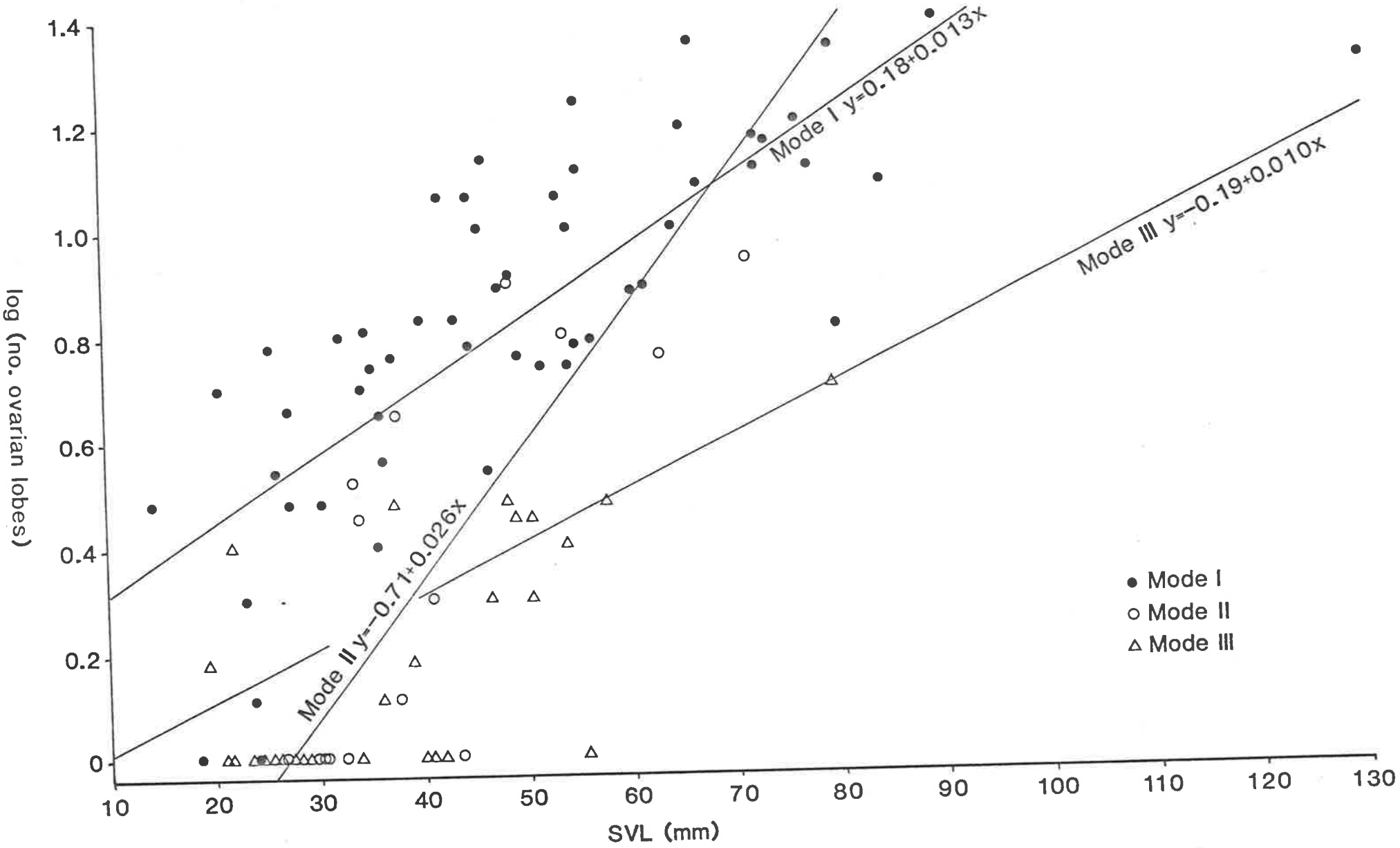
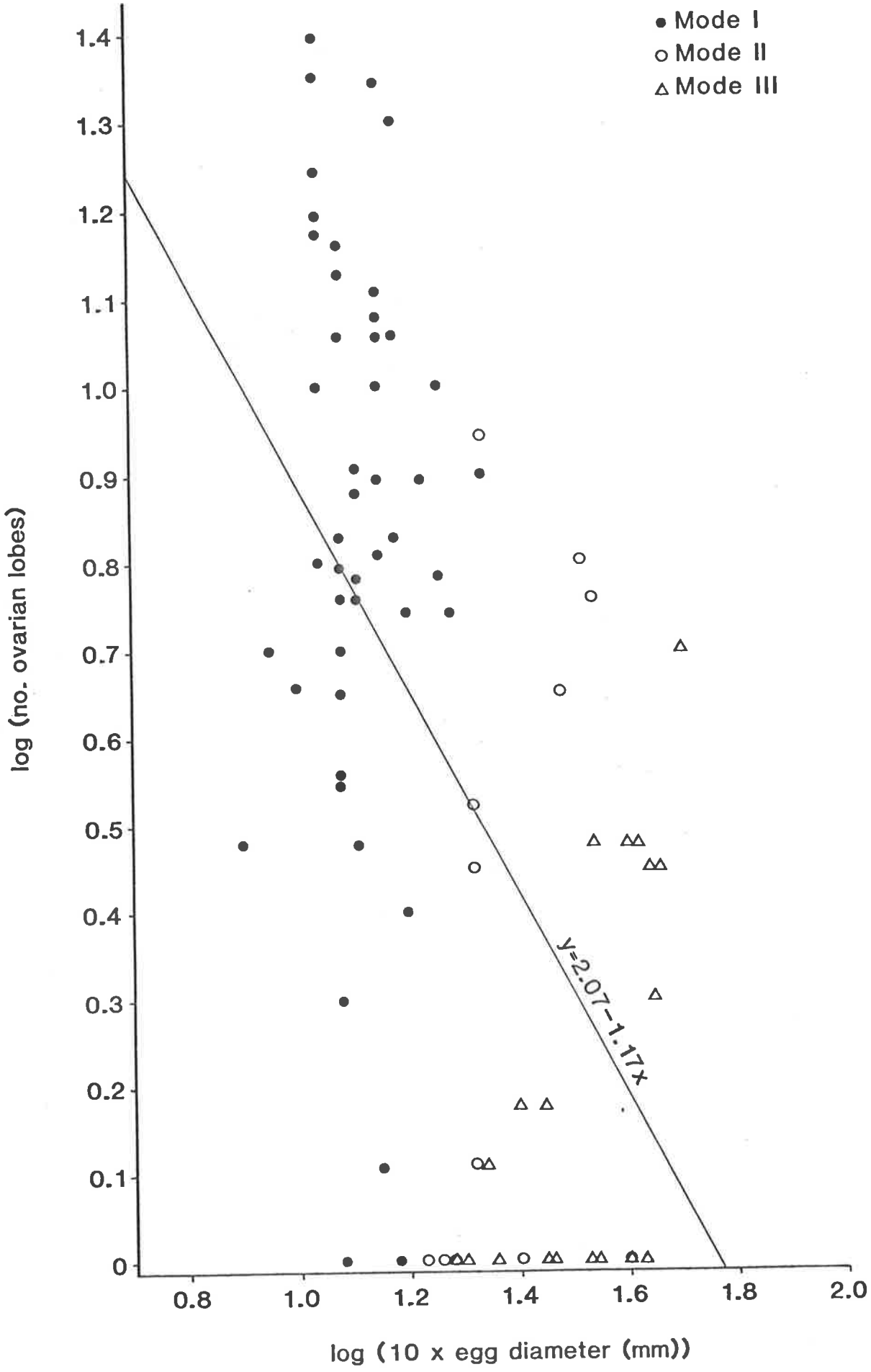

log (no. ovarian lobes)
SVL (mm)
Mode I y=0.18+0.013x
Mode II y=−0.71+0.026x
Mode III y=−0.19+0.010x
Mode I
Mode II
Mode III
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
10
20
30
40
50
60
70
80
90
100
110
120
130

FIG. 11 Log (ovarian lobe number) vs log (10 x egg diameter) for species of Modes I, II and III combined.


Mode I
Mode II
Mode III
y=2.07−1.17x
log (no. ovarian lobes)
log (10 x egg diameter (mm))
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
1.2
1.3
1.4
0.8
1.0
1.2
1.4
1.6
1.8
2.0

significant negative correlation ($P < 0.001$). Within each mode there is considerable scatter of points (Fig. 11), and for Modes I and II species there is no significant correlation of lobe number with egg diameter (Kendall's coefficient). For Mode III species there is a significant positive correlation.

(iii) Differentiation of Gonads

Differentiation of the gonads was investigated in four species: *Limnodynastes dumerili*, *L. tasmaniensis*, *Litoria ewingi* and *Pseudophryne bibroni*. The point of differentiation was taken as being that stage at which in transverse section of the immature gonad the medullary cells had either degenerated, forming a presumptive ovary, or proliferated, forming a presumptive testis, or at which oogonia could be distinguished (particularly in *Pseudophryne bibroni* in which it was difficult to distinguish between cortical and medullary cells).

Three series of *Limnodynastes tasmaniensis* tadpoles were examined, and the gonads were found to differentiate at late stage 25 and stage 30 (Horton 1982 - Appendix II), and at stage 28 - 29, respectively. In two series of *Limnodynastes dumerili* tadpoles the gonads differentiated at stage 35 and at stage 36. Differentiation occurred at stage 41 in one series of *Litoria ewingi* tadpoles. In one series of *Pseudophryne bibroni* tadpoles the stage of differentiation was determined approximately as between stages 39 and 41.

Externally visible lobing of the ovaries was not apparent immediately after differentiation of the gonads, but formed when the ovary was still in a very immature state. In one series of *Limnodynastes tasmaniensis* the ovarian lobes were apparent at stage 32 - 33. In two series of

Limnodynastes dumerili they were apparent at stage 40 - 41 and at stage 41, respectively, and in *Litoria ewingi* they formed shortly after metamorphosis. The numbers of lobes which form in these immature stages correspond with the lobe numbers seen in adult specimens. Therefore it appears that the number of lobes developed initially is a set number that the ovary will retain throughout the life of the frog.

(iv) Ovarian Asymmetry

Sufficient numbers of specimens of a few species were examined to give some indication of inequality, if present, between the left and right ovaries in their numbers of lobes and complements of eggs. Twenty-one individuals of *Rheobatrachus silus* were examined; lobe numbers and ovarian complements are detailed for these in Horton and Tyler (1982) (Appendix IV). Among the 18 specimens for which left and right lobe counts were made, the left ovary possessed more lobes than the right in two specimens, the same number of lobes in three specimens, and fewer lobes in 13 specimens. Among the 14 specimens for which left and right ovarian complements were counted, there were more eggs in the left ovary than the right in one specimen, the same number of eggs in two specimens, and fewer eggs in the left ovary in 11 specimens.

Counts for nine other species are given in Table 7. Only the counts of lobe number for *Litoria dahli* were tested statistically; there is no significant difference in numbers between left and right ovaries in this species (Wilcoxon signed rank test). No significant asymmetry is apparent in *Limnodynastes tasmaniensis*, *Ranidella signifera*, *Eleutherodactylus achatinus* and *Litoria rothi*. In *Myobatrachus gouldi*, four of the five specimens possessed more oocytes in the left ovary than in the right, as did all *Eleutherodactylus curtipes* and *Cyclorana*

TABLE 7a: Numbers of specimens of nine species in which the number of ovarian lobes is equal in both ovaries (L = R) or is greater in the left ovary (L > R) or is smaller in the left ovary (L < R). n = total number of specimens for each species.

Species	n	Number of Specimens		
		L = R	L > R	L < R
Limnodynastes tasmaniensis	18	8	4	6
Myobatrachus gouldi	5	5	0	0
Ranidella signifera	12	8	3	1
Eleutherodactylus achatinus	5	0	2	3
E. curtipes	6	4	0	2
Cyclorana australis	8	2	4	2
Litoria dahli	38	9	21	8
L. rothi	7	2	1	4
L. rubella	6	2	4	0

TABLE 7b: Ovarian complements of left (L) and right (R) ovaries in individuals of five species. n = total number of specimens per species; L > R = more oocytes in the left ovary than in the right; L < R = fewer oocytes in the left ovary than in the right. Numbers of ovarian lobes are given in parentheses.

Species	n	Ovarian Complements			
		L > R		L < R	
		L	R	L	R
Myobatrachus gouldi	5	25 (1)	18 (1)	23 (1)	28 (1)
		30 (1)	27 (1)		
		64 (1)	61 (1)		
		71 (1)	46 (1)		
Ranidella signifera	6	58 (2)	50 (1)	38 (1)	54 (1)
		64 (1)	62 (1)	58 (2)	61 (1)
		89 (1)	64 (2)	69 (1)	75 (1)
Eleutherodactylus curtipes	5	20 (2)	15 (2)		
		22 (1)	15 (1)		
		23 (1)	10 (2)		
		23 (1)	19 (1)		
		23 (1)	22 (3)		
Cyclorana australis	7	1457 (26)	1246 (23)		
		2341 (21)	2222 (22)		
		2743 (25)	1283 (23)		
		2871 (18)	2607 (19)		
		3453 (26)	3056 (26)		
		3735 (19)	2440 (17)		
		4009 (24)	2998 (23)		
Litoria rothi	5	368 (9)	348 (10)	170 (6)	300 (8)
		372 (9)	325 (6)	995 (8)	1200 (8)
		541 (10)	433 (10)		

australis specimens for which counts were obtained. In two specimens of *Litoria rubella* the number of lobes was equal for both ovaries but in the remaining four the left ovary possessed more lobes.

(e) OVIDUCTS

(i) The Anuran Oviduct, General Description

Anuran oviducts are bilaterally paired and lie firmly held by peritoneum along the dorsal surface of the body cavity, extending from a position adjacent (usually ventral) to the lung apices posteriorly to the cloaca (Fig. 1). From its ostium, each oviduct is more or less discretely composed of three regions (Fig. 1): 1) the anterior-most *pars recta*, a short, straight, thin-walled tube which extends dorsolaterally from the ostium and then curves posteriorly; 2) the *pars convoluta*, an elongate and thick-walled tube which in the mature frog is irregularly folded into numerous convolutions; these convolutions are tightly bound by peritoneal folds and increase in size posteriorly as the oviduct cross-sectional diameter increases, although in many individuals the *pars convoluta* narrows near its termination so that the posterior-most convolutions are slightly smaller, as shown in Fig. 26B; and 3) the ovisac, a thin-walled and highly distensible chamber which enters the dorsal wall of the cloaca posteriorly, generally through a small papilla. The paired ovisacs remain separate and open into the cloaca independently, or else they unite at some point along their length so that there is only a single opening into the cloaca. Examples of anuran oviducts are illustrated for a variety of species of Modes I, II and III, in Figs. 20 - 27.

In some species a urinogenital sinus may be present; this is a cavity in the rectal wall which usually lies between the oviducts and the

rectum, and which ends blindly anteriorly and opens into the cloaca posteriorly. The oviducts may enter into the sinus before the latter opens into the cloaca, or else the oviducts may open into the cloaca, posterior to the entrance of the sinus into the cloaca. The function of the urinogenital sinus is not understood.

The oviduct wall consists of an outer serosa, a lamina propria, and an inner, simple, cuboidal or low-columnar epithelium. The epithelium is folded into longitudinal ridges which are deepest in the *pars recta* and become shallower posteriorly. Epithelial cells on the crests of the ridges generally are ciliated. Tubular, jelly-secreting glands in the lamina propria constitute the bulk of the wall in the *pars convoluta*, and may also occur in the posterior-most and anterior-most regions of the *pars recta* and ovisacs, respectively. The glands are of similar histological structure throughout the oviduct. Mucopolysaccharide compounds secreted from these glands coat the ova as they are propelled along the oviduct following ovulation.

(ii) Convolutions of the *pars convoluta*

The number of convolutions of the *pars convoluta* of each oviduct was counted for most specimens examined. In some individuals it was not possible to determine the number due to poor preservation and disintegration of the soft oviduct tissue, or because undue damage would have been caused to museum specimens in dissecting them. The results of statistical analyses concerning numbers of convolutions are summarized in Table 12.

Correlation between number of convolutions and oviduct length

The length of the *pars convoluta* was measured in 13 specimens of

seven species of *Litoria* all with relatively narrow oviducts at reproductive maturity. The measurements are given in Table 8 and plotted in Fig. 12. There is a significant increase in length with increasing numbers of convolutions, indicating that the latter is a measure of oviduct length. There are too few points on the graph to determine the nature of the relationship; it appears allometric rather than linear, but those individuals which diverge furthest from a straight line near which most points lie are *L. chloris* no.2 and *L. rothi* no.3 in which the oviducts were comparatively broad (thus lengthening the oviduct). Therefore the relationship may be linear, as would be expected if oviduct width remains the same.

Intraspecific variation in numbers of convolutions

For those species of which several individuals were examined, it was apparent that the number of convolutions remains relatively consistent within the species. For example, left and right oviducts of six individuals of *Cyclorana australis* yielded the following counts (smallest to largest individual):

L	185	169	166	163	214	187
R	183	176	169	166	190	180

and left and right oviducts of 11 *Ranidella signifera* (smallest to largest individual):

L	26	29	27	28	38	30	33	34	31	36	31
R	29	30	29	30	39	32	36	38	31	33	35

There is no correlation of the number of convolutions with time of year of collection, as is illustrated in 18 individuals of *Rheobatrachus silus* (Horton and Tyler, 1982). Thus there appears to be no seasonal variation in convolution number. Within a species there appears to be no significant increase in the number of convolutions with an increase in size of

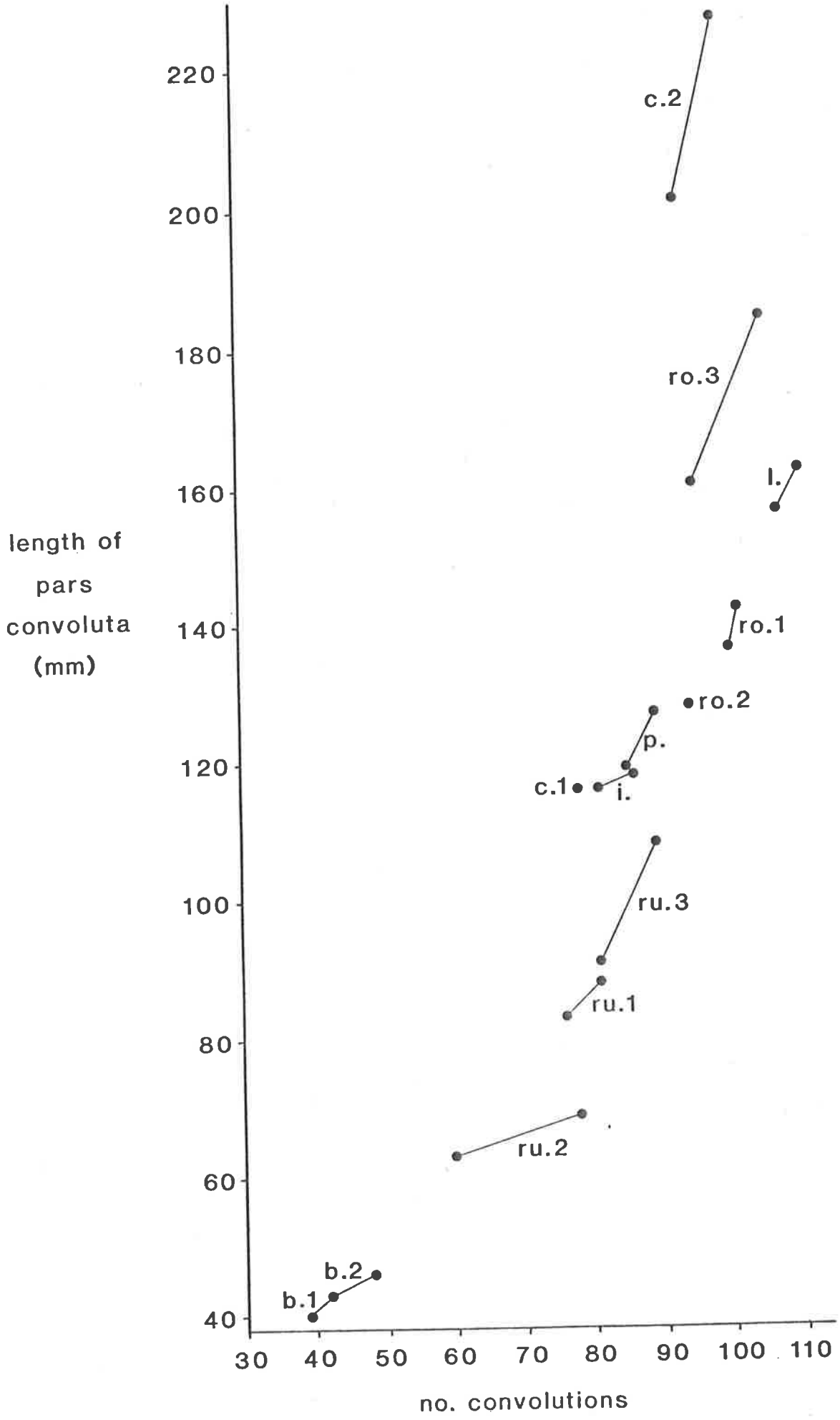
TABLE 8: Length and width of *pars convoluta*, and number of convolutions, in 13 individuals of seven *Litoria* species. L = left oviduct, R = right oviduct.

Species		SVL (mm)	Number of Convolutions L	Number of Convolutions R	Length (mm) L	Length (mm) R	Width (mm) L	Width (mm) R
L. bicolor	1	26.2	42	39	43	30	1.2	1.1
	2	27.8	48	42	46	43	1.0	1.0
L. chloris	1	49.3	-	78	-	116	-	1.4
	2	61.9	93	99	201	227	2.4	2.3
L. inermis		35.4	81	86	116	118	2.0	1.8
L. lesueuri		65.3	107	110	156	162	1.7	1.7
L. pallida		36.5	85	89	119	127	2.0	2.0
L. rothi	1	45.6	100	101	136	142	1.8	1.8
	2	48.2	-	94	-	128	-	1.6
	3	48.6	95	105	160	184	2.0	2.2
L. rubella	1	31.5	76	81	83	88	1.2	1.2
	2	31.6	78	60	69	63	1.0	1.1
	3	35.7	81	89	91	108	1.4	1.3

FIG. 12 Length of the *pars convoluta* vs number of convolutions of the *pars convoluta* in 13 individuals of seven *Litoria* species.

b. = *Litoria bicolor*; c. = *L. chloris*;
i. = *L. inermis*; l. = *L. lesueuri*;
p. = *L. pallida*; ro. = *L. rothi*;
ru. = *L. rubella*.

The data points for left and right oviducts of the same individual are joined by lines.


length of pars convoluta (mm)
220
200
180
160
140
120
100
80
60
40
30
40
50
60
70
80
90
100
110
no. convolutions
c.2
ro.3
l.
ro.1
ro.2
p.
c.1
i.
ru.3
ru.1
ru.2
b.2
b.1

the individuals. For example, in 11 reproductively mature *Ranidella signifera* (numbers of convolutions given above) with SVL ranging from 20.8 to 25.7mm there is no significant increase in convolution numbers from the smallest to the largest individual (Kendall's coefficient of rank correlation). Mean convolution numbers of left and right oviducts in 20 adult females of *Rheobatrachus silus* are plotted against SVL in Fig. 13 (data from Horton and Tyler, 1982), and the scatter of points is random with no apparent trends (no significant correlation; Kendall's coefficient).

Comparison of numbers of convolutions between modes

Means and standard deviations of numbers of convolutions per oviduct were calculated for each species and are given in Table 9. A histogram of convolution numbers for species of Modes I, II and III is given in Fig. 14. Ranges of convolution numbers are:

Mode I species: 11 - 179.8 (mean 89.76 ± 45.16)

Mode II species: 8.3 - 84.5 (mean 31.71 ± 21.03)

Mode III species: 7 - 52.5 (mean 26.61 ± 11.14)

Values of convolution numbers are from a population with normal distribution (Kolmogorov-Smirnov one-sample test), but the variances are significantly heterogeneous (F max test, $P < 0.01$). Values of log (number of convolutions) are also normally distributed and the variances are not significantly heterogeneous; these transformed values were therefore employed for parametric tests.

The mean of Mode I log (number of convolutions) values is significantly greater than those of Modes II and III (Student's t-test, $P < 0.001$), but the mean for Mode II is not significantly different from that for Mode III.

FIG. 13 Number of oviduct convolutions (mean of left and right oviducts) vs SVL in 20 individuals of *Rheobatrachus silus*.

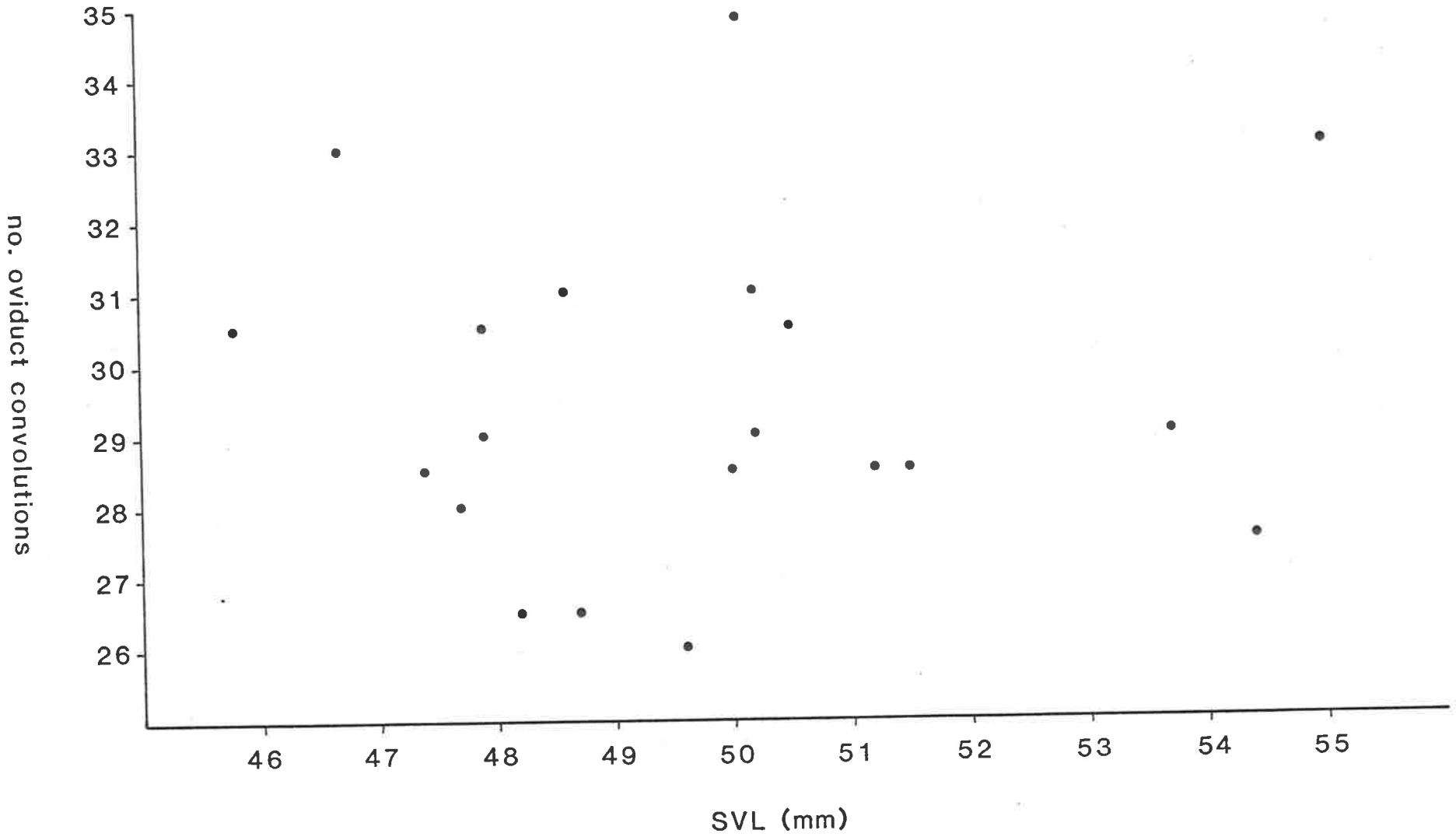

35
34
33
32
31
30
29
28
27
26
no. oviduct convolutions
46
47
48
49
50
51
52
53
54
55
SVL (mm)

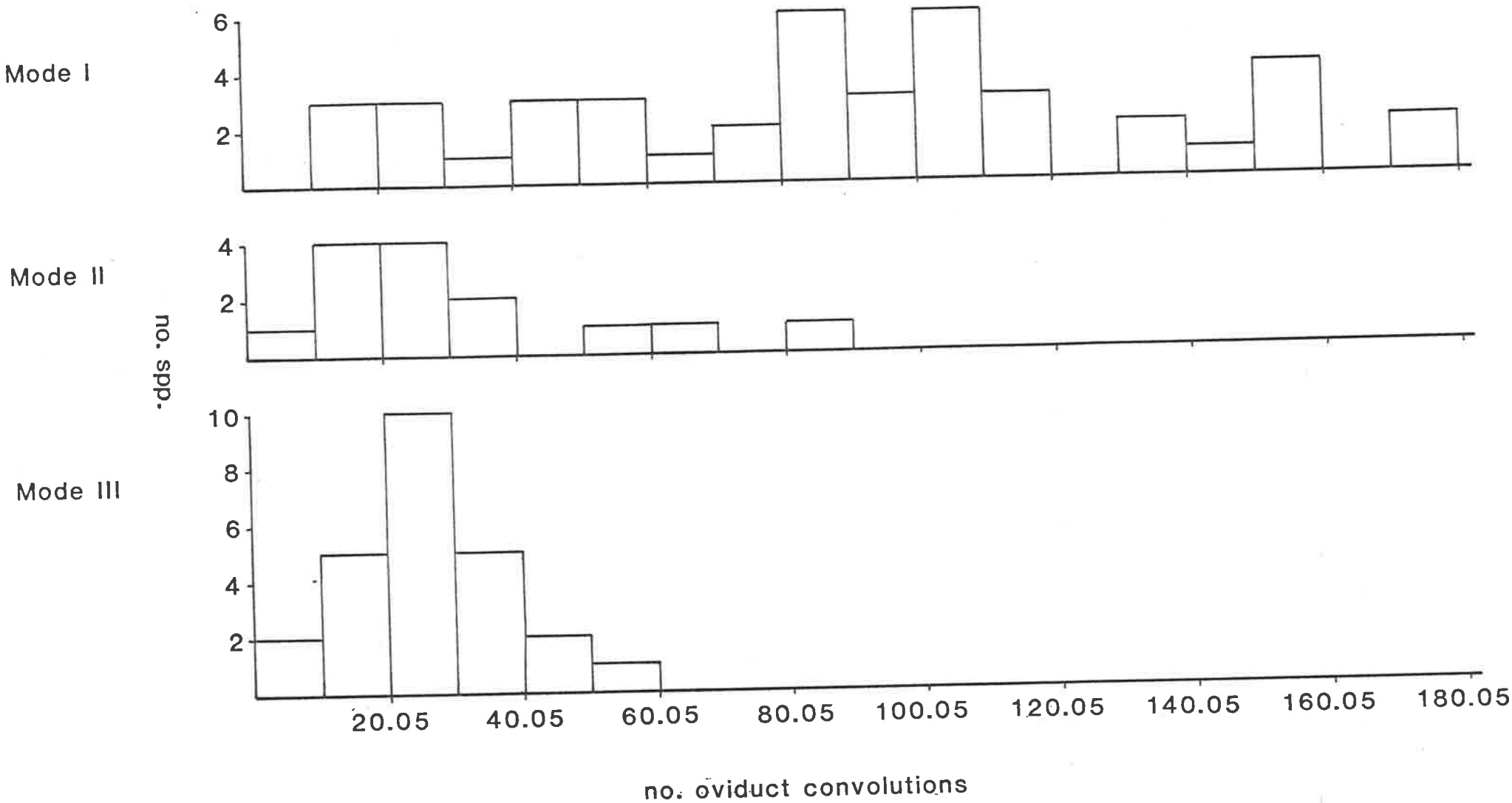
TABLE 9: Number of convolutions per oviduct, and oviduct width, for all species investigated. Each value is the mean for left and right oviducts for all specimens of that species. Standard deviations are in parentheses.

Taxa	Number of Convolutions	Oviduct Width (mm)
Leiopelmatidae		
Ascaphus truei	22.5 (± 0.7)	1.83 (± 0.04)
Leiopelma hochstetteri	32.0 (± 2.8)	3.68 (± 0.25)
Pipidae		
Xenopus laevis	156.5 (± 6.4)	1.83 (± 0.04)
X. muelleri	110.0 (± 8.5)	0.98 (± 0.04)
Pelobatidae		
Pelobates fuscus	90.0 (± 8.5)	-
Bufonidae		
Bufo marinus	110.0 (± 2.8)	2.60 (± 0.35)
Nectophrynoides malcolmi	14.5 (± 1.7)	-
N. tornieri	o	-
Leptodactylidae		
Limnodynastinae		
Adelotus brevis	-	-
Heleioporus eyrei	-	-
Lechriodus melanopyga	-	1.35 (± 0.35)
Limnodynastes dorsalis	-	1.53 (± 0.25)
L. dumerili	-	-
L. ornatus	-	1.25 (± 0.37)
L. peroni	-	1.70 (± 0.28)
L. tasmaniensis	-	1.63 (± 0.21)
Megistolotis lignarius	-	-
Neobatrachus ?centralis	65.0 (± 6.4)	1.35 (± 0.14)
N. sp.	87.5 (± 5.7)	1.54 (± 0.09)
Notaden melanoscaphus	115.0 (± 9.4)	1.90 (± 0.18)
N. nichollsi	152.0 (± 7.1)	1.38 (± 0.04)
Myobatrachinae		
Assa darlingtoni	7.0	2.35
Crinia georgiana	32.0 (± 2.8)	-
Myobatrachus gouldi	29.4 (± 3.4)	4.38 (± 0.11)
Pseudophryne bibroni	8.3 (± 3.4)	3.63 (± 0.30)
Ranidella bilingua	-	-
R. riparia	28.9 (± 2.4)	-
R. signifera	32.4 (± 3.7)	1.58 (± 0.36)
Taudactylus acutirostris	28.5 (± 2.1)	2.18 (± 0.10)
T. diurnus	23.5 (± 2.7)	1.26 (± 0.09)
Uperoleia inundata	48.5 (± 2.1)	-
Rheobatrachinae		
Rheobatrachus silus	29.3 (± 2.3)	2.72 (± 0.17)

Taxa	Number of Convolutions	Oviduct Width (mm)
Eleutherodactylinae		
Eleutherodactylus achatinus	37.0 (± 2.8)	-
E. chloronotus	28.0 (± 2.1)	3.23 (± 0.18)
E. curtipes	40.6 (± 5.4)	1.91 (± 0.05)
E. devillei	40.0 (± 2.6)	2.40 (± 0.07)
E. walkeri	21.0 (± 2.2)	1.35 (± 0.35)
Dendrobatidae		
Phyllobates aurotaenia	16.0 (± 1.8)	1.95 (± 0.35)
Hylidae		
Cyclorana australis	179.0 (±14.4)	2.80 (± 0.48)
C. brevipes	104.5 (± 3.5)	2.10 (± 0.09)
C. longipes	88.5 (± 2.1)	1.35
C. maini	92.5 (± 7.5)	-
Litoria alboguttata	135.0 (± 3.5)	-
L. bicolor	42.3 (± 3.5)	1.17 (± 0.13)
L. caerulea	179.8 (±44.5)	1.70 (± 0.70)
L. chloris	86.3 (±11.6)	1.86 (± 0.54)
L. coplandi	-	1.45 (± 0.07)
L. dahli	133.0 (±18.1)	-
L. eucnemis	74.0 (± 4.2)	-
L. ewingi	59.5 (± 0.7)	2.47 (± 0.17)
L. inermis	84.5 (± 3.1)	1.53 (± 0.43)
L. iris	32.3 (± 2.6)	2.22 (± 0.33)
L. lesueuri	108.5 (± 2.1)	1.65
L. microbelos	-	-
L. modica	19.8 (± 3.3)	2.39 (± 0.19)
L. nannotis	27.0 (± 0.8)	3.53 (± 0.02)
L. nasuta	99.3 (± 4.2)	2.28 (± 0.14)
L. pallida	99.4 (±11.7)	1.73 (± 0.19)
L. peroni	115.3 (± 7.3)	-
L. pratti	14.7 (± 5.5)	2.37 (± 0.29)
L. raniformis	155.5 (± 9.2)	3.30
L. rheocola	19.0	2.58 (± 0.09)
L. rothi	102.9 (± 7.2)	1.90 (± 0.28)
L. rubella	77.3 (± 8.6)	1.18 (± 0.15)
L. tornieri	-	1.45 (± 0.07)
L. wotjulumensis	89.5 (± 5.0)	2.20
Nyctimystes papua	60.8 (± 5.0)	3.30 (± 0.23)
Phrynohyas venulosa	146.0 (± 4.2)	-
Ranidae		
Arthroleptella lightfooti	7.0	-
Arthroleptis poecilonotus	-	2.73
Cacosternum boettgeri	45.5 (± 2.1)	-
Rana cascadea	55.0 (± 2.8)	2.50 (± 0.07)
R. grisea	-	-
R. papua	104.5 (± 3.5)	1.93 (± 0.04)

Taxa	Number of Convolutions	Oviduct Width (mm)
Hyperoliidae		
Afrixalus dorsalis	14.0 (± 1.4)	-
A. fornasini	17.5 (± 0.7)	-
A. quadrivittatus	11.0 (± 1.4)	-
Callixalus pictus	-	-
Cryptothylax greshoffi	30.0 (± 1.4)	-
Hyperolius marmoratus	-	-
Leptopelis bocagei	55.0	3.00
L. macrotis	84.5 (± 3.5)	-
Rhacophoridae		
Chiromantis petersi	102.0	-
C. xerampelina	-	-
Microhylidae		
Asterophryinae		
Asterophrys turpicula	-	-
Barygenys nana	14.0	1.55
Hylophorbus rufescens	19.0	1.63
Phrynomantis humicola compta	25.0	2.10 (± 0.07)
P. h. humicola	28.0	3.25
P. lateralis	32.3 (± 7.0)	-
P. louisiadensis	-	-
P. robusta	43.0	1.44
P. stictogaster	52.5 (±10.6)	-
P. wilhelmana	35.5 (± 4.7)	3.37 (± 1.23)
Xenobatrachus rostratus	23.5 (± 0.7)	-
Xenorhina bouwensi	18.5 (± 0.7)	-
Sphenophryninae		
Cophixalus darlingtoni	14.0 (± 1.4)	-
C. neglectus	28.0	-
C. ornatus	16.0	-
C. parkeri	29.0 (± 1.4)	-
C. riparius	-	-
Copiula fistulans	27.7 (± 4.9)	-
Oreophryne biroi	-	-
Sphenophryne schlaginhaufeni	-	-
Dyscophinae		
Calluella guttulata	-	-
Microhylinae		
Chaperina fusca	26.0 (± 1.4)	-
Kaloula pulchra	154.0	1.13
Microhyla heymonsi	53.0	1.0

FIG. 14 Numbers of species with oviduct convolution numbers in given size classes, for species of Mode I, Mode II and Mode III.


Mode I
Mode II
Mode III
6
4
2
4
2
10
8
6
4
2
no. spp.
20.05
40.05
60.05
80.05
100.05
120.05
140.05
160.05
180.05
no. oviduct convolutions

Correlation of numbers of convolutions with SVL

Log (number of convolutions) is plotted against SVL for species of each Mode, in Fig. 15. For a given SVL, log (number of convolutions) is generally greater in Mode I species than in Mode III species, but the values for Mode II species are widely scattered. There is a significant positive correlation between convolution numbers and SVL for both Modes I and III (Kendall's coefficient of rank correlation; $P < 0.001$), but there is no significant correlation for Mode II.

Correlation of numbers of convolutions with egg diameter

Values of log (number of convolutions) are plotted against log (10 x egg diameter) for each species of Modes I, II and III, in Fig.16. Overall, there is a trend towards a smaller number of convolutions with increasing egg diameter, and application of Kendall's coefficient of rank correlation indicates a significant negative correlation ($P < 0.001$). Within each mode there is considerable scatter of points about the regression line (Fig. 16), and for each mode there is no significant correlation between convolution number and egg diameter.

(iii) Ontogeny of the *pars convoluta*

The development of the *pars convoluta* was investigated in juveniles of four species. The oviducts do not develop until metamorphic climax in *Limnodynastes dumerili* and *L. tasmaniensis*, and shortly after the end of metamorphosis in *Litoria ewingi* and *Pseudophryne bibroni*. Initially they are straight, narrow cords of undifferentiated cells, later becoming hollow tubes, and finally convoluting when the frog approaches reproductive maturity. The convolutions form almost simultaneously along the entire length of the *pars convoluta*, so the full complement of convolutions can be seen shortly after the onset of convolution formation. The

FIG. 15 Log (number of oviduct convolutions) vs SVL for species of Modes I, II and III.

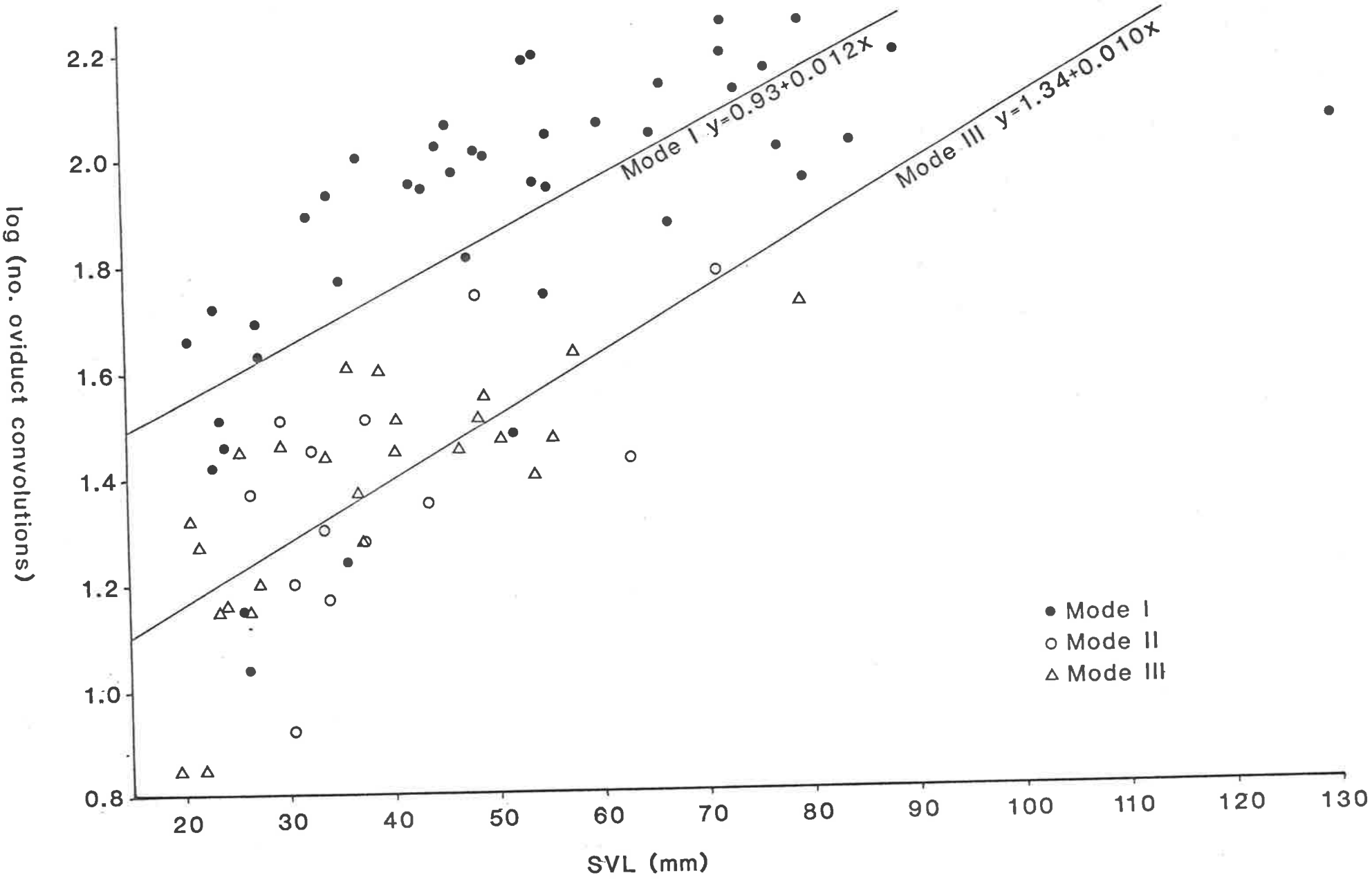
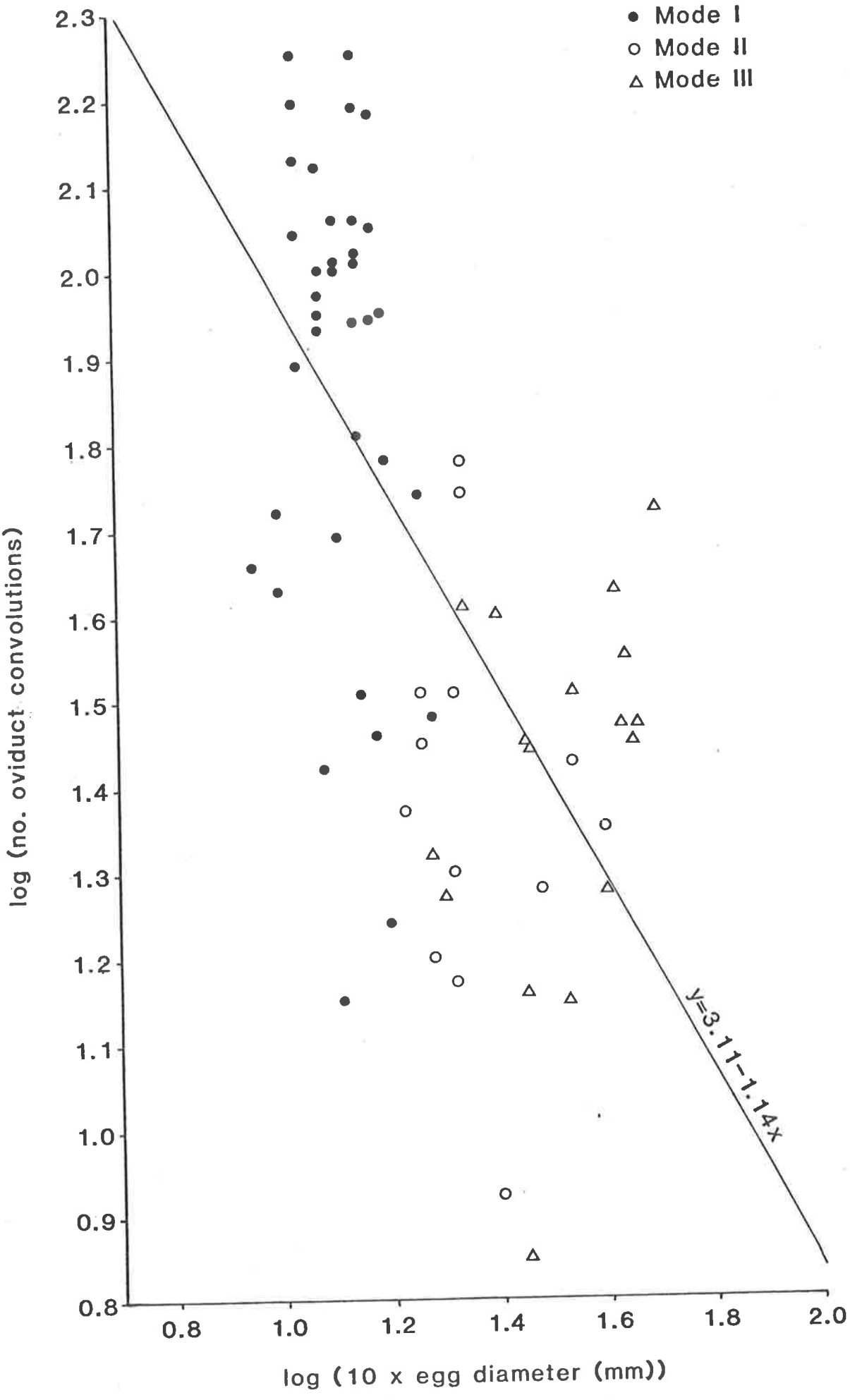

log (no. oviduct convolutions)
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
20
30
40
50
60
70
80
90
100
110
120
130
SVL (mm)
Mode I y=0.93+0.012x
Mode III y=1.34+0.010x
Mode I
Mode II
Mode III

FIG. 16 Log (number of oviduct convolutions) vs log (10 x egg diameter) for species of Modes I, II and III combined.


Mode I
Mode II
Mode III
y=3.11-1.14x
log (no. oviduct convolutions)
log (10 x egg diameter (mm))
2.3
2.2
2.1
2.0
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.8
1.0
1.2
1.4
1.6
1.8
2.0

numbers of convolutions in very immature oviducts correspond with the numbers seen in adult individuals. Therefore it is almost certain that the convolutions developed initially are a set number that the *pars convoluta* will retain throughout the life of the frog.

(iv) Diameter of the *pars convoluta* in Transverse Section

The transverse-sectional diameter of the *pars convoluta* of each oviduct, hereafter termed "oviduct width", was measured in many specimens. The results of all statistical analyses concerning oviduct width measurements are summarized in Table 12.

Intraspecific variation in oviduct width

Despite the fact that measurements were confined to individuals which were reproductively mature or approaching reproductive maturity, it is apparent that oviduct width varies substantially within a species. For example, the oviduct widths (mm) for left and right *pars convoluta* of five *Cyclorana australis* were (smallest to largest individual):

L	2.8	2.9	3.7	3.0	1.9
R	2.8	3.0	3.2	3.2	2.4

(mean of the 10 measurements: 2.89 ± 0.48 mm). Nonetheless there is also considerable interspecific variation, for example oviduct widths (mm) for left and right *pars convoluta* of six *Ranidella signifera* were (smallest to largest individual):

L	2.1	1.4	1.2	1.9	1.5	1.7
R	2.0	1.4	1.2	1.8	1.4	1.7

(mean of the 12 measurements: 1.61 ± 0.30 mm); these are considerably smaller than the measurements for *Cyclorana australis*. Therefore oviduct width measurements were subjected to similar analyses as other variables,

although for those species of which only one or a small number of individuals was examined the measurements may not be particularly representative. Within a species there were no apparent trends of oviduct width with size of the individuals.

Comparison of oviduct width between modes

Means and standard deviations of oviduct width were calculated for each species and are given in Table 9. Ranges of oviduct widths are:

Mode I species: 0.98 - 3.30 mm (mean 1.76 ± 0.54 mm)

Mode II species: 1.26 - 3.63 mm (mean 2.52 ± 0.72 mm)

Mode III species: 1.35 - 4.38 mm (mean 2.54 ± 0.91 mm)

Values of oviduct width are from a population with normal distribution (Kolmogorov-Smirnov one-sample test), and the variances are not significantly heterogeneous (F max test).

The mean of Mode I oviduct width values is significantly smaller than those of Modes II and III (Student's t-test, $P < 0.001$), but the mean for Mode II is not significantly different from that for Mode III.

Correlation of oviduct width with SVL

In Fig. 17, oviduct width is plotted against SVL for species of each mode. For Mode I there is a significant positive correlation between oviduct width and SVL (Kendall's coefficient of rank correlation, $0.001 < P < 0.01$). For Modes II and III the points are scattered and there is no significant correlation.

Correlation of oviduct width with egg diameter

Values of oviduct width are plotted against log (10 x egg diameter) for each species of Modes I, II and III, in Fig. 18. There is a trend

FIG. 17 Oviduct width vs SVL for species of Modes I, II and III.

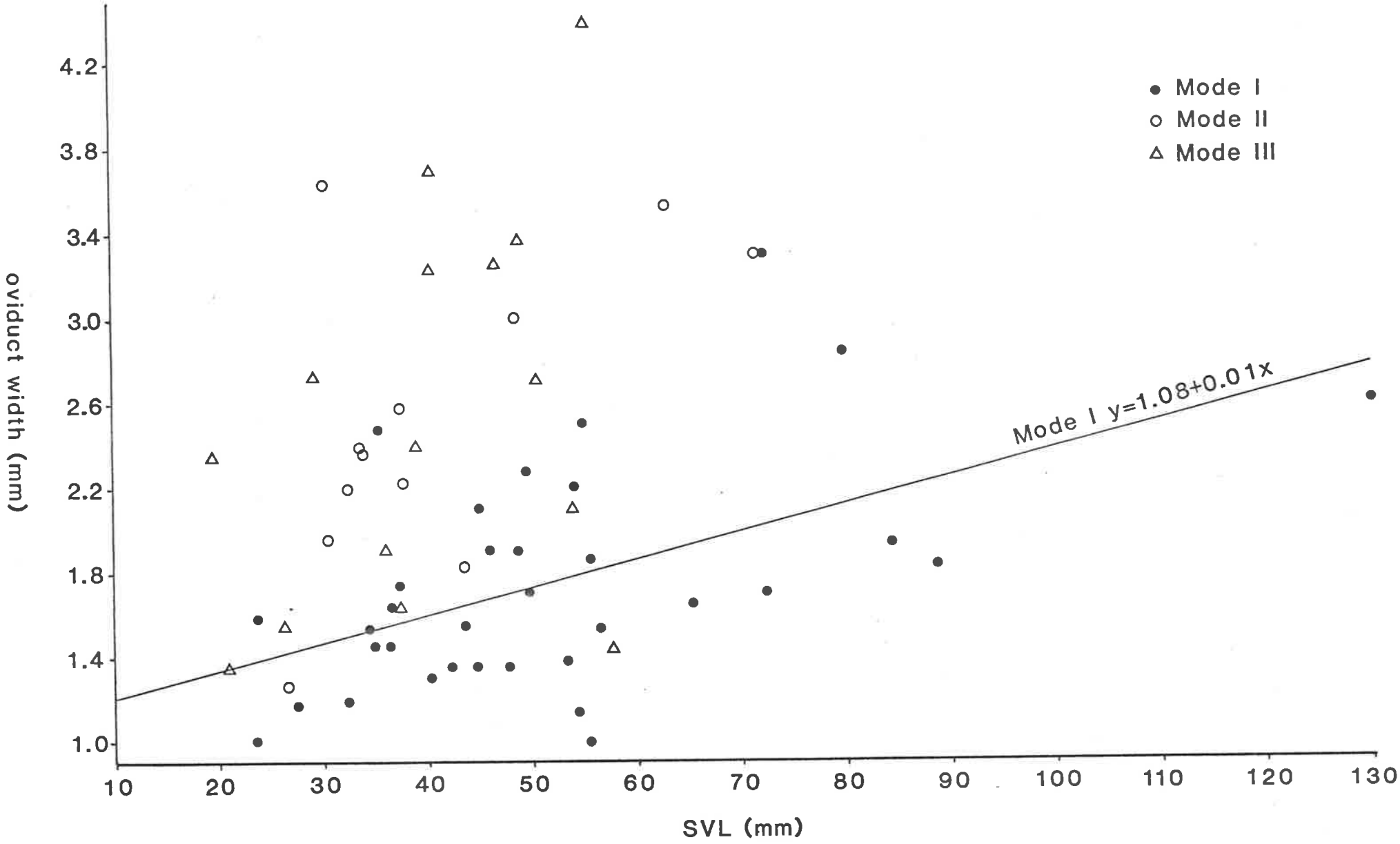
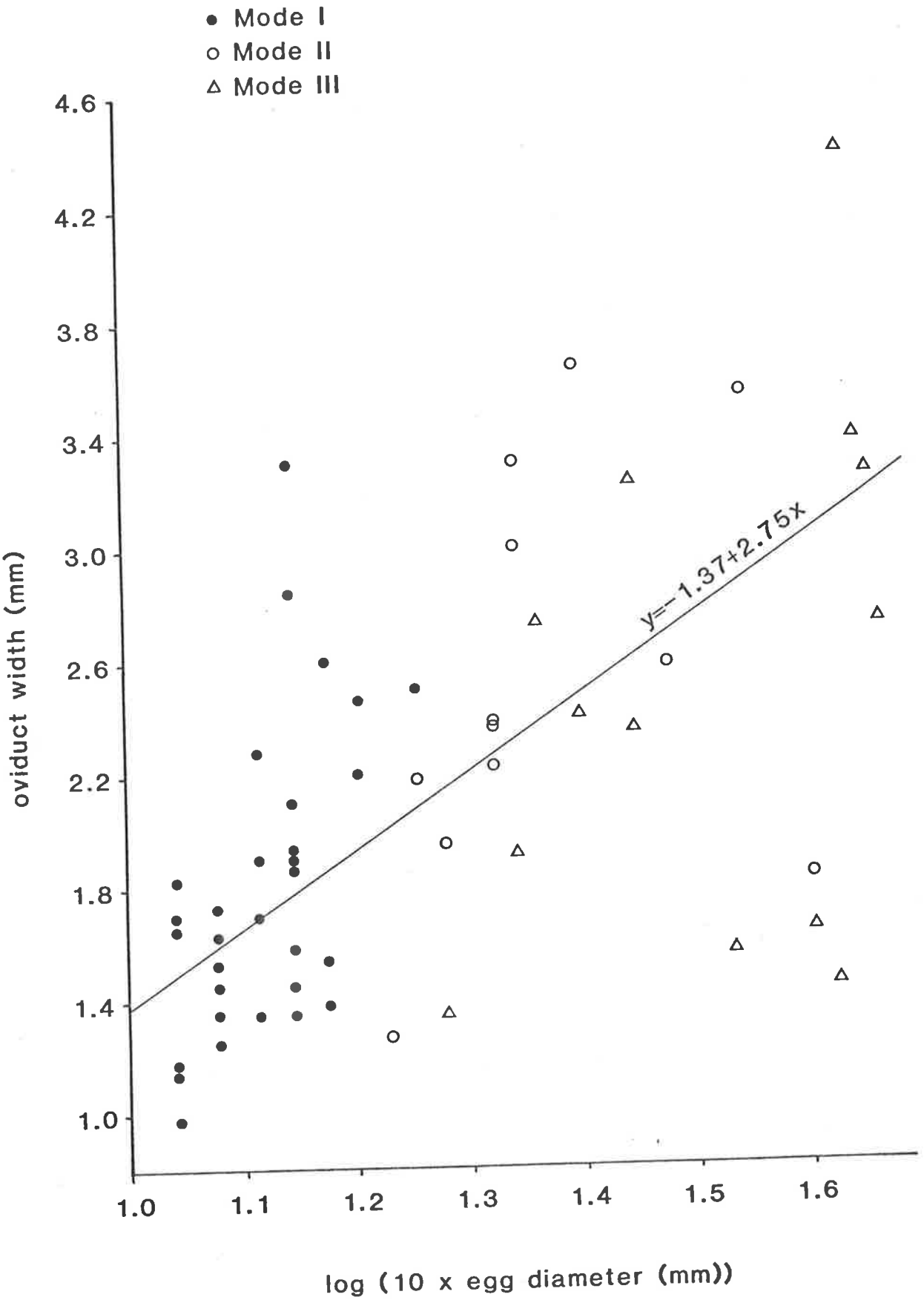

oviduct width (mm)
4.2
3.8
3.4
3.0
2.6
2.2
1.8
1.4
1.0
10
20
30
40
50
60
70
80
90
100
110
120
130
SVL (mm)
Mode I
Mode II
Mode III
Mode I y=1.08+0.01x

FIG. 18 Oviduct width vs log (10 x egg diameter) for species of Modes I, II and III combined.


Mode I
Mode II
Mode III
4.6
4.2
3.8
3.4
3.0
2.6
2.2
1.8
1.4
1.0
oviduct width (mm)
y=-1.37+2.75x
1.0
1.1
1.2
1.3
1.4
1.5
1.6
log (10 x egg diameter (mm))

towards a greater oviduct width with increasing egg diameter, and application of Kendall's coefficient of rank correlation indicates a significant positive correlation ($P < 0.001$). Within each mode there is a considerable scatter of points about the regression line (Fig. 18), but for Modes I and II there is a significant positive correlation of oviduct width with egg diameter ($P < 0.001$ and $0.01 < P < 0.05$ respectively); there is no significant correlation for Mode III species.

Correlation of oviduct width with numbers of convolutions

There is no significant correlation between oviduct width and convolution number, either within each mode or over all three modes (Kendall's coefficient of rank correlation).

(v) The *pars convoluta* in Foam-nesting Species

Eleven species which lay their eggs in a nest of oviducal mucopolysaccharides converted to foam (Modes Ib and IIc) were examined:

LEPTODACTYLIDAE
Adelotus brevis
Heleioporus eyrei
Lechriodus melanopyga
Limnodynastes dorsalis
L. dumerili
L. ornatus
L. peroni
L. tasmaniensis
Megistolotis lignarius

RHACOPHORIDAE
Chiromantis petersi
C. xerampelina

In each species at least the posterior-most convolutions of the *pars convoluta* are greatly enlarged, to several times the width of convolutions

immediately anterior, and are tightly bound together and more or less coalesced into a large mass of glandular tissue anterior to the ovisacs (Fig. 20). The number of convolutions involved in this enlargement is difficult to determine because the convolutions are not readily distinguishable externally. There is much variation in the extent of enlargement, from involving only the posterior two or three convolutions (*Megistolotis lignarius*) to involving most of the oviduct (*Adelotus brevis*). Such enlargement of the posterior regions of the *pars convoluta* occurs only in the species listed above; it does not occur in any of the species examined which do not lay eggs in foam nests.

Portions of the greatly enlarged region of *pars convoluta* were removed, sectioned, and stained, for the following species: *Adelotus brevis*, *Lechriodus melanopyga*, *Limnodynastes ornatus*, *L. peroni*, *L. tasmaniensis* and *Chiromantis petersi*. In each species the structure of the enlarged region is similar to that of normal regions of *pars convoluta*. However, the tubular jelly-secreting glands are greatly enlarged and more numerous, often several layers deep, so that the oviduct walls are very much thicker than in more anterior regions.

(vi) Fusion of the Ovisacs

In many specimens the degree of fusion of the ovisacs was noted. In some, particularly those with completely united ovisacs, it was possible to determine the degree of fusion *in situ* without sectioning, but in others it was necessary to determine the extent from serial sections. Usually material from only one specimen of each species was sectioned. For a number of species the degree of fusion is unknown because it was not possible to remove material from museum specimens for sectioning. The degree of fusion was observed in reproductively mature

or maturing individuals only, because in species with united ovisacs, fusion may not be complete in juveniles (as in *Pseudophryne bibroni*, see below).

The ovisacs were found a) to remain separate, condition "0" (Figs. 28, 29A) or b) to unite at some point anywhere between near their anterior end to near their entry into the cloaca, condition "1" (Fig. 29B), or c) to be completely united, condition "2" (Fig. 29C). The ovisac condition is given in Table 10 for species for which it was determined.

Correlation with reproductive mode

Table 11 gives the observed frequencies of species of each of Modes I, II and III with ovisac conditions 0, 1 and 2, together with the frequencies expected if there is no association between mode and ovisac condition. The observed frequencies diverge significantly from the expected ($P < 0.001$, chi-squared distribution) and there is a significant association between ovisac condition and reproductive mode. Separate ovisacs are found only in Mode I species, and completely united ovisacs occur largely in Mode III species; there is a trend towards increased ovisac fusion from Mode I to Mode III.

Egg diameter and SVL are plotted for species of ovisac conditions 0, 1 and 2, in Fig. 19. There is a trend for partly or completely united ovisacs to occur in species with large egg diameter and small SVL, with some outstanding exceptions such as *Bufo marinus* (SVL 130 mm, egg diameter 1.5 mm) and *Xenopus laevis* (SVL 88.9 mm, egg diameter 1.1 mm).

Ovisac fusion in an ontogenetic series of *Pseudophryne bibroni*

Tissues from a series of juvenile *Pseudophryne bibroni* (a species in

TABLE 10: Ovisac condition (0 = separate; 1 = partly united; 2 = completely united), and presence (+) or absence (o) of a urinogenital sinus, for all species investigated.

Taxa	Ovisac Condition	Urinogenital Sinus
Leiopelmatidae		
Ascaphus truei	1	+
Leiopelma hochstetteri	2	-
Pipidae		
Xenopus laevis	1	+
X. muelleri	1	+
Pelobatidae		
Pelobates fuscus	1	o
Bufonidae		
Bufo marinus	1	o
Nectophrynoides malcolmi	1	-
N. tornieri	2	-
Leptodactylidae		
Limnodynastinae		
Adelotus brevis	0	o
Heleioporus eyrei	1	o
Lechriodus melanopyga	0	o
Limnodynastes dorsalis	-	-
L. dumerili	0	o
L. ornatus	0	o
L. peroni	0	+
L. tasmaniensis	0	o
Megistolotis lignarius	0	+
Neobatrachus ?centralis	-	-
N. sp.	-	-
Notaden melanoscaphus	0	o
N. nichollsi	0	o
Myobatrachinae		
Assa darlingtoni	2	-
Crinia georgiana	2	-
Myobatrachus gouldi	2	-
Pseudophryne bibroni	2	o
Ranidella bilingua	0	o
R. riparia	0	+
R. signifera	0	o
Taudactylus acutirostris	2	-
T. diurnus	1	o
Uperoleia inundata	-	-
Rheobatrachinae		
Rheobatrachus silus	1	o

Taxa	Ovisac Condition	Urinogenital Sinus
Eleutherodactylinae		
Eleutherodactylus achatinus	2	-
E. chloronotus	2	-
E. curtipes	2	-
E. devillei	2	-
E. walkeri	2	-
Dendrobatidae		
Phyllobates aurotaenia	2	-
Hylidae		
Cyclorana australis	0	o
C. brevipes	-	-
C. longipes	0	o
C. maini	-	-
Litoria alboguttata	-	-
L. bicolor	1	o
L. caerulea	0	o
L. chloris	0	o
L. coplandi	0	o
L. dahli	-	-
L. eucnemis	-	-
L. ewingi	0	o
L. inermis	-	-
L. iris	1	-
L. lesueuri	1	o
L. microbelos	1	o
L. modica	2	-
L. nannotis	-	-
L. nasuta	1	o
L. pallida	-	-
L. peroni	0	o
L. pratti	2	-
L. raniformis	0	o
L. rheocola	-	-
L. rothi	1	o
L. rubella	1	o
L. tornieri	-	-
L. wotjulumensis	0	o
Nyctimystes papua	1	o
Phrynohyas venulosa	0	o
Ranidae		
Arthroleptella lightfooti	-	-
Arthroleptis poecilonotus	1	-
Cacosternum boettgeri	1	o
Rana cascadea	1	o
R. grisea	-	-
R. papua	0	+

Taxa	Ovisac Condition	Urinogenital Sinus
Hyperoliidae		
Afrixalus dorsalis	2	-
A. fornasini	2	o
A. quadrivittatus	1	-
Callixalus pictus	-	-
Cryptothylax greshoffi	-	-
Hyperolius marmoratus	2	-
Leptopelis bocagei	-	-
L. macrotis	-	-
Rhacophoridae		
Chiromantis petersi	-	-
C. xerampelina	-	-
Microhylidae		
Asterophryinae		
Asterophrys turpicula	-	-
Barygenys nana	2?	-
Hylophorbus rufescens	2?	-
Phrynomantis humicola compta	-	-
P. h. humicola	-	-
P. lateralis	2	-
P. louisiadensis	-	-
P. robusta	2?	-
P. stictogaster	-	-
P. wilhelmana	2	-
Xenobatrachus rostratus	2	-
Xenorhina bouwensi	-	-
Sphenophryninae		
Cophixalus darlingtoni	2	o
C. neglectus	-	-
C. ornatus	2	-
C. parkeri	-	-
C. riparius	2	-
Copiula fistulans	2	-
Oreophryne biroi	2	-
Sphenophryne schlaginhaufeni	-	-
Dyscophinae		
Calluella guttulata	-	-
Microhylinae		
Chaperina fusca	-	-
Kaloula pulchra	-	-
Microhyla heymonsi	-	-

TABLE 11: Contingency table for the number of species of each of Modes I, II and III with ovisacs separate (0), partly united (1), or completely united (2).
O = observed frequency, E = expected frequency if no association between mode and ovisac condition.
$X_4^2 = 46.99$ ***.

Ovisacs	Reproductive Mode I	II	III	
0	O = 23 E = 12.3	O = 0 E = 3.5	O = 0 E = 7.2	23
1	O = 13 E = 11.2	O = 5 E = 3.1	O = 3 E = 6.7	21
2	O = 3 E = 15.5	O = 6 E = 4.4	O = 20 E = 9.1	29
	39	11	23	73 spp.

FIG. 19 SVL vs egg diameter for species with ovisacs which remain separate (condition 0), with ovisacs which are partly united (condition 1), and with ovisacs which are completely united (condition 2).

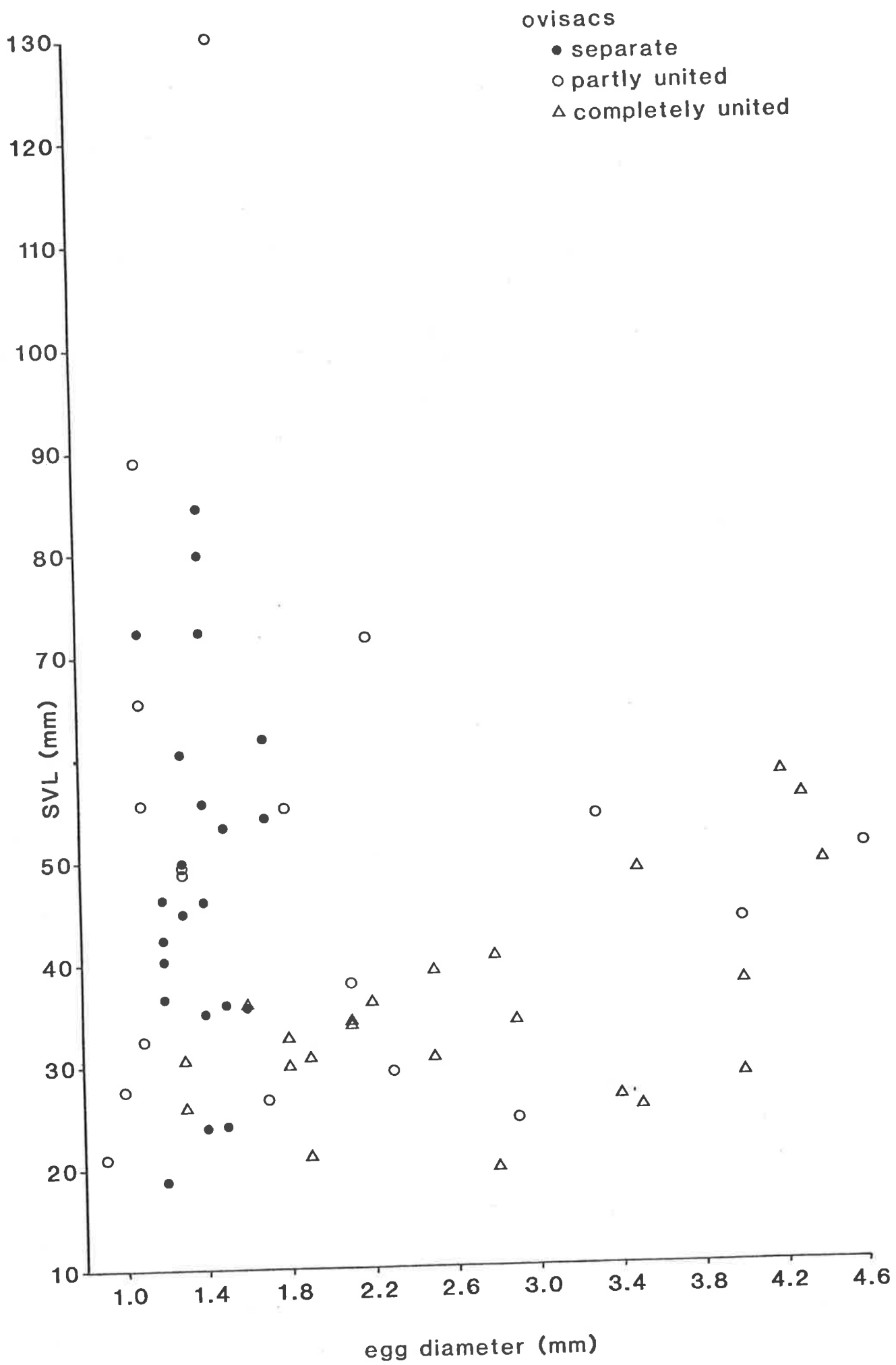

ovisacs
separate
partly united
completely united
130
120
110
100
90
80
70
50
40
30
20
10
SVL (mm)
1.0
1.4
1.8
2.2
2.6
3.0
3.4
3.8
4.2
4.6
egg diameter (mm)

FIG. 20 Female reproductive system (left oviduct, immature right ovary), ventral view, Mode I species. *Limmodynastes dumerili* (St Peters, S. Aust., 13.x.1981, M. Thompson).

enlgd p.con. = enlarged portion of *pars convoluta*; os. = ostium; o.sac = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.

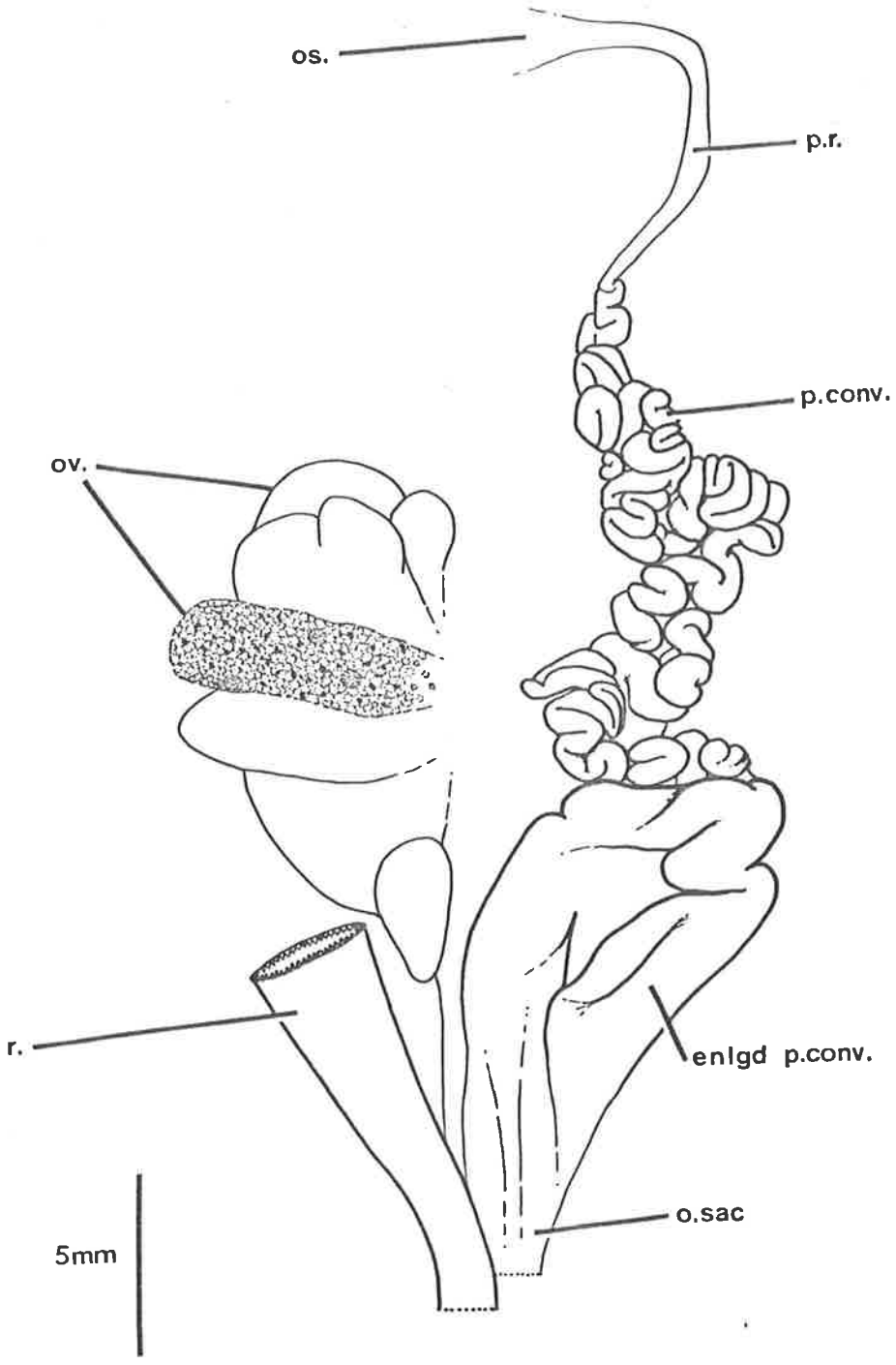

os.
p.r.
p.conv.
ov.
r.
enlgd p.conv.
o.sac
5mm

FIG. 21 Female reproductive system (left oviduct, right ovary) ventral view, Mode I species.

A. *Litoria rubella* (Mitchell Plateau, W. Aust., Jan. 1978, M.J. Tyler *et al.*)

B. *Cyclorana longipes* (131 km S. of Northern and Duncan Hwys junction, W. Aust., 24.i.1978, M.J. Tyler *et al.*)

os. = ostium; o.sac = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.

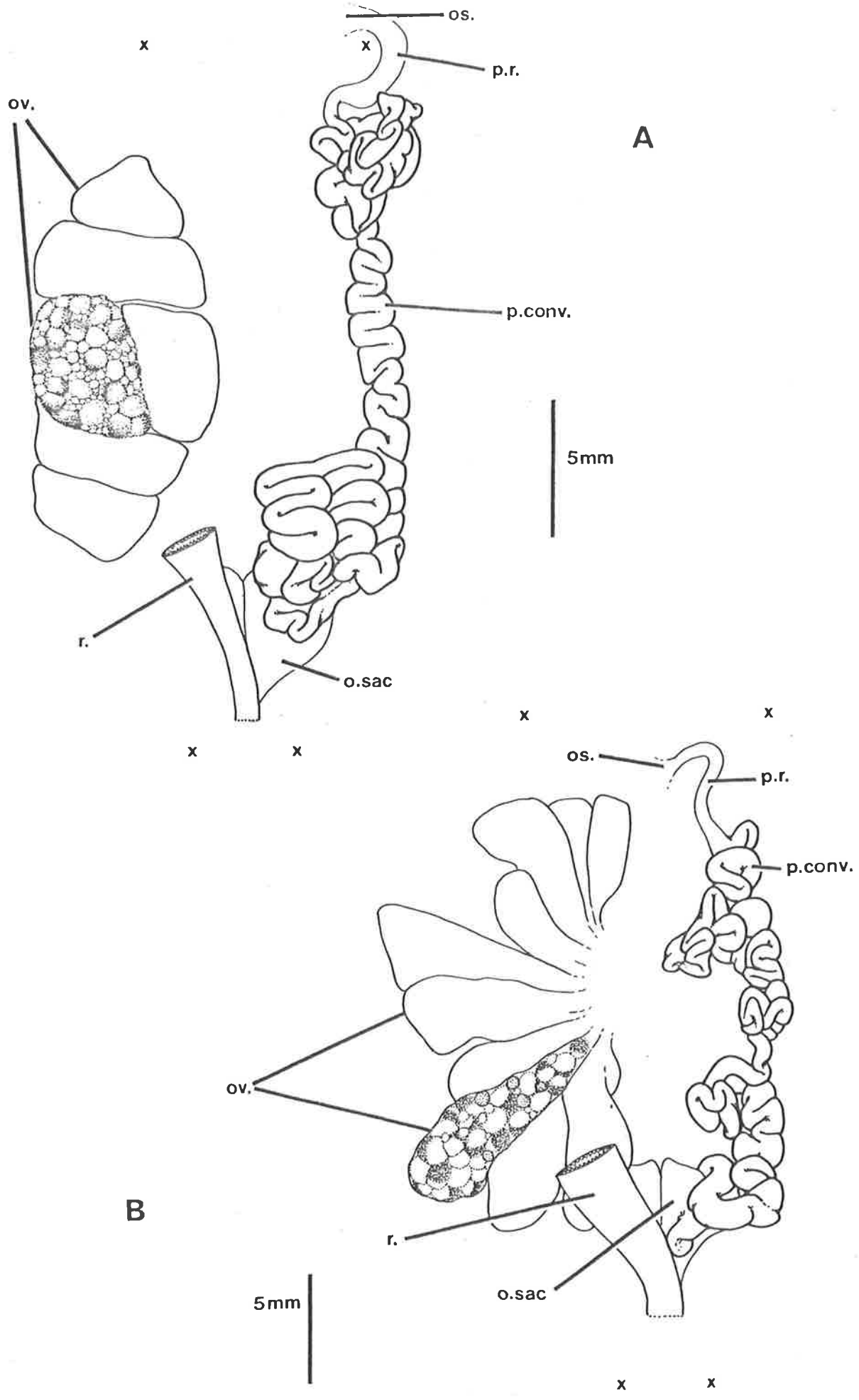

os.
p.r.
ov.
A
p.conv.
5mm
r.
o.sac
os.
p.r.
p.conv.
ov.
B
r.
5mm
o.sac

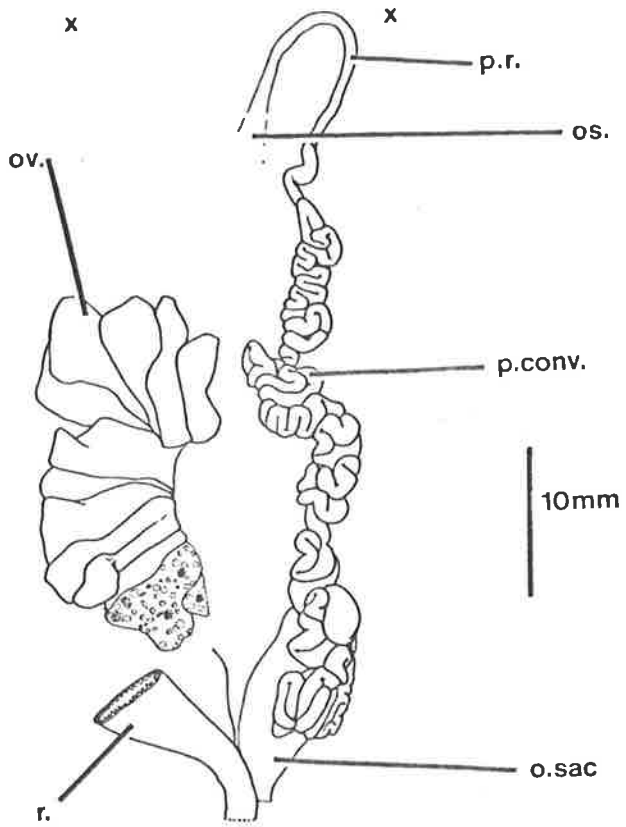
FIG. 22 Female reproductive system, Mode I species.

A. *Phrynohyas venulosa* (Tunapuna, Trinidad, 17.ix.1967, N. Gradwell), left oviduct and right ovary, ventral view;

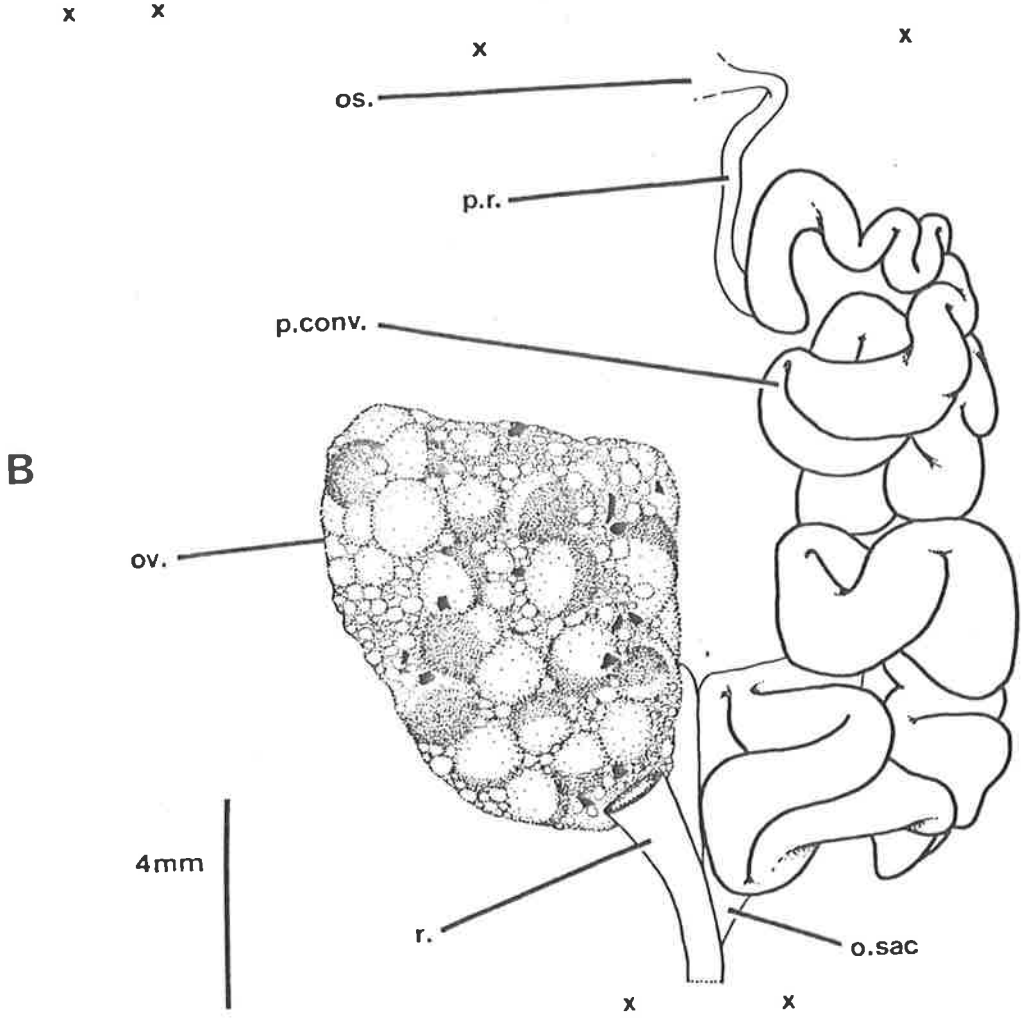
B. *Ranidella signifera* (Balhannah, S. Aust., 29.viii.1981, P. Horton), left oviduct (ventral view) and left ovary (dorsal view).

os. = ostium; o.sac = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.



A



B

FIG. 23 Female reproductive system (left oviduct, right ovary), ventral view, Mode II species.

A. *Leptopelis macrotis* (CAS 103699);

B. *Ascaphus truei* (Touchet R., Oregon, U.S.A., Sept. 1970, N. Gradwell).

os. = ostium; o.sac. = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.

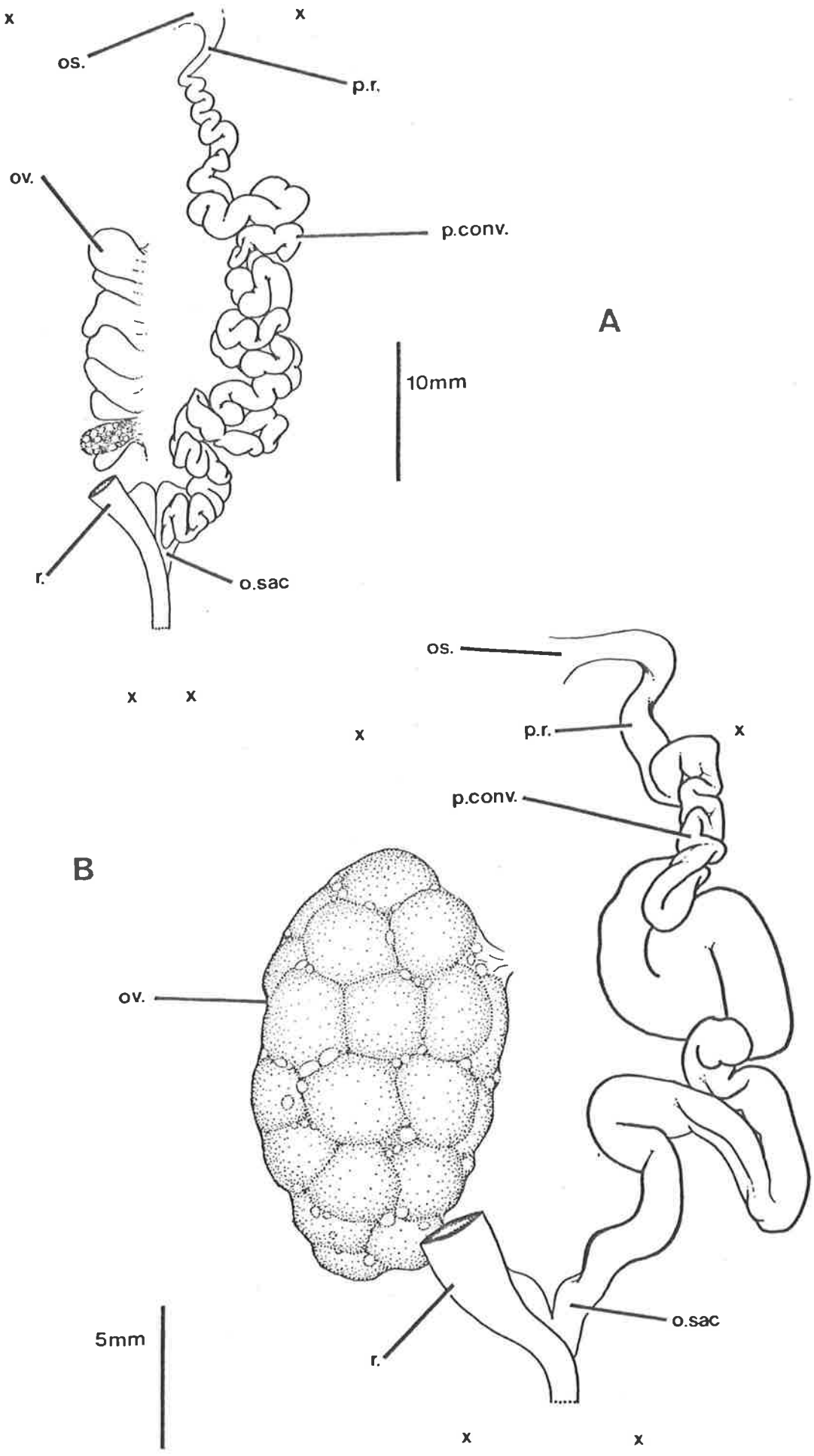

os.
p.r.
ov.
p.conv.
A
10mm
r.
o.sac
os.
p.r.
p.conv.
B
ov.
5mm
r.
o.sac

FIG. 24 Female reproductive system (left oviduct, right ovary), ventral view, Mode II species.

A. *Phyllobates aurotaenia* (SAM R13567);

B. *Litoria iris* (SAM R9141).

os. = ostium; o.sac = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.

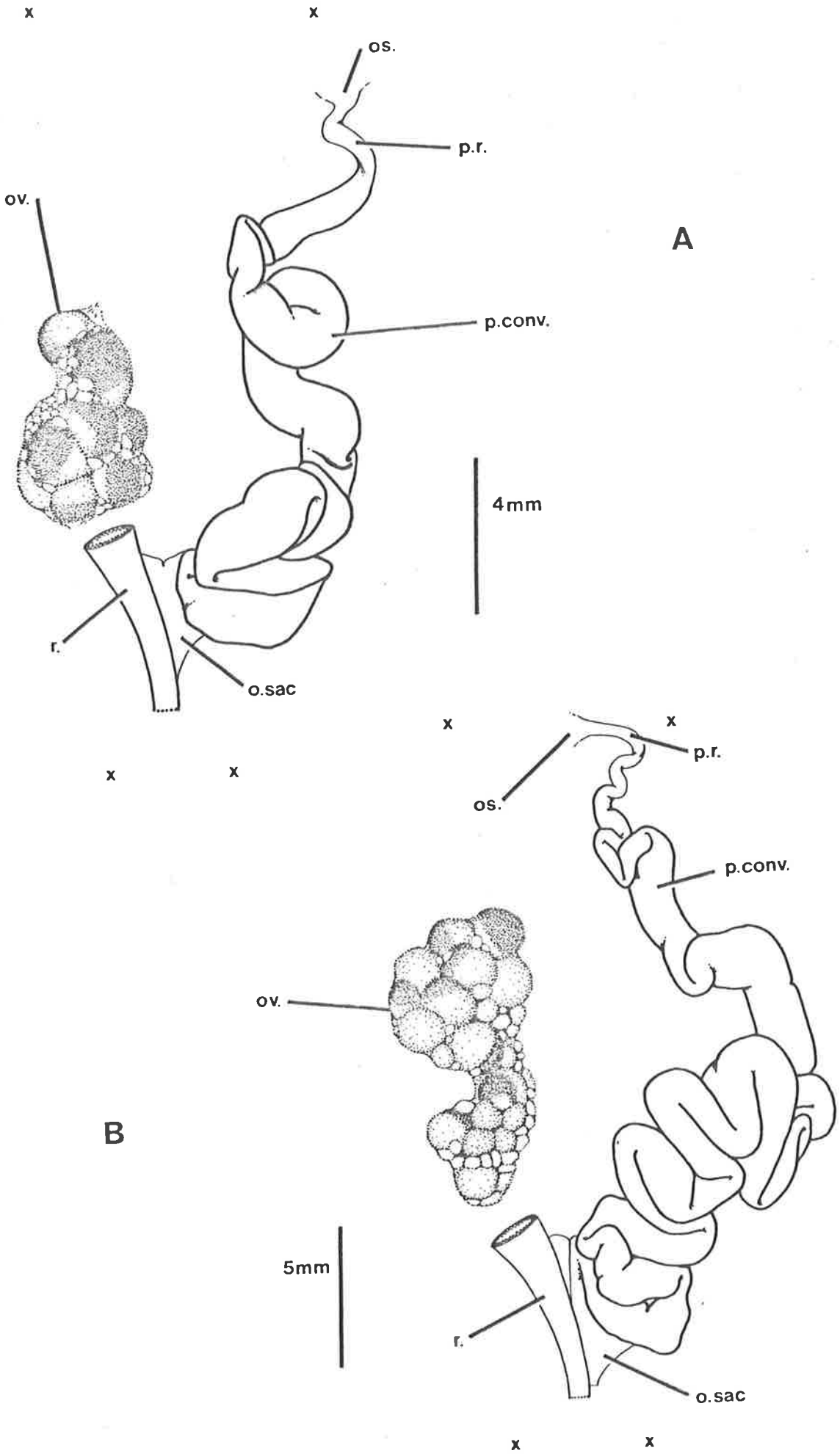

os.
p.r.
ov.
A
p.conv.
4mm
r.
o.sac
p.r.
os.
p.conv.
ov.
B
5mm
r.
o.sac

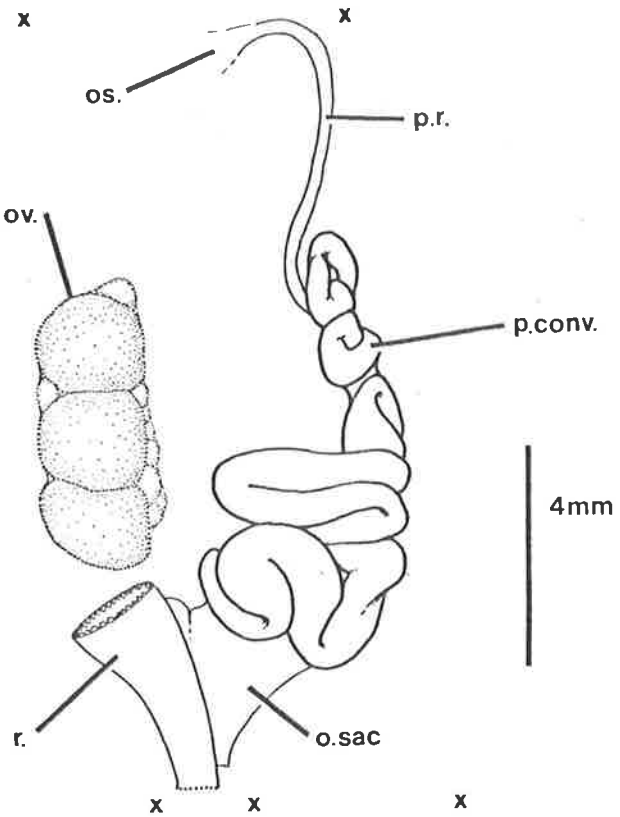
FIG. 25 Female reproductive system (left oviduct, right ovary), ventral view, Mode III species.

A. *Eleutherodactylus walkeri* (Santo Domingo de los Colorados, Ecuador, J.D. Lynch);

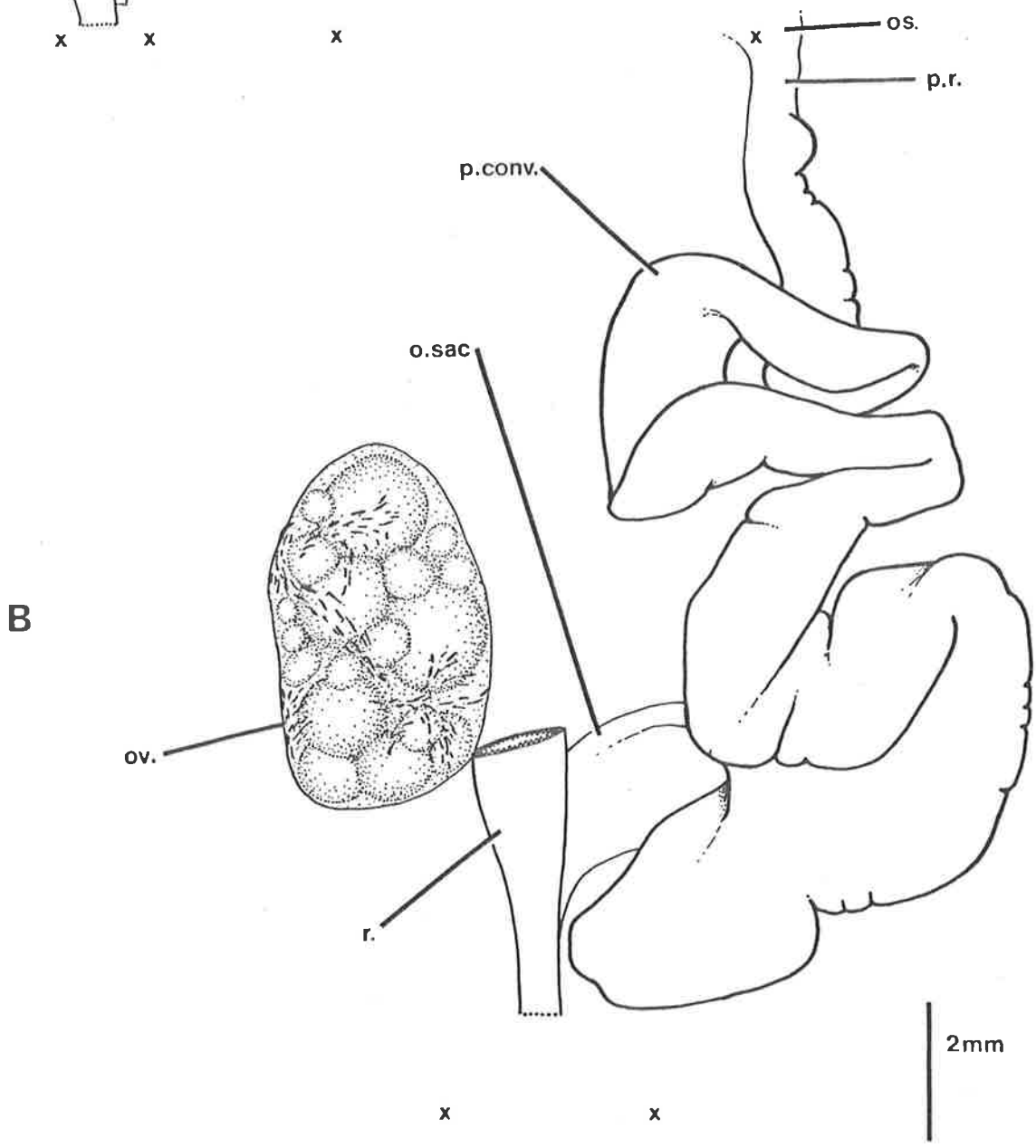
B. *Cophixalus darlingtoni* (Tomba, Mt Hagen, P.N.G., 5.i.1982, T.C. Burton).

os. = ostium; o.sac = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.



A



B

FIG. 26 Female reproductive system (left oviduct, right ovary), ventral view, Mode III species.

A. *Eleutherodactylus devillei*;

B. *Eleutherodactylus curtipes*,

(A and B both coll. 1-3 km E. of Papallacta, Ecuador, July 1977, J.D. Lynch).

os. = ostium; o.sac = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.

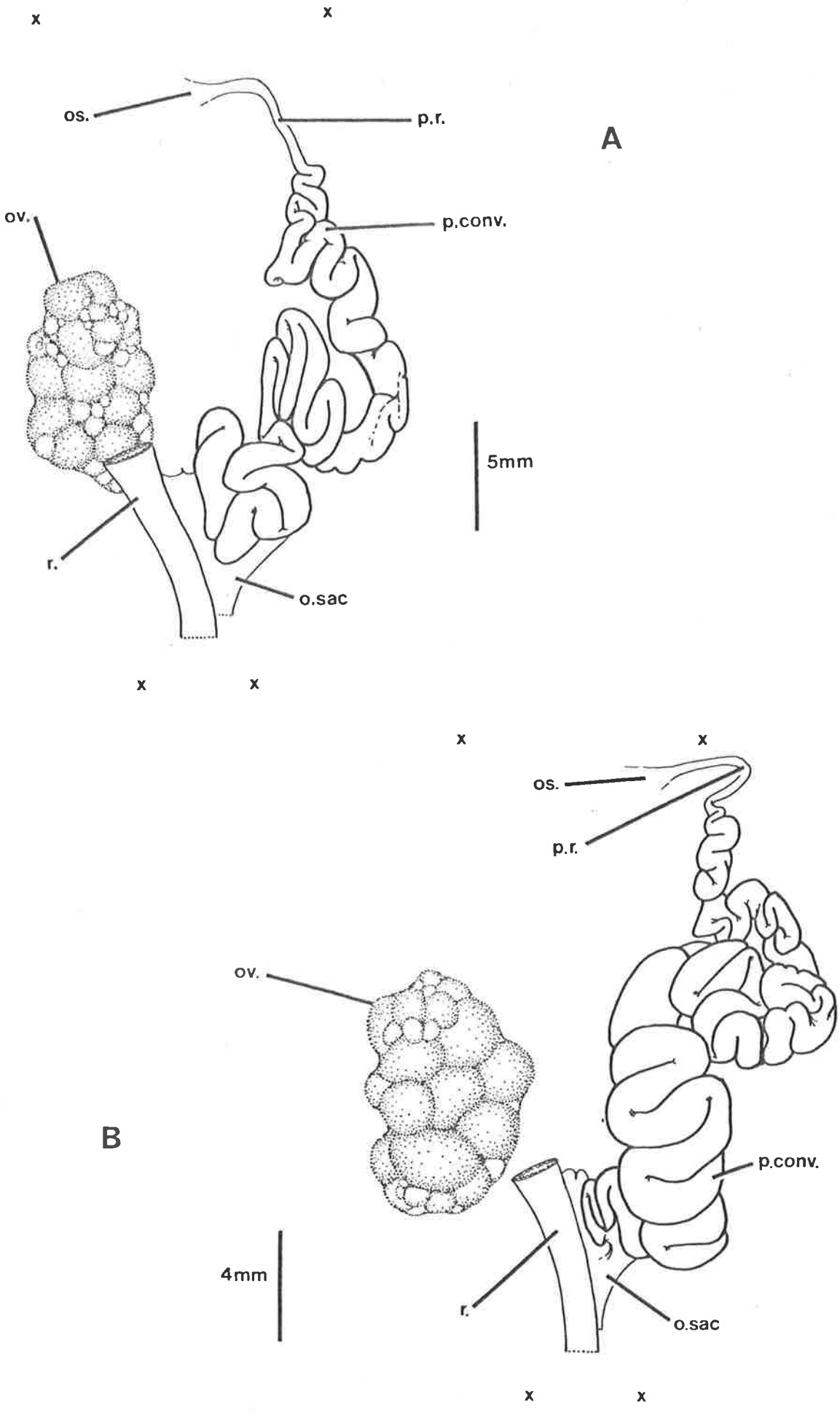

os.
p.r.
A
ov.
p.conv.
5mm
r.
o.sac
os.
p.r.
ov.
B
p.conv.
4mm
r.
o.sac

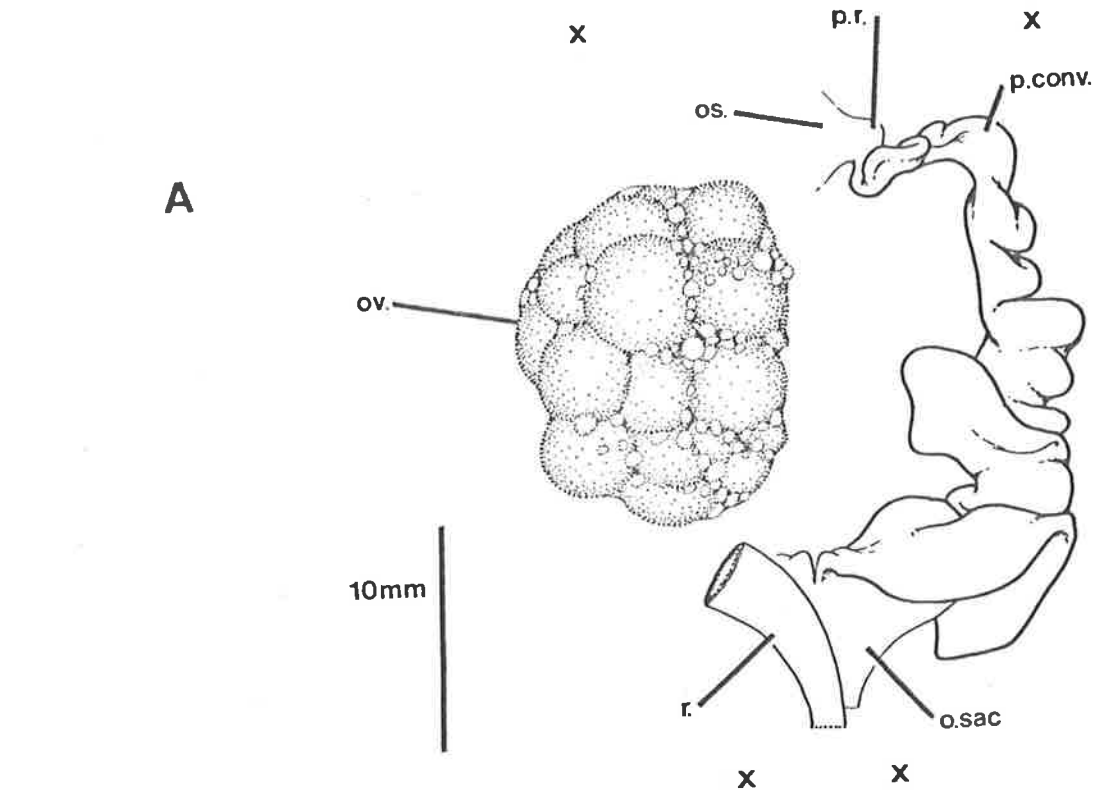
FIG. 27 Female reproductive system (left oviduct, right ovary), ventral view, Mode III species.

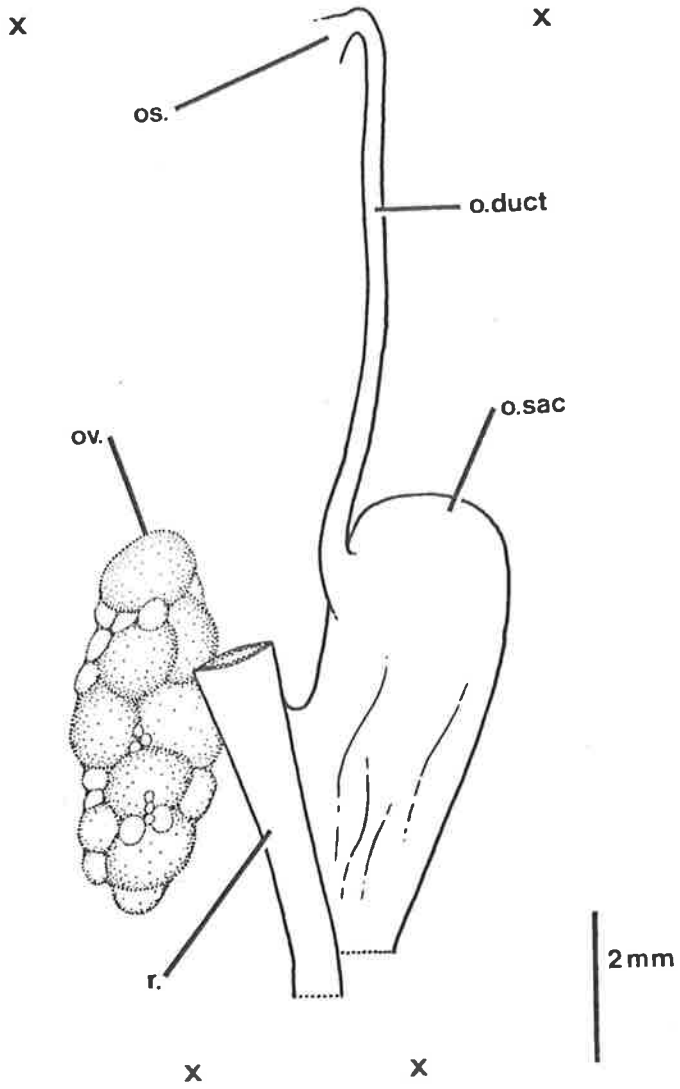
A. *Myobatrachus gouldi* (WAM R58108);

B. *Nectophrynoides tornieri* (BM 1974.446).

o.duct = undifferentiated oviduct; os. = ostium; o.sac = ovisac; ov. = ovary; p.conv. = *pars convoluta*; p.r. = *pars recta*; r. = rectum.

Crosses represent bases of limbs.





B

which the ovisacs are completely united in the adult) were sectioned to follow ovisac development. In the youngest individual, in which the oviducts had only just developed and the ovisac walls were only a single cell layer thick, the ovisacs were separate except at their posterior extremity where they united, immediately before ending blindly in the cloacal wall. In the oldest individual, in which the oviducts were beginning to convolute, the septum dividing the ovisacs was breaking down so at intervals the latter were united. Individuals of intermediate ages displayed intermediate degrees of fusion. Thus complete ovisac fusion was taking place at the onset of reproductive maturity. Such may be the case in other species, but it was not possible to test this hypothesis because series of juveniles were not available.

(vii) Occlusion of the Ovisacs

In order to determine whether or not the ovisacs open into the cloaca only at reproductive maturity, the fate of the ovisacs as they approach the cloaca was followed by sectioning tissue from one specimen of each of 43 species. Amongst these, the ovisacs were occluded from the cloacal lumen and ended blindly in the rectal wall in eight specimens. Four of these eight (*Limnodynastes peroni*, *Litoria microbelos*, *Nyctimystes papua*, *Rana cascadea*) were reproductively mature with mature oocytes in the ovaries; two (*Litoria lesueuri*, *Ranidella riparia*) were approaching reproductive maturity; one (*Ranidella bilingua*) was maturing but the oviducts were not fully convoluted, and the eighth (*Cyclorana australis*), although possessing mature oocytes, had been held in captivity and the oviducts had regressed. In the remaining 35 specimens the ovisacs opened into the cloaca; most of these were reproductively mature, but some were approaching maturity, or were fully grown but possessed no mature oocytes (probably post-oviposition), or were immature. The most

immature specimen was a *Litoria rothi* in which the oviducts had not convoluted, clearly suggesting that opening of the ovisacs is not necessarily associated with the attainment of reproductive maturity.

The ovisacs of series of juvenile *Limnodynastes dumerili*, *L. tasmaniensis* and *Pseudophryne bibroni* were also sectioned in order to determine whether or not ovisac occlusion might be related to stage of development. In *Limnodynastes dumerili* juveniles in which the oviducts were beginning to convolute, the connections between ovisacs and cloaca had not developed (in fact the ovisacs were united posteriorly with the urinary ducts); no more mature specimens were available. In the most mature *Limnodynastes tasmaniensis* individual available, in which the oviducts had convoluted and the ovaries contained some almost mature oocytes, the ovisacs ended blindly in the rectal wall. The most mature *Pseudophryne bibroni* juvenile available was one in which the oviducts were beginning to convolute and in this and in all less mature specimens the ovisacs were also occluded from the cloaca. Thus in these species at least, it appears that the ovisacs may remain occluded from the cloaca until a late stage of development.

(viii) The Urinogenital Sinus

The cloacal regions of individuals of 43 species were sectioned primarily to follow the course of the ovisacs, but presence or absence of a urinogenital sinus adjacent to the posterior end of the ovisacs was also recorded (Table 10). Seven species of six genera from four families were found to possess a urinogenital sinus. In six of the species the sinus is of similar form (Fig. 28B), anteriorly ending blindly in the rectal wall between the cloaca and the ovisacs and urinary ducts, and extending posteriorly until it unites with the cloaca before either

ovisacs or urinary ducts enter either it or the cloaca (except in *Ranidella riparia* in which the urinary ducts fuse with the sinus before the latter enters the cloaca). The seventh species, *Rana papua*, exhibits a different pattern: the sinus is situated dorsal to the ovisacs and urinary ducts as well as the rectum, and both sets of ducts fuse with it before it enters the cloaca (Fig. 28C). There is no apparent correlation of presence of a urinogenital sinus with reproductive mode.

FIG. 28 Transverse sections through posterior regions of intestine and ovisac in female frogs.

A. *Ranidella signifera*, in which the ovisacs remain separate;

B. *Limnodynastes peroni*, in which the ovisacs remain separate and there is a urinogenital sinus between them and the rectum;

C. *Rana papua*, in which the ovisacs remain separate and open into a urinogenital sinus which lies dorsal to them (the urinary ducts entered the sinus anterior to this section).

b = bladder; o = ovisac; r = rectum;
u = urinary duct; ugs = urinogenital sinus.

The line represents 400µm.

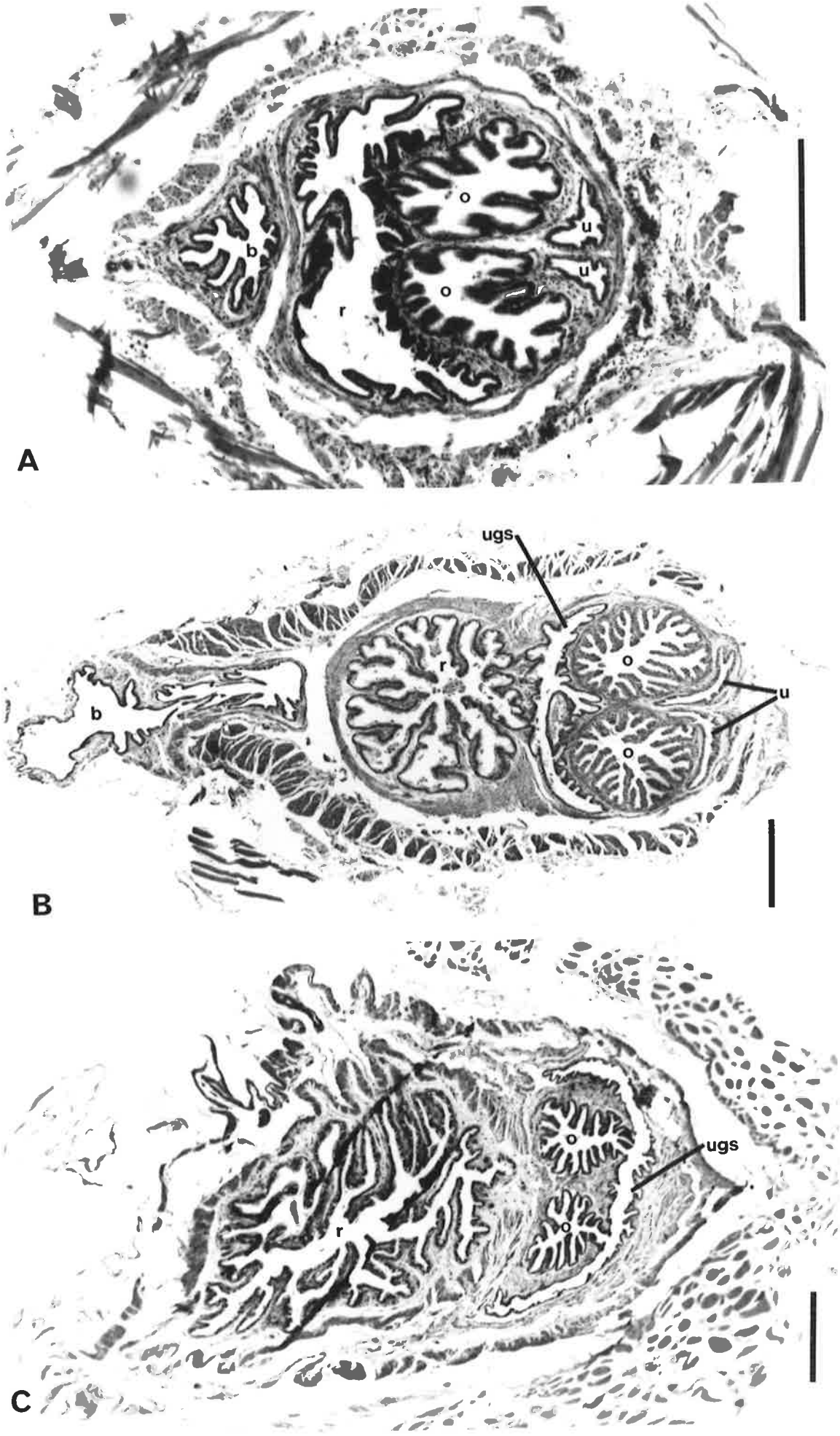

A
b
o
o
u
u
r
B
ugs
b
r
o
o
u
C
r
o
o
ugs

FIG. 29 Transverse sections through posterior regions of intestine and ovisac in female frogs.

A. *Limnodynastes tasmaniensis*, in which the ovisacs remain separate;

B. *Taudactylus diurnus*, in which the ovisacs unite near their posterior end;

C. *Pseudophryne bibroni*, in which the ovisacs are entirely united.

b = bladder; o = ovisac; r = rectum;
u = urinary duct; uo = united ovisacs;
uu = united urinary ducts.

The line represents 400µm.

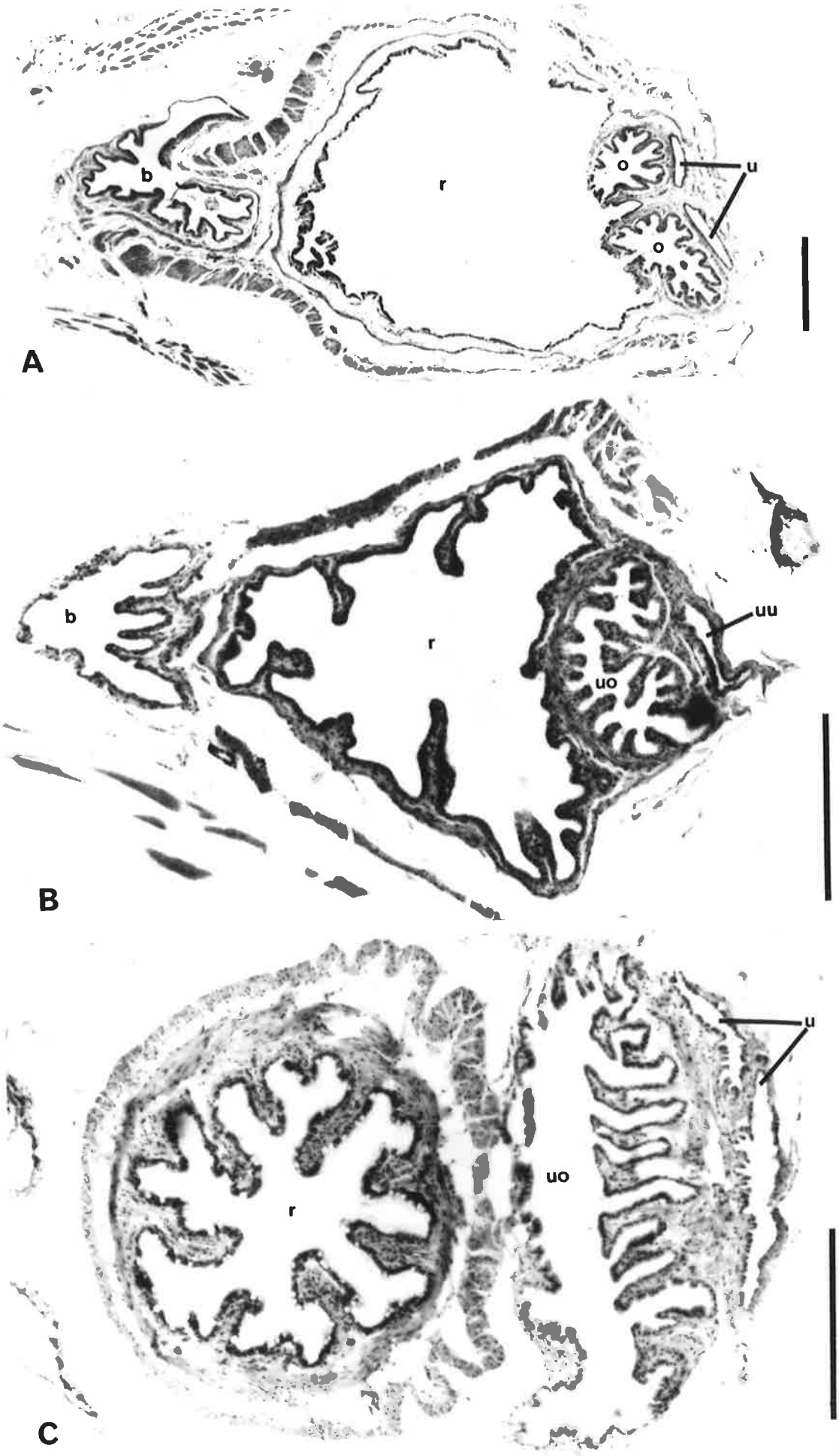

b
r
o
u
o
A
b
r
uu
uo
B
r
uo
u
C

TABLE 12: Summary of results of statistical analyses. (n.s. = not significant; * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$; reproductive modes represented as I, II and III).

Purpose of analysis, and Test Employed	Results
Detect heterogeneity of variances; F max test	SVL: n.s. egg diameter: ** log (10 x egg diameter): n.s. ovarian complement: ** log (ovarian complement): ** number of lobes: ** log (number of lobes): n.s. number of convolutions: ** log (number of convolutions): n.s. oviduct width: n.s.
Detect divergence from normal distribution; Kolmogorov-Smirnov one-sample test	SVL: n.s. egg diameter: n.s. log (10 x egg diameter): n.s. ovarian complement: ** log (ovarian complement): n.s. number of lobes: n.s. log (number of lobes): n.s. number of convolutions: n.s. log (number of convolutions): n.s. oviduct width: n.s.
Comparison of means; Student's t-test	SVL: I vs II n.s.; II vs III n.s.; I > III ** log (10 x egg diameter): I < II & III ***; II < III ** log (ovarian complement): I > II & III ***; II > III *** log (number of lobes): I > II & III ***; I > III * log (number of convolutions): I > II & III ***; II vs III n.s. oviduct width: I < II & III ***; II vs III n.s.
Detect correlation; Kendall's coefficient of rank correlation	egg diameter & SVL: I n.s.; II & III +'ve ** ovarian complement & SVL: all +'ve, I ***, II & III * ovarian complement & egg diameter: I, II & III n.s.; I + II + III -'ve *** number of lobes & SVL in 35 *Litoria dahli*: n.s. number of lobes & SVL: all +'ve, I ***, II **, III *

Purpose of Analysis, and Test Employed	Results
	number of lobes & egg diameter: I & II n.s.; III +'ve *; I + II + III -'ve ***
	number of convolutions & SVL in 11 *Ranidella signifera*: n.s.
	number of convolutions & SVL in 20 *Rheobatrachus silus*: n.s.
	number of convolutions & SVL: I & III +'ve ***; II n.s.
	number of convolutions & egg diameter: I, II & III n.s.; I + II + III -'ve ***
	oviduct width & SVL: I +'ve **; II & III n.s.
	oviduct width & egg diameter: I +'ve ***; II +'ve *; II n.s.; I + II + III +'ve ***
	oviduct width & number of convolutions: I, II & III n.s.; I + II + III n.s.
Detect divergence between observed and expected frequencies; chi-squared	reproductive mode vs ovisac condition: ***
Comparison of medians of paired populations; Wilcoxon signed rank test	number of lobes of left vs right ovaries in 38 *Litoria dahli*: n.s.

IV

DISCUSSION

Reproductive morphology is clearly correlated with reproductive mode. I will now discuss the associations between modes and particular features of morphology, and the possible functional pressures underlying variations in morphology. Discussion of each parameter or feature investigated will follow the order of presentation of data in Section III.

(a) SNOUT-VENT LENGTH

Within each reproductive mode there is a wide range in SVL, so that if trends in morphological features with increasing or decreasing SVL are present among species of the same mode, they should be discernible. The mean SVL for Mode I species does not differ significantly from that for Mode II species, nor does that for Mode II species from that for Mode III species, so significant differences in reproductive features between these modes should not be due to divergence in body size. However, the mean SVL for Mode I species is significantly greater than that for Mode III species, so any comparisons of reproductive features between these two modes must take into account the discrepancy in body size.

Salthe and Duellman (1973) tentatively suggested that small body size in frogs is a preadaptation for reproductive experimentation towards

more terrestrial modes, because clutch sizes in small species are already comparatively small and great reduction in clutch size is not favoured in them. Of the species which I considered, those of Modes II and III have undergone such "reproductive experimentation". The mean SVL of the Mode II species is smaller than that of the Mode I species but not significantly so. However, that for Mode III species is significantly smaller, thus lending support to Salthe and Duellman's (1973) suggestion.

(b) EGGS

(i) Egg Diameter

The criterion which I have chosen to distinguish between reproductive modes is the degree of dependence of the embryo or larva on energy supplied by the egg yolk. Thus there is an increase in yolk supply within each egg from Mode I to Mode III as the young rely progressively less on external food sources. The relative amounts of yolk contained in anuran eggs should be reflected by their diameters, so I measured egg diameters for as many species as possible, and predicted a significant increase in egg diameter from Mode I to Mode III. For reasons given in Section II, I did not use egg volume as an indicator of yolk content.

Ranges of egg diameter for each mode overlap, particularly between Modes II and III (Fig. 3), therefore it is not possible to apply an egg diameter range to define each reproductive mode more clearly. However, the mean egg diameter is significantly different between modes. As predicted, the smallest mean is that of Mode I and the largest that of Mode III, reflecting the increase in yolk content from Mode I to Mode III. I discuss the bearing on reproductive morphology of this increase in egg diameter in later sections.

Salthe and Duellman (1973) indicated that within a given reproductive mode there is a positive correlation between egg size and female SVL. This correlation holds for Modes II and III in my study, as illustrated in Fig. 4, and is statistically significant. However, although there is a slight positive correlation for Mode I it is not significant, contrary to Salthe and Duellman's (1973) generalization. The embryos in smaller eggs develop more quickly than those in larger ones (Salthe and Duellman, 1973), and a shorter time to hatching would be advantageous in an aquatic environment so that the young are motile as soon as possible, thus for Mode I species selection probably favours the retention of small eggs even in larger species. For a given SVL, egg diameter in Mode I species is always smaller than in species of Modes II and III, and generally smaller in Mode II species than in Mode III species (Fig. 4), again reflecting the increase in yolk content from Mode I to Mode III.

(ii) Ovarian Complement

A large frog is able to possess larger ovaries than a small individual, because of its greater abdominal volume. Increase in ovarian volume leading to increased reproductive output may be achieved in two ways: 1) by increasing the size of each oocyte, or 2) by increasing the number of oocytes, i.e. increasing ovarian complement. Among individuals of the same size, assuming that the ovaries always grow to a maximum volume within the constraints of abdominal volume and availability of energy resources for vitellogenesis, oocyte size may differ as demonstrated above, and the only means whereby an increase in oocyte size may be achieved is for the complement to decrease. Ovarian complement is therefore closely associated with egg diameter, and may also have some bearing on reproductive morphology, so I estimated complement values for

as many species as possible in this study.

The following comparisons of ovarian complement between groups of species are solely comparisons of the reproductive potential of species at a given time, i.e. of the number of eggs to which energy can be diverted for vitellogenesis at one time. They are not necessarily comparisons of clutch sizes or of reproductive potential over an entire breeding season (even though for most species ovarian complement would be a close estimate of these two parameters). This is for two reasons: 1) following oviposition there are usually several mature oocytes remaining in the ovaries and there may be some ova scattered in the body cavity or in the ovisac; and more importantly 2) not all anurans confine their entire reproductive effort for one breeding season to one clutch. Some species such as *Hyla rosenbergi* (Kluge, 1981), *H. regilla*, *H. cinerea* and *H. gratiosa* (Perrill and Daniel, 1983), *H. rhodopepla* (Crump, 1974), and *Rana clamitans* (Wells, 1976), may lay two or more clutches per season if suitable breeding conditions exist over an extended period of time. Under such circumstances, clutches following the initial one may be relatively small if food sources are limited, i.e. only a relatively small number of oocytes may be matured in the ovaries at one time although others may be in an advanced stage of vitellogenesis ready for the next clutch. Opportunistic breeding with multiple clutches has been reported in *Limnodynastes tasmaniensis* (Tyler, 1978; and in a laboratory colony - John, 1980), and may occur in other species which I examined, therefore not all ovarian complement values may be entirely comparable. However, gross differences in ovarian complement between groups of species should still be apparent.

Ranges of ovarian complement values of the species I investigated overlap between modes, but the means are significantly different between

modes. The mean for Mode I is greater than those of Modes II and III, and that for Mode II is greater than that for Mode III. This is correlated with the increase in egg diameter from Mode I to III since in an ovary of a given volume a larger egg size must be accompanied by a decrease in ovarian complement (although the decrease in SVL from Mode I to III may also bear upon the decrease in ovarian complement; see below). Salthe and Duellman (1973) indicated that regardless of reproductive mode there is a negative correlation between clutch size and ovum size. There should be a similar correlation between ovarian complement and egg diameter, and my data for all modes combined demonstrate that there is a significant negative correlation (Fig. 6; the regression line in this figure is a poor fit, suggesting that Bartlett's three-group method for linear regression is not well suited to these data). Within each mode, however, there is no correlation of ovarian complement with egg diameter, probably reflecting differences in SVL between species.

A third correlation documented by Salthe and Duellman (1973) is that within a given reproductive mode there is a positive correlation between clutch size and female SVL. A similar positive correlation should exist between ovarian complement, and indeed this correlation holds for all three modes in this study, as illustrated in Fig. 5, and is statistically significant. Whilst there is overlap in complement between modes, this is not usually so if only species of similar SVL are considered. For a given SVL, ovarian complement is generally greater in Mode I species than Mode II, generally greater in Mode II species than Mode III, and always greater in Mode I than Mode III. Thus the differences in mean ovarian complements between modes are not entirely due to differences in SVL.

Among species of a similar size, one would expect that under optimal conditions of energy input the total ovarian volume should remain similar,

i.e. as large as possible within the constraints of the abdominal cavity (assuming that in frogs reproductive potential is maximized when possible), regardless of reproductive mode. Thus a species with many, small oocytes should possess ovaries of a similar volume to those of a similarly-sized species with a small number of large oocytes. I did not measure ovarian volume but calculated a value approximating this: complement volume - the total volume of mature oocytes in an ovary, i.e. the reproductive effort of the ovary at a given time. Fig. 7 indicates that in fact complement volume is similar in similarly sized species of any mode. Thus body size (represented by SVL) appears to be a significant constraint upon the total reproductive output, as also noted by Kaplan and Salthe (1979) for salamanders. Scattering of points in Fig. 7 is probably partly due to inaccuracy of data but may also reflect that some species have approached a maximum level of reproductive output more closely than others, due to, for example, a greater supply of energy for vitellogenesis.

(iii) Egg Pigmentation

Melanin pigmentation covering the animal hemispheres of anuran eggs occurs in all species which lay their eggs in sites exposed to sunlight, and absence of pigmentation occurs in many species which lay their eggs in sites sheltered from sunlight (Tyler, 1968; Heyer, 1969). It is suggested that pigmentation aids in protecting the eggs against damaging levels of ultra-violet radiation, and/or in raising egg temperature (Salthe and Mecham, 1974), or in camouflaging them (Passmore and Carruthers, 1979).

There is a clear trend towards lack of pigmentation from Mode I to Mode III, with only a few of the Mode I species, about half of the Mode II species, and all but one of the Mode III species possessing unpigmented

eggs. All of those species which usually oviposit in exposed sites possess pigmented eggs, and all of those which lay unpigmented eggs do so in cryptic or protected situations where pigmentation is obsolete and presumably lost through selective pressures. However, three of the Mode II species with pigmented eggs may lay them in unexposed sites: *Pseudophryne bibroni*, *Taudactylus acutirostris* and *T. diurnus*. *Pseudophryne bibroni* individuals frequently conceal their eggs under logs, rocks or leaf litter (Woodruff, 1976; personal observation), but may also lay them in exposed situations such as between grass roots in waterlogged paddocks, or in small depressions in the ground (Jacobson, 1963; Tyler, 1976b). Such apparent adaptability to a variety of oviposition sites is probably the reason for retention of pigmentation that might otherwise be lost in a species which usually conceals its eggs. *Taudactylus diurnus* lays its eggs under rocks in water, and *T. acutirostris* amongst rocks in water usually in heavy shade (Liem and Hosmer, 1973). Particularly *T. diurnus* would therefore be expected to possess unpigmented eggs; the reasons for retention of egg pigmentation in these two species are not clear. The solitary Mode III species with pigmented eggs, *Nectophrynoides malcolmi*, deposits its eggs "...at the base of short, herbaceous vegetation, ...and only rarely beneath logs and leaves". (Grandison, 1978), so they may be exposed to low levels of ultra-violet radiation; camouflage from predators may also be a significant benefit of egg pigmentation in this species.

(iv) Egg Jelly Capsules

The jelly capsule protects the egg against damage following oviposition. It is possible that the amount of jelly which coats each egg differs according to the environment in which the eggs are deposited, and may therefore be related to reproductive mode. For example, eggs of Mode III species may possess particularly thick jelly capsules as

protection against excessive desiccation. Thicker capsules would require extra mucopolysaccharide jelly to be secreted from the oviducts, and this may be reflected in either the number of convolutions of the oviduct or its width (q.v.).

I was able to measure capsule thickness for only a few species - those which were collected with eggs or which had ova in the ovisacs at the time of collection - and these were supplemented by other values taken from the literature. Sample sizes are too small for statistical analysis, but it is apparent that amongst these few values there is no trend in thickness with reproductive mode. Capsules both thick and thin occur in all three modes. Four of the thickness values given in Table 5 may not be comparable with the remainder because I measured them from ova within the ovisac instead of from fertilized eggs. Egg capsule jelly swells following oviposition due to uptake of water (Rugh, 1951), but jelly surrounding eggs in the confines of the ovisac of a preserved frog may not absorb as much water, therefore these four figures may be unrealistically small. Beattie (1980) has demonstrated that the ionic concentration of the water in which eggs are deposited dramatically affects capsule thickness in *Rana temporaria*. The variability of my data on capsule thicknesses may be caused in part by ionic concentration effects.

(c) OVARIES

(i) Morphological Variation in Vertebrate Ovaries

The morphology of the vertebrate ovary remains relatively uniform within major vertebrate groups: elongate organs that extend from near the anterior end of the opisthonephros posteriorly along most of the length of the abdomen in cyclostomes, most teleosts and elasmobranchs,

and more or less compact, globular, and sometimes lobulated bodies in tetrapods (Frye, 1977). Little distinctive morphological variation in ovaries of different species has been reported. Jones *et al.* (1982) surveyed a number of lizard species and reported the occurrence of either one or two germinal beds per ovary, or several (4 - 6) in two species of *Eumeces*. They found the number of germinal beds to be closely related to geographic distribution of the species, and possibly to taxonomic status at the familial level. Anuran ovaries frequently are lobed, and Spengel (1876) and Bhaduri (1953) noted that the number of lobes may vary considerably. My study documents the variation, both intra- and interspecific, in lobe number of anuran ovaries and indicates some relationship with reproductive mode.

(ii) Lobing of Anuran Ovaries

The surface area of an organ of given volume can be increased by folding or lobing of its surface. Such a consideration should be important in the case of the anuran ovary which is essentially a hollow sac with oocytes developing in a single layer under the epithelium. To increase ovarian complement, the surface area of ovarian epithelium must increase. The ovary could simply be expanded to form a larger and larger sac, but this is impossible within the confines of the abdominal cavity, so the epithelium must become folded. The lobing seen in many anuran ovaries must be a result of this necessity for folding, in species with large ovarian complements.

The results of my study demonstrate that the number of lobes of the ovary varies widely in the Anura. Such variation may be due to: 1) random intraspecific variation, 2) increase of lobe numbers with increasing age or size of the individual, 3) seasonal variation, or 4) interspecific variation.

For those species of which I examined more than one specimen it is clear that there is a small degree of intraspecific variation in lobe numbers but that this variation is insufficient to account for gross differences between species, which may be more than ten-fold. In general the lobe number is similar within a species. The greatest discrepancy I observed was in *Litoria caerulea* in which one individual possessed ovaries both with 13 lobes, and the other individual one ovary with 12 and one with 21 lobes. Such a substantial difference between the two ovaries of one individual is extremely unusual and may have been due to a developmental abnormality of the ovary with 21 lobes.

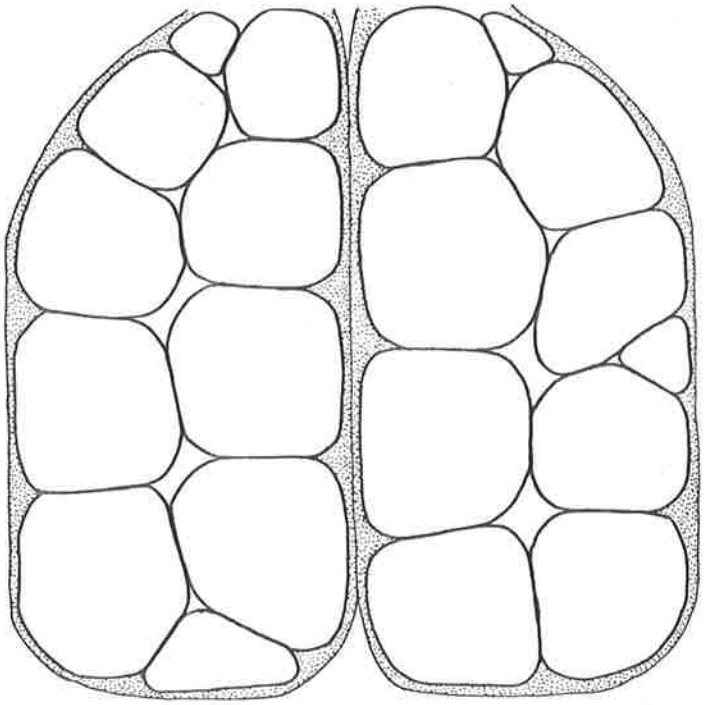
In *Limnodynastes dumerili* and *L. tasmaniensis*, young of which I reared from eggs to sub-adults or adults, the lobing of the ovary becomes apparent early in ontogeny and the numbers of lobes in tadpoles or individuals at metamorphic climax correspond with those in adult individuals. Thus the number of lobes does not increase with increasing age, as I also found in other species of which I dissected both juveniles and adults. Bhaduri (1953) quoted van den Broek (1933) as writing that in old specimens several lobes may unite into one. I found no evidence for this assertion, as lobe numbers for all conspecific adult specimens were always similar. It could be predicted also that conspecific individuals at the same stage of reproductive maturity but of different body sizes may differ in lobe numbers because of different abdominal volumes. Fig. 8 for 35 sub-adult *Litoria dahli*, all at a similar stage of reproductive maturity but of widely differing body sizes, shows that at least for this species such a prediction does not hold.

For those species of which several specimens collected at various times of the year were available there is no correlation of lobe number with the month of collection, so there is no evidence to suggest that

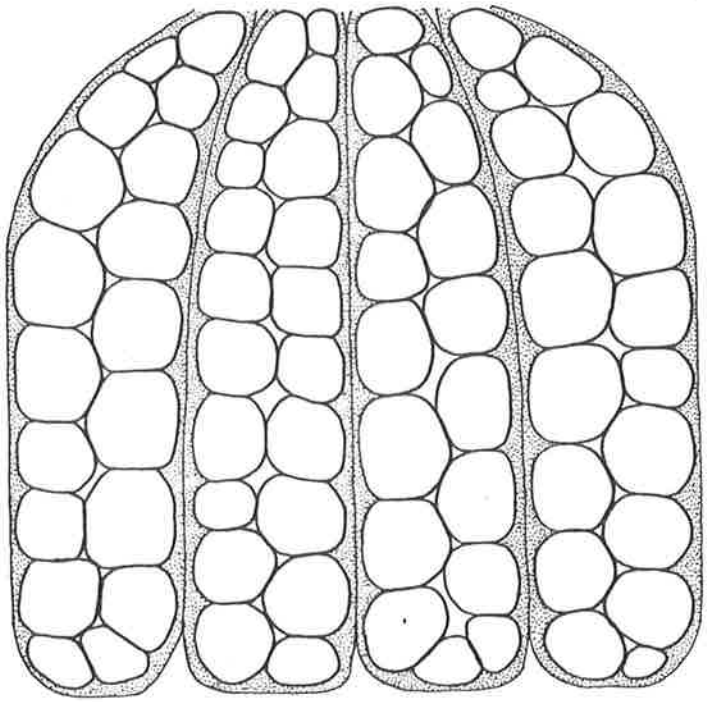
lobe numbers vary temporally, for example increasing at the onset of the breeding season.

Interspecific variation accounts for much of the variation in numbers of lobes. Such interspecific variation could be related to 1) size of the species, and/or 2) egg size and ovarian complement, i.e. reproductive mode. Fig. 10 displays the relationship between SVL (i.e. body size) and numbers of lobes. There is a significant positive correlation between the two variables, as expected since in larger species ovarian complement is greater, so a greater surface area of ovarian epithelium is required to accomodate the additional oocytes; thus there are more ovarian lobes. For Modes II and III the increase in lobe number is seen more clearly among larger species, because most of the smaller species (less than about 35 mm SVL) possess unlobed ovaries. Any decrease in body size below about 35 mm SVL cannot be accompanied by a decrease in lobe numbers because the maximum decrease in ovarian lobing has already been achieved, i.e. the ovaries are unlobed. Fig. 10 indicates that for a given SVL, the number of lobes is generally greater in Mode I species than in Mode III species. The points for Mode II are scattered, but tend to be intermediate between those of Modes I and III. A comparison of mean lobe numbers for each mode reveals that the mean for Mode I is significantly greater than those for Modes II and III, and that for Mode II is significantly greater than that for Mode III. Thus there is a decrease in lobing from Mode I to III. The reason probably lies in surface area considerations. A frog with a large number of small oocytes will require a certain number of ovarian lobes so that ovarian epithelium can reach each oocyte (Fig. 30). A similarly sized frog (and one therefore with a similarly sized ovary) with a small number of large oocytes will not require as large an area of epithelium to subtend each oocyte because, although the ovary is the same size, there are fewer eggs, and

FIG. 30 Diagrammatic anuran ovaries of similar size, with a small number of large oocytes (A) or a large number of small oocytes (B).



A



B

so not as many layers of epithelium are required within the bounds of the ovarian mass (Fig. 30).

Since it is the egg diameter (and thus reproductive mode) as well as body size of a species which determines the number of lobes, a relationship between the values I obtained for egg diameter and number of lobes should be discernible; a decrease in lobing with increasing egg diameter would be predicted. This relationship is shown in Fig. 11 and is not particularly clear, but for all species combined there is a significant negative correlation between egg diameter and number of lobes, as predicted. (The regression line in Fig. 11 is a poor fit, suggesting that Bartlett's three-group method for linear regression is not well suited to these data.) Within each mode, however, this does not apply. For Modes I and II there is no correlation at all and for Mode III there is a significant positive correlation. For Mode I the egg diameter remains fairly similar for most species, so trends with lobe number would not be expected. For Modes II and III, in which there are significant positive correlations between egg diameter and SVL, I would suggest that the effect of increasing SVL increasing the number of lobes overrides the effect of increasing egg diameter decreasing the number of lobes.

Among the published accounts of anuran reproductive morphology, some include the number of ovarian lobes of the species in question. Marshall (1912) found *Rana temporaria* to possess 15 "pouches" to each ovary, and Rugh (1951) observed 8 - 13 lobes in *Rana pipiens*. These are large Mode I species and so would be predicted to possess such numbers of lobes. *Eleutherodactylus jasperi* and *Nectophrynoides malcolmi* being relatively small species with few, large eggs (Drewry and Jones, 1976; Grandison, 1978), and classed as Mode III, could be expected to possess unlobed ovaries, as indeed Wake (1978, 1980) reported. *Nectophrynoides occidentalis* (Mode IV) possesses very small eggs, but they are few in

number and the species is small (Angel and Lamotte, 1944) so again it would be expected to possess unlobed ovaries, as Angel and Lamotte (1944) found. *Rheobatrachus silus*, also Mode III with few, large eggs, is a larger species than those discussed previously (adult female SVL 44.5 - 53.9 mm, Tyler and Davies, 1983) so a small number of lobes would be predicted and in fact is observed (Horton and Tyler, 1982). Spengel's (1876) account gives the number of lobes for several species, and most tally with what would be expected from my study, except that his report of unlobed ovaries in *Pelodytes punctatus*, a Mode I species of up to 45 mm SVL (Mertens, 1960), is unexpected. Bhaduri and colleagues noted lobe numbers for most species they examined (Table 2). Three of these species I also examined, and the numbers observed in both studies correspond for two (*Ascaphus truei* - 1 lobe, and *Cacosternum boettgeri* - 5 lobes), but not so closely for the third (*Hyperolius marmoratus* 5 - 6 lobes (Bhaduri and Basu, 1957); 3 lobes, this study). Lobe numbers for most of the remaining species fit reasonably closely with my data when plotted against SVL and according to reproductive mode, as in Fig. 10.

(iii) Ovarian Asymmetry

With the exception of Horton and Tyler (1982) (Appendix IV), in which my observations on *Rheobatrachus silus* are detailed, no authors have reported significant ovarian asymmetry in any species, other than that which may have been due to developmental abnormality, such as that noted by Watson and Saunders (1959) in one specimen of *Myobatrachus gouldi* in which the right ovary was rudimentary. Horton and Tyler (1982) observed that in *Rheobatrachus silus* there are frequently more lobes in the right ovary than in the left, and the number of oocytes similarly is higher on the right side. Horton (1983) (Appendix III) suggested that because the anuran stomach is sinistral, and ventral to the left ovary, a large meal consumed by a gravid *R. silus* may press on the left ovary

and distort the large eggs. Such a problem might be lessened by a reduction in size of the left ovary and the number of its oocytes.

If this hypothesis were correct, one would expect other Mode III species to show such a trend towards reduction of the left ovary. I examined several specimens of each of three other Mode III species (*Eleutherodactylus achatinus*, *E. curtipes* and *Myobatrachus gouldi*) and none of these species exhibited sinistral ovarian reduction (Tables 7a and b). However, in each of five specimens of *Eleutherodactylus curtipes* there were more oocytes in the left ovary than in the right, as there were also in four of five individuals of *Myobatrachus gouldi* (Table 7b). If this trend towards a greater ovarian complement on the left side is real (and it may not be since samples were small) then it is the opposite to the situation in *Rheobatrachus silus*. Thus the hypothesis of pressure from the engorged stomach leading to sinistral ovarian reduction is unlikely. Pressure from a brooding stomach full of developing young should not be the cause either, since brooding follows ovulation and subsequent vitellogenesis cannot occur until brooding has ended and the female may resume feeding. Thus there can be no mature oocytes in the ovaries during brooding. In addition, the brooding stomach fills the abdominal cavity almost entirely (Tyler and Carter, 1981), so that the right ovary should be affected as much as the left. No other explanation is apparent for this characteristic of *R. silus*.

Sufficient numbers of six Mode I species were dissected to observe possible trends towards ovarian asymmetry (Table 7). There are no definite trends apparent in *Limnodynastes tasmanienis*, *Litoria rothi*, *L. rubella*, or *Ranidella signifera*. There is no trend in lobe number for *Cyclorana australis*, but in each of the seven specimens for which I obtained oocyte counts there were more oocytes in the left ovary than in

the right. *Litoria dahli* exhibited a tendency for more lobes in the left ovary than the right, but this trend is not statistically significant.

Possible trends towards ovarian asymmetry are rendered less plausible by the fact that a larger number of eggs in an ovary, either left or right, is not always associated with a larger number of lobes in that same ovary (Table 7b). Some specimens of several species possessed ovaries with the smaller number of oocytes and the larger number of lobes (or *vice versa*) in the same ovary.

I can draw no firm conclusions regarding ovarian asymmetry other than that (except in *Rheobatrachus silus*) there may be a tendency for the left ovary to possess more lobes or to contain more eggs. There is no apparent relationship between ovarian asymmetry and reproductive mode.

(d) OVIDUCTS

(i) Oviducal Modifications

Among most vertebrates the female reproductive tract essentially consists of paired oviducts and the cloaca (Frye, 1977). Specialization of regions of the oviduct has occurred, for example for secretion of calciferous shells or for gestation. In the Anura the oviduct is specialized for the secretion of gelatinous mucopolysaccharide material which forms protective capsules around the eggs. Further specialization of the oviduct may be expected amongst anurans for two reasons: 1) the environments into which the eggs are deposited vary greatly from species to species, therefore the chemical composition of the secreted jelly may be altered, and 2) the size and number of ova passing through the oviducts following ovulation differ widely between species, and may influence the quantity of jelly secreted and the morphology of the oviduct.

The possibility of chemical diversity of oviducal secretions has been addressed by several workers, such as Freeman (1968), Lee (1969), Pereda (1970), Shivers and James (1970a), Steinke and Benson (1970), de Martinez *et al.* (1975) and Suvarnalatha *et al.* (1975). Their results indicate that the chemical composition of the secretions differs both between species and according to the region of oviduct from which they are secreted. Several discrete layers of jelly material can be distinguished in the capsules of eggs which have traversed the full length of the oviduct and these layers correspond with the chemically distinguishable regions of the oviduct (Shivers and James, 1970a). Attention has been directed to the role of these jelly layers in fertilization, but none to their properties in relation to the environment in which the eggs are deposited. It is unlikely that their chemical properties can be correlated with reproductive mode since different numbers of jelly layers with divergent chemical properties have been found within a species (for example by Shivers and James, 1970, and Steinke and Benson, 1970, both on *Rana pipiens*).

The possibility of the nature of the eggs affecting the morphology of the oviducts is one which has received scant attention. Bhaduri (1953), Bhaduri and Basu (1957), and Coe (1974), considered the greatly enlarged posterior region of the oviduct in several foam-nesting species to be related to the production of mucus for foam-nest construction. Bhaduri (1953), Griffiths (1959), Watson and Saunders (1959), and Bhaduri and Mondal (1965), suggested that broadened oviducts and united ovisacs may be associated with large eggs, i.e. with modified reproductive modes, but they were not able to substantiate this prediction. I consider these and other possibilities in the following sections.

(ii) Convolutions of the Oviduct

It is logical to assume that the reason for the extreme folding or convolution of anuran oviducts is to lengthen the oviduct between ostium and ovisac, i.e. to increase the number of oviducal glands so that sufficient mucopolysaccharide jelly can be produced to coat a large number of eggs. Presumably a straight oviduct is too short, since it has been found in no frogs other than *Nectophrynoides occidentalis* (Xavier, 1973) and *N. tornieri* (personal observation), both of which retain their eggs and are live-bearing, and therefore would require no egg jelly coating other than that which may be necessary for fertilization (Shivers and James, 1970b). No information is available on the third live-bearing species of this genus, *N. viviparus*, but in another ovoviviparous species, *Eleutherodactylus jasperi*, the oviducts possess very few convolutions (M.H. Wake, *in litt.*). Alternatively, the jelly-secreting capacity of an oviduct could be increased by increasing the thickness of its walls and thus increasing the number of jelly glands in the wall, rather than by increasing its length. However, except in the case of foam-nesting species, I did not observe appreciable thickening of the walls in any anurans (but see section c)); possibly the viscosity of the jelly would render its transport from the outermost glands in to the oviduct lumen impossible if the walls were thickened to any great extent.

If the oviduct is lengthened by an increase in its convolution, then the number of convolutions should be proportional to the length of the *pars convoluta*, so long as the oviduct remains the same in cross-sectional diameter. Measurements I made of the oviducts of a few individuals indicates that this is so, as shown in Fig. 12. The number of convolutions as an indicator of oviduct length is preferable to oviduct length itself since the latter is awkward and time-consuming and requires

removal of the oviduct from the specimen. In addition, if only juvenile specimens are available so that the mature oviduct length cannot be measured, length can still be estimated from the number of convolutions which appears to remain the same throughout the life of the frog (see below).

The results of my study demonstrate that the number of convolutions varies widely among numbers of the Anura. Such variations may be related to: 1) random intraspecific variation, 2) increasing number of convolutions with increasing age or size of the individual, 3) seasonal variation, 4) interspecific variation.

For those species of which I examined more than one specimen, it is apparent that there is intraspecific variation but that it is insufficient to account for gross differences between species, which may be fifty-fold or more. Generally the number of convolutions remains similar within a species. The greatest intraspecific variation which I observed was in *Litoria caerulea* (as also for the number of ovary lobes) in which one individual possessed oviducts with 136 and 147 convolutions respectively, and the other individual oviducts with 215 and 221 convolutions, respectively. Such wide discrepancy was not encountered in any other species.

Beddard (1908a) suggested that in a *Breviceps verrucosus* which he dissected, and which he suspected to be relatively young, "It may be ... that the oviducts are not as complicated in their coiling as they would have been had the frog lived longer". I found no evidence supporting an increase in oviducal convolution with increasing age. In young of *Limnodynastes dumerili*, *L. tasmaniensis*, and *Pseudophryne bibroni* which I reared from eggs to sub-adults or adults, the numbers of convolutions

of juveniles in which convolution had just occurred corresponded with those in reproductively mature individuals. In other species in which both juvenile and adult individuals were available for dissection the number of convolutions was similar in both. Therefore I conclude that the number of convolutions is almost certainly determined at the onset of convolution and that there is no increase with increasing age of the individual. Among conspecific individuals of different body sizes, the larger individuals may develop more eggs, so a longer oviduct, i.e. one with more convolutions, would be required. However, I did not observe such a trend in any species of which I dissected several specimens, nor did Horton (1983) (Appendix III) among 20 *Rheobatrachus silus* (Fig. 13).

For those species of which I examined several specimens collected at different times of the year, there was no apparent correlation of number of convolutions with the month of collection. There is no evidence to suggest that the number of convolutions varies temporally, for example increasing at the onset of the breeding season.

Much of the variation in convolution numbers is interspecific. Such variation may be related to 1) size of the species, and/or 2) egg size and ovarian complement, i.e. reproductive mode. The relationship between body size (SVL) and the number of convolutions is displayed in Fig. 15. For species of Mode I and of Mode III this relationship is a significant positive correlation. This would be expected since in larger species the egg complement is generally greater therefore more muco-polysaccharide jelly would be required and so a longer oviduct would be necessary - achieved by an increase in convolution. For Mode II species there is a slight positive correlation but it is not statistically significant. For a given SVL, the number of convolutions is generally greater in Mode I species than in Mode III species (Fig. 15). The values

for Mode II are scattered but tend to lie amongst those of Mode III. The mean number of convolutions for Mode I species is significantly greater than those for Modes II and III, and the mean for Mode II is greater than that for Mode III but not significantly so. Thus there is a trend towards a smaller number of convolutions from Mode I to Mode III, although there is little difference between Modes II and III. Such a trend may be related to two factors. Firstly, it can be shown by simple calculation that a small number of large eggs requires a considerably smaller volume of jelly to encapsule the eggs than does a large number of small eggs of equivalent total volume, assuming that the eggs are coated to the same thickness (which they are not in different species, but there appear to be no trends in thickness with reproductive mode; see part (b)(iv)). Thus in species with large eggs probably less jelly is required, so the oviducts need not be so long, i.e. the number of convolutions may be smaller. Secondly, if the eggs are larger, then the oviduct lumen may be larger to accomodate them, assuming that there is a maximum elasticity of the oviduct wall beyond which it cannot stretch without damage during ovulation. Thus the diameter of the oviduct in transverse section, or oviduct width, must be greater. If this is so, then for a given length of oviduct there must be fewer convolutions, since each convolution covers a greater distance.

Since the egg diameter of a species may influence the number of convolutions, a relationship between the values I obtained for egg diameter and number of convolutions may be discernible; a decrease in convolution with increasing egg diameter would be predicted. The relationship between egg diameter and number of convolutions is shown in Fig. 16 (the regression line in this figure is a poor fit, suggesting that Bartlett's three-group method for linear regression is not well suited to these data). Overall, there is a significant negative correlation between the

two variables, as expected, although the points are widely scattered. Within each mode, however, there is no correlation at all. For Mode I, egg diameter remains similar for most species, so trends with numbers of convolutions would not be expected. For Modes II and III, the effect of increasing SVL increasing convolution number probably overrides the decrease in number of convolutions due to increasing egg diameter.

Few published accounts of anuran reproductive morphology include a precise count of convolution numbers. Wake (1980) reported "five or six pronounced curves" per oviduct in *Nectophrynoides malcolmi*, about one half the number that I found; possibly the curves counted by Wake do not correspond with my definition of convolutions, or else Wake counted only the major curves whereas I also include the minor ones. Horton and Tyler (1982) (Appendix IV) listed convolution numbers in 20 individuals of *Rheobatrachus silus*. Bhaduri and co-workers did not give numbers of convolutions, but illustrated the reproductive system of each species so that some idea can be gained of the number of convolutions in these, but no direct comparisons can be made with my results. In general, those species seen by Bhaduri which were Mode I species possessed many convolutions, and Modes II and III species possessed fewer.

(iii) Oviduct Width

Anuran oviduct walls are elastic and during ovulation they bulge around each egg as it descends. If egg diameter increases, the oviduct lumen may increase in diameter to accomodate the larger eggs. Thus there may be discernible correlations between lumen diameter and egg diameter or reproductive mode. I used oviduct width as an index of lumen diameter, but a combination of factors which may affect the thickness of the oviduct wall (discussed in section II) is likely to render width measurements highly variable, even though lumen diameter may remain relatively

stable. Therefore any trends in oviduct width between species may be masked. In fact I found oviduct width measurements to be quite variable within a species; thus measurements for species of which only one specimen was available are of dubious value. Nonetheless, I observed even greater differences between species; this interspecific variation may be related to the size of the species, and to its egg size and ovarian complement; i.e. reproductive mode.

Plotting oviduct width against egg diameter (Fig. 18) demonstrates that, as predicted, there is a positive correlation between these two variables, although the points are widely scattered. There is also a significant positive correlation for Mode I species considered alone, and also for Mode II species. There is no significant positive correlation for Mode III species, probably because of the unexpectedly low width measurements (shown on the lower right in Fig. 18) which I obtained for three New Guinean microhylid species. These three measurements were all based on one oviduct only and so may not be representative for their species; excluding them leaves a series of points which appear to be positively correlated. Since egg diameter apparently does influence oviduct width, a trend towards increasing oviduct width from Mode I to III would be predicted. The mean for Mode I species is indeed significantly smaller than those for Modes II and III, but although the mean for Mode II is slightly smaller than that for Mode III, it is not significantly so.

The differences in oviduct widths between modes are shown more clearly in Fig. 17 (oviduct width vs SVL), from which it can be seen that for a given SVL oviduct width is usually smallest in Mode I, but that width values are mostly intermingled in Modes II and III. The overlap in widths (and convolution numbers) between Modes II and III suggests either

that the morphology of the oviduct is altered to a similar degree in species with modified reproductive modes regardless of how much larger or fewer their eggs may be, or else that oviduct width may not be a satisfactory reflection of lumen diameter. In the latter case, the lumen diameter may be larger in Mode III, but the oviduct walls may be slightly thinner since less jelly need be produced, thus leaving oviduct width almost the same. I noticed no appreciable difference in wall thickness between species of Modes II and III, but since I made no measurements I cannot test the validity of the preceding suggestion. However, it is perhaps supported by the fact that there is a significant positive correlation between SVL and oviduct width in Mode I species (Fig. 17). There is a slight increase in egg diameter with increasing SVL in Mode I, but it is not significant, so the increase in oviduct width may be due to slight thickening of the walls.

A multi-dimensional analysis of SVL, egg diameter, ovarian complement, number of convolutions, lumen diameter and wall thickness would be necessary to determine the precise effects of the former three variables on the latter three. Similarly, there are too many interdependent variables involved to determine the relationship, if any, between oviduct width and the number of convolutions; I found no correlation between these two variables.

(iv) The Oviduct in Foam-nesting Species

Frogs which lay their eggs in foam nests produce large quantities of mucus which is filled with air bubbles by one or other parent, or both parents, to form foam. This mucus is exuded from the cloaca, therefore must be produced either in the cloaca or in the oviduct. It is almost certainly not produced in the cloaca which upon dissection appears indistinguishable from the cloaca of any non-foam-nesting species. In section,

the cellular structure of the cloaca also appears quite normal; there are no distinctive or unusual glandular cells. It is far more likely that the oviduct is the site of foam-mucus production, since it is already involved in mucus production for reproductive purposes.

If foam-mucus originates from the oviduct, it is most likely to do so from the posterior-most regions of the duct, because it must be secreted around the outside of the jelly capsule surrounding each egg. Therefore the jelly capsule must be laid down first, i.e. in the anterior regions of the oviduct, so that foam-mucus does not interfere with its formation. Thus one might expect to find the cellular or even gross structure of the posterior regions of the oviduct to be distinctive in foam-nesting species. I examined 11 foam-nesting species and indeed in each one the posterior region of the oviduct is modified by gross enlargement and proliferation of the glands, suggesting greatly heightened secretory potential. In none of the non-foam-nesting species was this gross thickening of the oviduct walls present. Oviducal enlargement was also observed by Coe (1974) in *Chiromantis rufescens*. He found the enlarged region to consist of swollen convolutions held tightly together by connective tissue, as I found, and he termed it the "foam gland". This term is misleading since the structure is not a discrete organ, or pad of tissue as Coe (1974) described it, but merely a region of the oviduct. Bhaduri and Basu (1957) found the same oviducal morphology in *Chiromantis rufescens*, and Bhaduri (1953) also in the foam-nesting species *Leptodactylus melanonotus*, *L. pentadactylus*, *L. podicipinus*, and *Pleurodema cinerea*. Bhaduri (1932) briefly examined the female reproductive system of *Rhacophorus maximus* but made no mention of any distinctive oviducal structure. Bhaduri (1953) also dissected *Pachymedusa dacnicolor* (as *Phyllomedusa dacnicolor*) which lays its eggs on leaves overhanging water but not in a foam nest (Pyburn, 1970), and found the

posterior portion of the oviduct to be similarly enlarged. No other species investigated by Bhaduri and colleages were foam-nesting species and in none was there gross enlargement of the posterior end of the oviduct.

There is no direct proof that the enlarged region at the posterior end of the oviduct in foam-nesting species functions as the site of manufacture of large quantities of mucus for foam production. That could only be gained from a detailed chemical analysis of the glandular secretions of each region of the oviduct and of the foam-mucus and egg capsules. But since the oviduct is modified in the same manner in all foam-nesters investigated to date, and since the region of the oviduct involved is that where one would expect modification, it seems almost certain that this enlarged region is the site of foam-mucus production. The only non-foam-nesting species so far described with the posterior enlargement of the oviduct is *Pachymedusa dacnicolor*, and Bhaduri's (1953) illustration shows that the oviduct is extremely enlarged. Other phyllomedusine hylids have been described as laying their eggs in folded leaves with plugs of jelly protecting the exposed ends of the clutch (Lamotte and Lescure, 1977); these jelly plugs have been demonstrated to serve in water retention in *Phyllomedusa hypochondrialis* (Pyburn, 1980). *Pachymedusa dacnicolor* simply lays its eggs exposed on the flat surfaces of leaves and Pyburn (1970) made no specific reference to large quantities of extra jelly surrounding the eggs. However, he did refer to the males aiding in oviposition by "pulling eggs *and jelly* from the female's vent" (italics mine), suggesting that there is mucus produced in addition to that of the egg capsules. Pyburn (1970) also described the necessity for a considerable quantity of water, supplied from the female's bladder, to be added to the egg mass at oviposition in order to swell the jelly and prevent its desiccation. The requirement of a

bladder-full of water per clutch suggests that a large quantity of extra jelly is produced with each clutch, presumably to aid in water balance of the clutch. If this is so, the additional mucus presumably originates from the posterior enlarged region of the oviduct.

Substantial thickening of any part of the oviduct wall does not appear to occur otherwise in the Anura. Lengthening of the oviduct appears to be involved in increasing mucus output, rather than thickening of the walls, as discussed in section b) on oviduct convolutions, possibly because viscous egg capsule jelly would not flow readily into the oviduct lumen from the outside of the wall if the latter were very deep with many glands. The mucus produced for foam-nesting is relatively fluid (Coe, 1974; personal observations), and is considerably less viscous than the jelly constituting the outermost layers of the egg capsules. Therefore, thickening of the region of oviduct wall which produces foam-mucus should not unduly inhibit the flow of foam-mucus inwards to the oviduct lumen.

(v) The Ovisac

(1) Degree of fusion

Spengel (1876) discovered that in some species he dissected the terminal portions of the oviducts, the ovisacs, do not enter the cloaca separately as they do in many other species. Bhaduri (1953) looked at ovisac fusion in some detail and described three states: *uterus separatus*, *uterus septatus* and *uterus communis* (which I term conditions 0, 1 and 2, respectively). Bhaduri (1953) and Bhaduri and Mondal (1965) suggested that fusion of the ovisacs may be a result of the evolution of large eggs, but they were not able to substantiate this claim.

Spengel (1876) raised the possibility that intraspecific variation

may occur in ovisac fusion. He dissected eight specimens of *Bombina bombina* (as *Bombinator igneus*) and seven possessed united ovisacs whilst in the eighth the ovisacs remained separate. Bhaduri and colleagues examined only one specimen of each species and so could not comment on intraspecific variability. For the majority of species which I considered, I was able to determine the degree of ovisac fusion in only one specimen, but for 16 species I determined the degree of fusion from two to four specimens, and for *Eleutherodactylus curtipes* from six specimens. In each of these 17 species the degree of fusion was the same among conspecific individuals. Ovisac condition is also relatively consistent among congeners, with exceptions such as *Litoria* in which all three conditions occur. For example in five *Eleutherodactylus* species seen by me and three other species seen by Bhaduri (1953) the ovisacs are completely united. Limited intrageneric variation suggests that the character is likely to be stable within a species. If intraspecific variation were to occur, it would be likely to be in a species with united ovisacs, and take the form of variation in the point at which the ovisacs united, whether half way down or a third of the way down for example. In fact this might be seen in *Cacosternum boettgeri* which Bhaduri and Basu (1957) reported as possessing completely united ovisacs but in which I found the ovisacs to be separate anteriorly and to unite at about one third of the way along their length. However, Bhaduri and Basu's (1957) illustration shows the ovisacs separated for some distance and then uniting as they converge, so the discrepancy is probably due to personal interpretation rather than to intraspecific variation. The difference between separate and united ovisacs is a drastic one, therefore Spengel's (1876) report of both conditions in *Bombina bombina* is unexpected, particularly as it involves a change from two to one openings into the cloacal wall. Thus, despite Spengel's (1876) observation, I will assume that the degree of ovisac fusion remains the same within a species.

Of all the species which I examined, there are similar numbers possessing separate, and partly united, and completely united ovisacs. But they are not equally distributed amongst reproductive modes; there is a strong trend towards complete ovisac fusion from Mode I to Mode III (Table 11). Since the ovisac serves simply as a temporary storage sac for ovulated eggs prior to oviposition, any changes in its morphology, i.e. fusion with its opposite, is likely to be associated with changes in the size and number of eggs. Body size may also be involved particularly in very small species in which the egg diameter:SVL ratio may be particularly large. In Fig. 19 egg diameter is plotted against SVL for species of each ovisac condition. There are no apparent trends with SVL, but there are with egg diameter. All species with large or fairly large eggs (diameter 1.8 mm or more) possess ovisacs either partially or completely united, and the only species with separate ovisacs are those with small eggs (diameter 1.7 mm or less). Presumably fusion of the ovisacs and a single opening into the cloaca are necessary to avoid impaction of large eggs as they are about to enter the cloaca at oviposition. If two ovisacs and cloacal openings were present, then eggs could descend and enter the cloaca simultaneously; if they are large eggs they may become irreparably distorted or jammed. United ovisacs and a single opening would allow only one egg through at a time. It should be noted, however, that in *Bufo* species, which produce strings of eggs often in a double row (the left row presumably from the left ovisac and the right row from the right ovisac), the ovisacs unite shortly before the single opening into the cloaca [at least in *Bufo marinus*, which I examined, and in *B. melanostictus* (Bhaduri and Banerjee, 1939), and in three species examined by Spengel (1876)]. The eggs are very small and do not impact upon entering the cloaca, as in the strings of spawn two eggs may lie at the same transverse level. Ovisac fusion in *Bufo* species must have occurred for some other reason than avoidance of impaction. Fusion may

facilitate the formation of a single compact string of eggs derived from both oviducts simultaneously. The formation of strings of spawn also occurs in species of *Neobatrachus* (Watson and Martin, 1973), although the eggs may also be laid separately or in clumps (Littlejohn, 1963; Watson and Martin, 1973). If terminal fusion of the ovisacs also occurs in species of *Neobatrachus* which oviposit in strings, then the hypothesis of fusion facilitating string formation would be supported. I was not able to examine the terminal portions of the ovisacs in the two species I considered because they were not present in the material available to me, which had been dissected previously. *Litoria lesueuri*, *L. nasuta*, *L. rothi*, *Xenopus laevis* and *X. muelleri*, are also, like *Bufo*, moderate to large species with small eggs and ovisacs which unite shortly before entering the cloaca. None of these five species lays eggs in strings (Martin, 1967; Passmore and Carruthers, 1979; Tyler *et al.*, 1983), so ovisac fusion must serve some other function in these frogs.

From Fig. 19 it is apparent that there is almost complete overlap in egg diameter between species with partially and those with completely united ovisacs (if the above mentioned species with small eggs but partially united ovisacs are discounted), i.e. completely united ovisacs are not restricted to species with very large eggs and partially united ovisacs to those with moderately large eggs. Functionally there would be little difference between the two conditions since they both have the same effect of joining the two groups of ova before oviposition and reducing access to the cloaca to one aperture. However, condition 2 is strongly correlated with Mode III, as amongst the species I considered, of 29 species with condition 2 ovisacs, 20 are Mode III (Table 11). It has been proposed that aquatic reproduction, or Mode I, is the ancestral or primitive reproductive mode, and that delayed hatching of feeding larvae (Mode II) is an intermediate stage in the evolution of direct

development (Mode III) (Jameson, 1957; Martin, 1967; Tyler, 1979). If this is so, then probably ovisac condition 2 is the most derived one, which evolved only after condition 1 had been attained, by progressive reduction of the septum dividing the ovisacs.

The ovisacs of species dissected by other authors fall into this pattern also. *Litoria aurea* (Briggs, 1940), *Rana pipiens* (Rugh, 1951) and *R. temporaria* (Marshall, 1912), all Mode I species, possess separate ovisacs. *Breviceps verrucosus* (Beddard, 1908a), *Eleutherodactylus jasperi* (Wake, 1978), *Leiopelma archeyi* (Stephenson and Stephenson, 1957) and *Sminthillus limbatus* (Griffiths, 1959), all Mode III species, possess completely united ovisacs. Of the species which Bhaduri and associates dissected, most Mode I species possess separate ovisacs, notable exceptions being the pelobatids with united ovisacs (but the two illustrations given suggest that, as for *Cacosternum boettgeri*, the ovisacs are condition 1, not 2). The Modes II and III species they examined are fairly evenly apportioned between ovisac conditions 1 and 2.

(2) Occlusion from the cloaca

Bhaduri (1946) suggested that the anuran oviduct may open into the cloaca at the onset of the breeding season and close some time after spawning, i.e. the ovisacs would be occluded from the cloaca for most of the individual's life-span. I examined the terminal portion of the ovisacs in 43 species and found little evidence to support Bhaduri's suggestion, since the ovisacs were open in some juvenile specimens and in some which had probably oviposited shortly before collection, and were occluded in some which were reproductively mature and apparently ready to ovulate. However, evidence from developmental series of *Limnodynastes dumerili*, *L. tasmaniensis*, and *Pseudophryne bibroni*, indicates that the ovisacs remain occluded in juveniles for some time

after their formation.

Occlusion of the ovisacs in adult individuals may be related to the frequency of breeding in a given season. For species with one well-defined breeding season per year, the ovisacs may well behave as Bhaduri (1946) suggested, but for opportunistic breeders or those which lay several clutches per breeding season they may not occlude for the potentially brief periods between ovipositions. The evidence which I have gathered here is too scanty to test this hypothesis. There seems no obvious advantage of occlusion for long periods over occlusion for short periods, however.

(3) Disposition of the ovisacs and urinary ducts

The anuran urinary ducts always lie dorsal to the oviducts after leaving the kidneys, and in general they remain in this dorsal-most position throughout their length and terminate in the cloaca posterior to the termination of the ovisacs. However, there are a few exceptions to this pattern. Bhaduri (1953) noted that in *Scaphiopus couchi* and *S. holbrooki* each urinary duct passes laterally around the ovisac of that side and comes to lie ventro-lateral or ventral to it; the urinary ducts also enter the cloaca anterior to the ovisacs' entry. He did not observe this pattern in any other species, nor did I in any I examined. However, I did find in a few miscellaneous species with separate ovisacs that the urinary ducts moved ventro-medially to the ovisacs and came to lie medial to them, opening into the cloaca slightly posteriorly or even at the same level. This pattern is developed further in *Lechriodus melanopyga* in which the urinary ducts come to lie medial to the ovisacs and enter the cloaca anterior to them. The functional significance of such arrangements is not obvious; they have no apparent relationship with a particular reproductive mode.

Displacement of the urinary ducts laterally around the ovisacs, as displayed in *Scaphiopus*, is not known to occur in any species with partly or completely united ovisacs. Displacement of the ducts between the ovisacs, as in *Lechriodus melanopyga*, is impossible in species with completely united ovisacs, and among species with partially united ovisacs it has been reported only in *Rheobatrachus silus* (Horton and Tyler, 1982; and Horton, 1983; Appendices IV and III). As illustrated by Horton (1983), in one *Rheobatrachus silus* specimen sectioned the urinary ducts pass ventrally between the ovisacs just anterior to the point of fusion of the latter, fuse themselves as they do so, and come to lie ventral to the now united ovisacs and immediately dorsal to the rectum. I sectioned a second specimen and found the same arrangement of ducts. Whether it is the urinary ducts which have moved anteriorly or the ovisacs posteriorly or both cannot be determined, and there is no apparent reason why the ducts have reversed positions. The bladder of *R. silus* enters the cloaca anterior to both urinary ducts and ovisacs, so perhaps the anterior position of the bladder opening has influenced the position of the urinary duct opening, i.e. the urinary ducts moved anteriorly so as to enter the cloaca as close as possible to the bladder. But in a number of other species I sectioned, the bladder also enters anterior to the urinary ducts and ovisacs, but the latter do not reverse positions. So it is unlikely that the position of the bladder has influenced the disposition of the urinary ducts and ovisacs in *R. silus*.

The majority of Mode III species possess completely united ovisacs. *Rheobatrachus silus*, a Mode III species with extremely large eggs of about 5 mm diameter, is a species in which one would also expect to find completely united ovisacs. But the ovisacs of *R. silus* are united only near their posterior end, and they are effectively prevented from fusing further by the urinary ducts which run between them. Reversal

of duct positions in *R. silus* might therefore have occurred very early in the evolutionary history of the species.

The situation described above in anurans is partially analogous to that seen in a comparison of marsupial and eutherian mammals. In moving ventrally to open directly into the bladder, the urinary ducts of marsupials have passed medially between the gential ducts, and those of eutherians have negotiated the genital ducts by passing laterally around them (Tyndale-Biscoe, 1973). Thus, *Scaphiopus* parallels the eutherian condition, and *Rheobatrachus silus* and to a lesser extent *Lechriodus melanopyga* parallel the marsupial condition, except that the urinary ducts still open into the cloaca, not the bladder. Two different strategies to achieve the same end have therefore been adopted in both groups of animals. As in *R. silus*, the posterior portions of the genital ducts, the vaginae, remain separate in marsupials because the urinary ducts divide them. In *R. silus* fusion nonetheless has occurred, because the ovisacs simply unite after the urinary ducts have traversed them, and it has also occurred in marsupials but by different means: a median vaginal cul-de-sac has formed at the anterior ends of the vaginae, and this opens into the urinogenital sinus at parturition (Tyndale-Biscoe, 1973). The major difference between the mammalian condition and that seen in these few anurans is that in the former it has an obvious functional advantage - to drain kidney wastes directly into the bladder, but such a function has not been achieved by duct reversal in anurans.

(4) The urinogenital sinus

Bhaduri and Rudra (1944) discovered the presence of a diverticulum in the rectal wall of a female *Microhyla ornata*; they termed it a Wolffian sinus since the urinary (Wolffian) ducts united with it. Bhaduri (1953), who referred to the sinus as a urinogenital sinus, found

the same in a female *Ascaphus truei*, and Bhaduri and Basu (1957) found a similar sinus in a female *Arthroleptis sylvaticus*. I observed a urinogenital sinus in six other miscellaneous species, in addition to *Ascaphus truei*. In four of these (*Limnodynastes peroni*, *Megistolotis lignarius*, *Xenopus laevis* and *X. muelleri*) the spatial relationship of ovisacs and urinary ducts to the sinus is similar to that in *Ascaphus truei*, i.e., the sinus lies dorsal to the cloaca and ventral to the ovisacs and urinary ducts and enters the cloaca first (in which case the term "urinogenital sinus" is inappropriate; "cloacal sinus" would be preferable). In *Ranidella riparia* the situation is as Bhaduri and Rudra (1944) observed in *Microhyla ornata*: the urinary ducts fuse with the sinus before the latter enters the cloaca. In *Rana papua* the situation is as has not previously been observed: both ovisacs and urinary ducts first enter the sinus, which is dorsal to them, and which therefore is the most appropriately termed "urinogenital sinus". Thus the sinus is not directly analogous in all species, so probably it has evolved independently in most - supported by the phylogenetic diversity of species in which it occurs.

Bhaduri (1953) suggested that the urinogenital sinus may function as a spermatheca in *Ascaphus truei*, in which fertilization is internal. But of all the species in which the sinus has been observed, *Ascaphus truei* is the only one known to have internal fertilization, so the sinus may not serve as a spermatheca at all. Bhaduri's (1953) suggestion may be supported if a urinogenital sinus were found in the only other oviparous species for which internal fertilization has been reported - *Eleutherodactylus coqui* (Townsend *et al.*, 1981). In the three species for which Bhaduri and colleagues reported the presence of a urinogenital sinus in the female, they also reported such a sinus in the male. In addition, Bhaduri and Basu (1957) found that the males of *Kassina*

argyreivittis and *Phrynobatrachus natalensis* possess a urinogenital sinus but not the females. They suggested therefore that it may serve some purpose in the male, perhaps as a vesicula seminalis, but that in the female it is a vestige. I did not dissect males of the species in which I found a sinus and so cannot further illuminate this point. There is no obvious similarity in reproductive mode shared by all these species that might suggest a function for the urinogenital sinus in the female.

(e) SYSTEMATIC IMPLICATIONS OF REPRODUCTIVE MORPHOLOGY

The review of Lamotte and Lescure (1977), concerning those anuran reproductive modes which diverge from the totally aquatic mode, indicates not only that the diversity of reproductive modes is very extensive, but also that many taxonomic groups are involved. I have summarized the occurrence of reproductive modes in all anuran families, in Table 13. It is clear that none of Modes I, II and III is restricted to a particular family or group of families. Evolutionary experimentation and alteration in reproductive mode has occurred many times (with the exception of Mode IV which is known only in one species), and presumably independently in all or most families. Not only have the broad categories of Modes I, II and III arisen in different systematic groups, but specific patterns of breeding behaviour have evolved apparently independently on more than one occasion, for example the transportation of young (eggs or larvae) on the back of a parent in pipids, dendrobatids, hylids and sooglossids, and foam-nesting in Australian and South American leptodactylids (as noted by Martin, 1970) and rhacophorids (although the mechanism by which the foam-mucus is converted to foam differs between groups: by beating of the hindlimbs of both male and female in *Chiromantis* (Coe, 1974), by beating of the hindlimbs of the male only in *Leptodactylus pentadactylus* and *Physalaemus pustulosus* (Heyer and Rand, 1977), and by air bubbles created

TABLE 13: The occurrence of reproductive modes in anuran families (familial classification of Duellman, 1975). (Asterisks indicate data taken from Goin *et al.*, 1978).

Family	Reproductive Mode			
	I	II	III	IV
Leiopelmatidae	-	+	+	-
Discoglossidae	+	+	-	-
Pipidae	+	+	+	-
Rhinophrynidae	+	-	-	-
Pelobatidae	+	-	+	-
Pelodytidae	+	-	-	-
Leptodactylidae	+	+	+	-
Bufonidae	+	+	+	+
Brachycephalidae	+*	-	-	-
Rhinodermatidae	-	-	+	-
Dendrobatidae	-	+	-	-
Pseudidae	+*	-	-	-
Hylidae	+	+	+	-
Centrolenidae	-	+	-	-
Microhylidae	+	+	+	-
Sooglossidae	-	+*	-	-
Ranidae	+	+	+	-
Hyperoliidae	+	+	-	-
Rhacophoridae	+	+	+*	-

by paddling of the hands of the female in Australian leptodactylids (Tyler and Davies, 1979). Nonetheless the end product is the same - a foam nest).

The results of my analysis of reproductive morphology demonstrate that variation in morphology is usually associated with differences in reproductive mode. Therefore the extensive parallelism in reproductive modes between taxonomic groups should be reflected in parallelism in reproductive morphology, and indeed this is what I have found. For example, foam-nesting Australian leptodactylids, *Chiromantis*, and from Bhaduri's (1953) work foam-nesting South American leptodactylids, all possess grossly enlarged oviducts. Reduction in ovarian lobe numbers or numbers of oviduct convolutions is found in many unrelated genera. Fusion of the ovisacs occurs in members of many families. There is no single peculiarity of reproductive morphology which is confined to a group of closely related species or genera (other than sinistral ovarian reduction in *Rheobatrachus silus*). Thus the diversity of reproductive morphology bears no taxonomic significance, and only reflects the parallel evolution of various reproductive modes.

(f) PREDICTIVE AND COMPARATIVE VALUE OF REPRODUCTIVE MORPHOLOGY

Salthe and Duellman (1973) were able to summarize their observations concerning the physical factors related to reproductive mode, in a number of generalized principles, some of which I have substantiated statistically in the course of my own work, as described earlier. Some of my observations on the relationships between reproductive mode and morphology can also be summarized in a similar way:

(1) the number of ovarian lobes is positively correlated with SVL

(2) the number of ovarian lobes is negatively correlated with egg diameter and tends to decrease from Mode I to Mode III

(3) the number of oviducal convolutions is usually positively correlated with SVL

(4) the number of oviducal convolutions is negatively correlated with egg diameter and tends to decrease from Mode I to Mode III

(5) oviduct width is positively correlated with egg diameter and tends to increase from Mode I to Mode III

(6) the tendency towards ovisac fusion increases from Mode I to Mode III.

In the case of species for which the reproductive mode is unknown or uncertain, it should therefore be possible to make predictions about the reproductive mode, based on the morphology of the reproductive system. If ova or mature oocytes are available, predictions can be made from these alone, but if for example only immature or post-ovipository females are collected so that the size and number of eggs are unknown, then the reproductive morphology may give some clues as to reproductive mode. For example, a frog may be 30 mm SVL, and possess five lobes per ovary and fifty convolutions per oviduct, whilst another of 35 mm SVL may possess unlobed ovaries and 20 convolutions per oviduct. One would predict that the first example is a Mode I species, and the second a Mode II or probably Mode III species. A species with completely united ovisacs is likely to be of Mode II or more probably Mode III, and one in which the posterior region of the *pars convoluta* is greatly enlarged is likely to exhibit foam-nesting.

The data which I have gathered describing the anuran reproductive

system also serve as a basis against which to compare the reproductive morphology of species of particular interest. The gastric brooding frog *Rheobatrachus silus* is one such species because of its bizarre reproductive behaviour. Modifications of *R. silus* which are associated with its breeding habits are likely to be centred around its digestive system, but the reproductive system is also modified and is largely typical of that of a moderately large Mode III species, possessing small numbers of ovarian lobes and oviducal convolutions, and broad oviducts. However, there are no unique features of the reproductive system, with the exception of the degree of fusion of its ovisacs, which unite only near their posterior ends. This feature is due to separation of the ovisacs by the urinary ducts, as discussed earlier, and bears no apparent relationship with the gastric brooding habit. The sinistral ovarian reduction of *R. silus* also appears to be unrelated to reproductive mode.

The reproductive system of *R. silus* illustrates two conclusions to be drawn from my study of anuran reproductive systems.

Firstly, it exemplifies the conservative nature of the female reproductive system. The reproductive biology of *R. silus* is perhaps the most divergent from the totally aquatic mode displayed, for example, by species of *Rana* and *Bufo*. Other species exhibit reproductive modes only marginally less bizarre, and yet their reproductive morphology is of the same general pattern as in most other members of the Anura, with only few exceptions such as *Sminthillus limbatus* in which one oviduct is vestigial (Griffiths, 1959) and *Nectophrynoides occidentalis* and *N. tornieri* in which the oviducts are unconvoluted. The reproductive system almost unvaryingly comprises paired, sacciform ovaries, and paired oviducts which extend along the length of the body cavity, consist of three distinct regions, and terminate in the cloaca. It is conservative in its general

morphology because in almost all species it serves the same function: to produce a number of eggs coated with mucopolysaccharide jelly and capable of being fertilized and developing outside the reproductive system.

Secondly, the reproductive system of *Rheobatrachus silus* illustrates that although the anuran reproductive system is conservative in form, it does display diversity in particular details, and this is associated with the physiological and developmental characteristics of reproductive modes, rather than with the behavioural characteristics. I have shown that despite their extreme diversity, anuran reproductive modes can be allocated to four categories, based on the amount of yolk stored in each egg and the proportion of development, prior to metamorphic climax, which is independent of external food sources. It is these factors which have apparently influenced specific features of reproductive morphology, so that instead of a wide diversity of morphology associated with the extreme diversity of reproductive mode (to which behavioural traits contribute significantly), there is limited but specific variation associated with the nature and development of the eggs. Thus the reproductive system of *R. silus* is characteristic of that of all other species with clutches of few, large eggs which are entirely independent of external energy sources.

APPENDIX I

SPECIMENS EXAMINED IN THE COURSE OF THIS STUDY

Abbreviations for Institutions:

AM	Australian Museum, Sydney
AMNH	American Museum of Natural History, New York
AUZ	Adelaide University Zoology Department
BM	British Museum (Natural History), London
CAS	California Academy of Sciences, San Francisco
CMNH	Field Museum of Natural History, Chicago
MCZ	Museum of Comparative Zoology, Harvard
RMNH	Rijksmuseum van Natuurlijke Historie, Leiden
SAM	South Australian Museum, Adelaide
UPNG	University of Papua New Guinea, Port Moresby
WAM	Western Australian Museum, Perth

(Number in brackets = number of individuals dissected)

LEIOPELMATIDAE

Ascaphus truei (1) AUZ, Touchet River, Oregon, U.S.A., Sept. 1970, N. Gradwell

Leiopelma hochstetteri (1) AUZ, Tokatea Ridge, Coramandel Peninsula, New Zealand, Feb. 1960, D. Baswell

PIPIDAE

Xenopus laevis (1) AUZ, no data

X. muelleri (1) AUZ, S. Africa

PELOBATIDAE

Pelobates fuscus (1) AUZ, Neusiedler-See-Gebiet (Ostafer) Germany, April 1969, Boeker

BUFONIDAE

Bufo marinus (1) AUZ, Qld

Nectophrynoides malcolmi (2) BM, 6-8 km S.E. of Goba, Balé Prov., Ethiopia

N. tornieri (2) BM, Amani, E. Usambara Mts, Tanzania, 1974, A.G.C. Grandison

LEPTODACTYLIDAE

Limnodynastinae

Adelotus brevis (2) AUZ, no data

Heleioporus eyrei (1) AUZ, Mt Barker, W. Aust., 1977, D. King

" " (1) AUZ, Forestfield, W. Aust., D. King

Lechriodus melanopyga (1) AUZ, Brown River, P.N.G., 29.xii.1977, K. Gowlett

Limnodynastes dorsalis (5) AUZ, 5-10 km W. of Narrinkap, S.W. Mt Barker, W. Aust., June 1976, D. King

L. dumerili (3) R. Torrens, St Peter's, S. Aust., 13.x.1981, M. Thompson

L. ornatus (1) Jabiru, N.T., Jan. 1981, M. Cappo

" " (1) AUZ, Conondale Ra., Qld, Jan. 1979, K.R. McDonald

L. peroni (1) AUZ, no data

L. tasmaniensis (numerous) S. Aust., various locations, dates and collectors

Megistolotis lignarius (1) AUZ, died in captivity

Neobatrachus ?centralis (3) SAM R20404, Roxby Downs, S. Aust., 11.ii.1981, M.J. Tyler

N. sp. (3) SAM R20214-8, Alice Springs, N.T., 27-28.i.1981, M. Gillam

Notaden melanoscaphus (1) AUZ, W. Aust.

" " (3) Jabiru, N.T., Jan.-Feb. 1981, M. Cappo

N. nichollsi (1) AUZ, 5 km N.E. of Broome, W. Aust.

Myobatrachinae

Assa darlingtoni (1) AUZ, no data

Crinia georgiana (1) AUZ, W. Aust., 27.vi.1980, D. King

Myobatrachus gouldi (1) WAM R19816, Dianella, W. Aust.

" " (1) WAM R22600, Narrogin, W. Aust., May 1964

" " (1) WAM R42963, West Popanyinning, W. Aust., 1972

" " (1) WAM R52494, 13 km E. of Guairading, W. Aust., 7.v.1975

" " (1) WAM R58108, Wanneroo, W. Aust., 1.xi.1977

Pseudophryne bibroni (1) Mitcham, S. Aust., 12.v.1980, P. Horton

" " (1) Fifth Ck, Montacute, S. Aust., 6.v.1981, J. Moller

Ranidella bilingua (1) AUZ, Port Essington, N.T.

R. riparia (4) Moralana Ck, Flinders Ras, S. Aust., 3.x.1982, P. Horton

" " (1) AUZ, no data

R. signifera (9) Balhannah, S. Aust., 4.x.1980 - 29.viii.1981, P. Horton

" " (1) Mitcham, S. Aust., 3.viii.1980, P. Horton

" " (2) AUZ, no data

Taudactylus acutirostris (1) AUZ, N. Qld, K.R. McDonald

T. diurnus (1) AUZ, K.R. McDonald

Uperoleia inundata (1) Jabiru, N.T., 2.ii.1981, M. Cappo

Rheobatrachinae

Rheobatrachus silus (21) S.E. Qld, various dates and collectors, held at various institutions

Eleutherodactylinae

Eleutherodactylus achatinus (5) SAM R25788-92, Tandapi, Ecuador

E. chloronotus (5) SAM R25807-11, 1-3 km E. of Papallacta, Ecuador, July 1977, J.D. Lynch

E. curtipes (6) SAM R25796-801, 1-3 km E. of Papallacta, Ecuador, July 1977, J.D. Lynch

E. devillei (5) SAM R25802-06, 1-3 km E. of Papallacta, Ecuador, July 1977, J.D. Lynch

E. walkeri (3) SAM R25812-14, Santo Domingo de los Colorados, Ecuador

DENDROBATIDAE

Phyllobates aurotaenia (3) SAM R13567, Choc6, Playa de Oro, Rio San Juan, Colombia

HYLIDAE

Cyclorana australis (2) AUZ, Kununurra area, W. Aust., Feb. 1977, M.J. Tyler *et al.*

" " (5) Jabiru, N.T., Jan. 1981, M. Cappo

" " (1) AUZ, Derby, W. Aust., early 1981, W.A. Dept Ag.

C. brevipes (1) AUZ, Townsville, Qld, Jan. 1981, K.R. McDonald

C. longipes (1) AUZ, 131 km S. of junction of Northern and Duncan Hwys, W. Aust., 24.i.1978, M.J. Tyler *et al.*

C. maini (2) SAM R20282-85, Alice Springs, N.T., 27/28.i. 1980, M. Gillam

Litoria alboguttata (2) AUZ, Townsville, Qld, 26.x.1980 & 3.i.1981, K.R. McDonald

L. bicolor (1) AUZ, Mitchell Plateau, W. Aust., 27.i.1978, M.J. Tyler *et al.*

" " (3) Jabiru, N.T., 31.i.1981, M. Cappo

L. caerulea (1) AUZ, Fitzroy R., Broome-Derby Rd, W. Aust., 17.ii.1980, M.J. Tyler *et al.*

Litoria caerulea (1) Cannon Hill, N.T., 27.iii.1980, G. Crook

L. chloris (1) AUZ, Conondale Range, Qld, Nov. 1976, M.J. Tyler *et al.*

" " (1) AUZ, no data

L. coplandi (1) AUZ, Crystal Ck, Mitchell Plateau, W. Aust., 17.ii.1979, M.J. Tyler *et al.*

L. dahli (numerous) Nankeen Billabong, N.T., 27.iii.1981, M. Cappo

" " (1) AUZ, Arnhem Hwy, nr Beaufort Hill, N.T.

L. eucnemis (1) SAM R20238-41, Johnston R. State Forest, Qld, 16.i.1981, K.R. McDonald

L. ewingi (1) Balhannah, S. Aust., 29.viii.1981, P. Horton

" " (1) AUZ, no data

L. inermis (4) Jabiru, N.T., 31.i.1981, M. Cappo

L. iris (4) SAM R9141, Ialibu District, Sthn Highlands, P.N.G., 30.x.1967

L. lesueuri (1) AUZ, no data

L. microbelos (1) AUZ, Mitchell Plateau, W. Aust., 29.i.1978, M.J. Tyler *et al.*

L. modica (2) SAM R6519, Busilmin, Star Mts, P.N.G., B. Craig

L. nannotis (2) SAM R20223-4, Mt Lewis, Qld, 25.i.1981, R.G. Zweifel & K.R. McDonald

L. nasuta (2) AUZ, Cooloola Nat. Pk, Qld, Nov. 1976, M. Davies & M.J. Tyler

L. pallida (5) Jabiru, N.T., Jan.-Feb. 1981, M. Cappo

L. peroni (2) AUZ, Conondale Ra., Qld, Jan. 1979

L. pratti (2) SAM R5714, Koko, P.N.G.

L. raniformis (1) AUZ, no data

L. rheocola (1) SAM R20247-8, Millaa Millaa, Atherton Tablelands, Qld, 16.i.1981, K.R. McDonald

" " (1) Mt Lewis, Qld, 25.i.1981, R.G. Zweifel & K.R. McDonald

Litoria rothi (1) AUZ, Roper R., 2 km W. of Mataranka H.S., N.T., 27.ix.1977, G. Crook

" " (1) AUZ, Mitchell Plateau, W. Aust., 31.i.1978, M.J. Tyler *et al.*

" " (5) Jabiru, N.T., Jan. 1981, M. Cappo

L. rubella (1) AUZ, Mitchell Plateau, W. Aust., Jan. 1978, M.J. Tyler *et al.*

" " (5) Jabiru, N.T., Jan.-Feb. 1981, M. Cappo

L. tornieri (1) Jabiru, N.T., 2.ii.1981, M. Cappo

L. wotjulumensis (1) AUZ, Crystal Ck, Mitchell Plateau, W. Aust., 17.ii.1979, M.J. Tyler *et al.*

Nyctimystes papua (4) SAM R5212, Okapa, P.N.G.

Phrynohyas venulosa (1) AUZ, Tunapuna, Trinidad, 17.ix.1967, N. Gradwell

RANIDAE

Arthroleptella lightfooti (1) CAS 85899, Plettenberg Bay, Cape Province, S. Africa, 23.iv.1958, Leech & Ross

Arthroleptis poecilonotus (1) CAS 153564, Nyabessan, 157 km S.W. of Ebolowa, Cameroun, 12.iv.1981, T. Papenfuss

Cacosternum boettgeri (1) AUZ, ca 32 km S.E. of Montague, S. Africa, 21.xi.1972, N. Gradwell

Rana cascadea (1) AUZ, Snowqualmie R., Washington, U.S.A., 30.viii.1969, N. Gradwell

R. grisea (1) no data

R. papua (1) AUZ, Brown R., P.N.G., 29.xii.1977, K. Gowlett

HYPEROLIIDAE

Afrixalus d. dorsalis (1) CAS 146260, Kade Agricultural Station, Ghana, 27.vii.1975, P. Williams

A. fornasini (1) AUZ, Durban, S. Africa, 15.xii.1972, N. Gradwell

A. quadrivittatus (1) CAS 141671, 1.3 km N. Kakamega at Lubao, Kenya, 5-6.vii.1976, R.C. Drewes

Callixalus pictus (1) CAS 145261, Upper Luvubu R., Itombwe Highlands, Uvira Terr., Kivu Prov., Zaire, 8-16.xii.1950, R.F. Laurent

Cryptothylax greshoffi (1) CAS 145279, Lowale R., Oneme Chadala, Lodja Terr., Sankuru Prov., Zaire, 20.viii.1959, Poelman

Hyperolius marmoratus (1) AUZ, Belair, Durban, S. Africa, 17.xii.1971, N. Gradwell

Leptopelis bocagei (1) CAS 141453, Chemelil, Kisumu Dist., Kenya, May - June 1976, L. Hoevers

L. macrotis (1) CAS 103699, Kade, Ghana, 12.i.1966, T. Papenfuss

RHACOPHORIDAE

Chiromantis petersi (1) CAS 130629, nr El Wak, Mandera Dist., Kenya, 13.vii.1971, R.C. Drewes

C. xerampelina (1) CAS 153644, 8 km W. of Ganda, Kilifi Dist., Kenya, 9.iv.1981, S. Reilly

MICROHYLIDAE

Asterophryinae

Asterophrys turpicula (1) RMNH 16655, Aifat, Vogelkop, Irian Jaya, 13.viii.1953, M. v.d.Nieuwenhuiren

Barygenys nana (1) AM R22802, Fungoi, Kaironk Valley, Schrader Mts, P.N.G.

Hylophorbus r. rufescens (1) UPNG 5714, Manga, Huon Peninsula, P.N.G.

Phrynomantis humicola compta (1) SAM R9387, Kaironk Valley, Schrader Mts, P.N.G., R. Bulmer

P. h. humicola (1) AMNH 66266-70, Kotuni, Mt Otto, P.N.G., 18.viii.1959, 6th Archbold Expedition

P. lateralis (1) MCZ 59000, Lae, P.N.G., 12.ii.1966, F. Parker

" " (1) UPNG 2621, Alotau, P.N.G.

" " (1) UPNG 5202, Alotau, P.N.G.

Phrynomantis lateralis (1) Taraka, 4 km N. of Lae, P.N.G., 10.i.1982, T.C. Burton & R. Stocks

P. louisiadensis (1) AMNH 60135-43, Rossel Island, P.N.G., Oct. 1956, R.F. Peterson

P. robusta (1) MCZ 81688, Derongo, P.N.G., 6.iv.1969, F. Parker

P. stictogaster (3) SAM R20887,89&90, Okapa, P.N.G., J.Y. Hancock

P. wilhelmana (1) AMNH 65868-86, Mt Wilhelm, P.N.G.

" " (1) MCZ 59895, Kogi, Suai Ra., P.N.G., 6.iii.1965, F. Parker

" " (1) Tomba, Mt Hagen, P.N.G., 5.i.1982, T.C. Burton

Xenobatrachus rostratus (2) SAM R9386, Kaironk Valley, Schrader Mts, P.N.G.

Xenorhina bouwensi (1) RMNH 16658, Kigonmedip, Ok Sibil Valley, Star Mts, Irian Jaya, 1959, Netherlands Star Mts Expedition

Sphenophryninae

Cophixalus darlingtoni (1) Tomba, Mt Hagen, P.N.G., 5.i.1982, T.C. Burton

C. neglectus (1) AUZ, Mt Bellenden Ker, Qld, 27.ii.1977

C. ornatus (1) South Bell Peak, Mallon Thompson Range, Qld, 6.xi.1980, K.R. McDonald

C. parkeri (1) SAM R5604, Kaironk Valley, Schrader Mts, P.N.G., R. Bulmer

C. riparius (1) SAM R5216, Okapa, P.N.G.

Copiula fistulans (1) SAM R14241, Agenchambo nr Popondetta, P.N.G., July-Oct. 1964, B.J. Brock

" " (1) Taraka, 4 km N. of Lae, P.N.G., Dec. 1981, R. Stocks

Oreophryne biroi (1) SAM R10899, Karrimui, P.N.G.

Sphenophryne schlaginhaufeni (1 egg mass) Trauna Ridge, 13 km N.E. of Baiyer River, P.N.G., 3.i.1982, T.C. Burton

Dyscophinae

Calluella guttulata (1) CMNH 143960, Kuala Tahan, Pahang, Malaya, 14.x.1958, E.R. Alfred

Microhylinae

Chaperina fusca (1) CMNH 77253, Deramakot, Kinabatangan Dist., N. Borneo, R.F. Inger

Kaloula pulchra (1) CMNH 175952, Siracha, Cholemlarb, Chon Buri, Thailand, E. Taylor

Microhyla heymonsi (1) CMNH 186029, Bukit Lanjan, Selangor, Malaya, Lim & Tang

APPENDIX II

HORTON, P. 1982. Precocious reproduction in the Australian frog *Limnodynastes tasmaniensis*. *Herpetologica* 38:486-489.

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Herpetologica, v. 38 (4), pp. 486-489, December 1982

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APPENDIX IV

HORTON, P. and M.J. TYLER. 1982. The female reproductive system of the Australian gastric brooding frog *Rheobatrachus silus* (Anura: Leptodactylidae). *Aust.J.Zool.* 30:857-863.

Horton, P. and Tyler, M.J. (1982) The Female Reproductive System of the Australian Gastric Brooding Frog, Rheobatrachus silus (Anura: Leptodactylidae).
Australian Journal of Zoology, v. 30 (6), pp. 857 – 863, 1982

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ADDENDUM TO THE THESIS :

"THE FEMALE ANURAN REPRODUCTIVE SYSTEM IN RELATION TO REPRODUCTIVE MODE"

by

PHILIPPA HORTON

PART ONE:

ANALYTICAL PROCEDURES

A. X^2 TEST: EXTENT OF OVISAC FUSION IN SPECIES OF REPRODUCTIVE MODES I, II AND III (Table 11, p.72 of thesis)

As one examiner noted, this test cannot be undertaken on the data presented, because some of the expected frequencies are smaller than the required minimum of five (Campbell, 1974). I propose deleting the test and leaving the data in the simple form presented in Table 11; the differences in observed and expected values are clear enough not to require a statistical test of significance.

B. SINGLE-FACTOR ANALYSIS OF VARIANCE FOR COMPARISON OF MEANS AMONG MODES I, II AND III

Values of the F-statistic are given for each case; significance at the 5% level is represented by: *, and at the 0.1% level by: ***. Page numbers for the incorporation of each result into the thesis are given in brackets.

Snout-vent length	:	$F_{2,101}$ =	4.74 *	(p.37)
Log (10x egg diameter)	:	$F_{2,86}$ =	137.09 ***	(p.41)
Log (ovarian complement)	:	$F_{2,86}$ =	118.55 ***	(p.42)
Log (number of lobes)	:	$F_{2,99}$ =	44.22 ***	(p.50)

Log (number of convolutions): $F_{2,80}$ = 33.31 *** (p.59)

Oviduct width : $F_{2,57}$ = 9.93 *** (p.65).

The results of these tests support my findings as already described.

C. A DEFENCE OF THE USE OF SINGLE SPECIMENS

One examiner questioned the use of data from single specimens of many species in the comparisons and statistical analyses that I made. Ideally I would have preferred to have used data only from those species of which I examined several specimens. However, I included data from single or few specimens in order to provide as many examples as possible from each of the three reproductive modes concerned. Had I excluded all data from species with solitary or few individuals, then I would have had no comparative information at all for Mode II and little for Mode III; only Mode I would have been adequately represented. My justification for the inclusion of these data is as follows:

For each morphological feature of the ovary and oviduct, I examined that feature in several species of which I had numerous specimens. By doing so I was able to determine the likely degree of intraspecific variability of that feature. Whilst each feature exhibited variability within a species, nonetheless I found that the degree of variability was small in comparison with the overall variability amongst all species I examined. Thus for example the range of number of ovarian lobes was 1 - 26. Within that range I found intraspecific variation such as illustrated in *Myobatrachus gouldi* in which both left and right ovaries were unlobed in all five specimens examined, in six individuals of *Eleutherodactylus chloronotus* in which the ovaries were unlobed or bilobed, and in 35 individuals of *Limnodynastes tasmaniensis* in which the number ranged from three to five, with one ovary

in one individual bilobed. Species with larger numbers of lobes tended to show greater variability, as observed in seven individuals of *Litoria rothi* (6-10 lobes, mean 8.1), and eight individuals of *Cyclorana australis* (18 - 26 lobes, mean 22.1). But the majority of species for which I sampled single specimens were of small size or represented Modes II and III, and such species generally exhibit low numbers of lobes. Despite the greater variability in those species exhibiting large lobe numbers, the figures are not randomly distributed throughout the total range (1 - 26), but occupy a discrete portion of it, so that the number of lobes from even a single specimen should give an indication of the magnitude of lobe number for the species. If comparisons were being made between different species with similar numbers of lobes then one specimen may not be sufficient, particularly for species with large lobe counts; however, in my thesis I make no comparisons between individual species, as I discuss below.

Similar arguments apply for number of oviduct convolutions and oviduct width, and I give examples in the main body of the thesis of convolution numbers and widths for species of which I dissected several specimens (pp.57 and 64). As described on p.104 I found no intraspecific variation in the degree of ovisac fusion in 17 species of which I dissected more than one specimen, so it is almost certain that the single individuals of the remaining species were representative for those species.

Thus I considered the variability of these morphological features sufficiently insignificant to warrant comparison of each feature between groups of species, and to allow the inclusion of data from single or few specimens because they were most likely to be reasonably representative for those species.

In addition, I was seeking the presence of any trends in the variation of these morphological features, rather than absolute differences between individual species, so that if a single datum happened to be unusual for that species, it would have represented a local disturbance in the trend rather than its demolition. The only instances in which I subjected individual species to analysis were those in which several specimens of that species were available, for example *Rheobatrachus silus*. In all other instances I made comparisons among Modes I, II and III, each of which had an acceptable sample size of data. In effect, I have made comparisons between series of observations, each series taken from individuals of the same reproductive mode rather than of the same species.

The parameters snout-vent length, egg diameter and ovarian complement are also variable within a species, but again I used values of these from single or few specimens because the comparisons I made were between reproductive modes, not individual species, and because I was looking at trends rather than absolute differences.

PART TWO:

THE FEMALE VERTEBRATE REPRODUCTION SYSTEM AND ITS RELATION TO REPRODUCTIVE MODE

INTRODUCTION

Reproductive diversity in vertebrates ranges from the laying and abandonment of shell-less eggs which are fertilized and develop externally, to the retention of eggs with internal fertilization, placentation, and extended intra-uterine development. As I have outlined in my thesis, almost this entire range of patterns of reproduction occurs amongst the Anura alone, the major exception being the absence of placentation in the only known viviparous species.

I have demonstrated an apparent association between the variations in morphology of the female anuran reproductive system and the broad category of reproductive mode of the species concerned. It is known that at least the female reproductive tract differs significantly in morphology among different vertebrate groups. Are there any disernible trends among these different morphologies, and perhaps also in the vertebrate ovary, that can be correlated with reproductive mode? If so, are they comparable with the changes in morphology found among anurans?

Data on female reproductive morphology are distributed widely in the literature. Most contributors have devoted attention to separate classes

of vertebrates, unless making specific cytological comparisons in which case the vertebrates may be considered as a whole. There has not been a broad review of female vertebrate reproductive morphology at a gross structural level. To place my findings on the Anura in perspective, I have undertaken this review and present the synthesis in the following pages. One limitation of such a review is that data on similar morphological features are not available for all vertebrate classes, therefore my descriptions for each group are not completely comparable.

I consider firstly the ovary and how the anuran ovary compares with that of other vertebrate groups, and secondly the reproductive tract, also comparing anurans with other vertebrates.

A. THE OVARY

i) Ovarian Form Among Vertebrates

a) Cyclostomes: Lampreys possess a single, mid-dorsal ovary formed as a result of fusion of the customary pair (Wake, 1979). It is lobate and extends the entire length of the body cavity which it fills and distends when mature (Dodd, 1977). Hagfish also possess only one elongate ovary, not formed by fusion but by atrophy of the left ovary at an early stage of development (Dodd, 1977). The largest and oldest of the oocytes lie along the border of the mesovarium, parallel to the intestine, each suspended by a stalk (Dodd, 1977). Thus the hagfish ovary has no particular shape; it is more or less a row of oocytes. Cyclostome ovaries are not hollow, but are a solid mass of follicles (Wake, 1979).

b) Elasmobranchs: These animals possess a saccular ovary, often slightly hollow. In general, egg-laying species have large, paired,

functional ovaries, whereas viviparous sharks have a functional right ovary only, and viviparous rays a functional left ovary only (Wake, 1979).

c) Teleosts: The ovaries are paired in many species, but there is only a single functional ovary in some (Wake, 1979); for example, almost all viviparous teleosts possess a single, median ovary (Wourms, 1981). Loss of an ovary in teleosts is due either to fusion of the paired rudiments, or to the arrested development of one of them (Brambell, 1956). The ovaries may be solid or hollow organs, the hollow state being characteristic of viviparous species (Wourms, 1981). Typically the ovary of fishes is elongate, and during the breeding season its surface assumes a beaded appearance as it becomes distended with maturing oocytes. In viviparous and ovoviviparous species smaller numbers of ooctyes mature at any one time, so the ovary often assumes the appearance of a bunch of grapes (Franchi, 1962). After spawning, fish ovaries rapidly shrink and may even be reduced to thin, thread-like organs (Franchi, 1962). Dodd (1977) remarked, "Bony fishes, especially teleosts, show a greater degree of diversity in reproduction than any other vertebrates and this is reflected by their range of ovarian structure. In teleosts, in which viviparity has arisen independently in at least eight of the large groups, ovarian structure may become markedly modified since viviparity invariably involves the ovary in a gestational role." However, Dodd (1977) went on to describe differences in follicular and epithelial structure; it appears that there are almost no particular interspecific variations in gross morphology documented for the teleost ovary. Hoar (1957) noted that the arrangement of follicles within the supporting tissue of the ovary varies greatly in different groups, and different morphological types can be distinguished, based on follicular arrangement. The diagrammatic illustrations of the fish ovaries that he presented do not indicate any lobing.

d) Amphibians (caudates and caecilians): The ovaries are paired and hollow (Wake, 1979). Those of caecilians are unlobed, narrow and elongate (Wake, 1968), and those of caudates are slightly elongate (Wake, 1979).

e) Reptiles: The ovaries are paired, compact, hollow, and irregularly ovoid in shape (Wake, 1979), or elongate in snakes (Jones, 1978). The ovaries of turtles are positioned symmetrically, but in lizards and snakes they are usually situated asymmetrically, with the right anterior to the left, and usually larger than the left in some snakes (Fox, 1977). Dodd (1977) commented that most of the differences between the ovaries of different species appear to be superficial and due mainly to differences in numbers of large vitellogenic oocytes present in the ovary.

f) Birds: The ovaries of birds are compact and hollow (Wake, 1979). As oocytes accumulate yolk, their rapid gross enlargement causes them to project from the surface of the ovary and ultimately to become pedunculate (Dodd, 1977); thus the ovary resembles a bunch of grapes at different stages of ripening. There are always two ovarian primordia, but in most species only the left matures (Dodd, 1977). However, both ovaries commonly mature in many species of the Falconiformes, and there is evidence of two ovaries in species belonging to at least 16 orders in which the norm is usually accepted to be one ovary (Gilbert, 1979). Kinsky (1971) discovered that the Kiwis (Apterygiformes) are the only group of birds in which paired ovaries occur consistently, and both ovaries are usually functional, with ovulation occurring alternately from the two if more than one egg is laid in the same season.

g) Mammals: Mammalian ovaries are small, compact and cellular throughout (Wake, 1979), except in the monotremes in which the medulla contains large lymph spaces (Brambell, 1956). They are paired and

approximately equal in size except in the platypus in which the right is atrophied (Hughes and Carrick, 1978), certain bats in which the left shows atrophy, and some Odontoceti, especially Delphinidae, in which ovulation occurs more frequently, or consistently, in the left ovary (Harrison and Weir, 1977). In mammals in which multiple ovulation is the rule (e.g. sow, rat, rabbit) the pedunculate follicles and corpora lutea give the ovary a grape-like appearance; in others (e.g. horse, sheep, primates) the regular outline of the ovary is only locally disturbed (Harrison and Weir, 1977).

ii) Trends in Vertebrate Ovarian Form and a Comparison with Anurans

The appearance of the ovary differs dramatically among vertebrates. Factors such as reproductive state, particularly whether pre- or post-ovulatory, and nutritional state, have considerable influence, largely in terms of ovarian mass relative to body mass. These are seasonal or environmental factors, but there are also factors associated with the nature of the animal itself which alter gross ovarian morphology between vertebrate groups. Two of the most obvious of these are body shape and the reproductive strategy of the species in question. I will consider these in turn.

Body form has its main influence in those species in which it is highly modified. Thus among the amphibians, as described in the previous section, the ovary is a pendulous sac in anurans, is slightly elongate in the more slender-bodied caudates, and is narrow and elongate in the vermiform caecilians. Similarly among reptiles, the ovary is ovoid in most lizards and turtles, but elongate in those with the most elongate bodies: snakes. Such variety in shape does not occur in birds or mammals, perhaps attributable to the fact that their body form, particularly abdominal proportions, is relatively more uniform.

Reproductive mode has a significant bearing on ovarian morphology, as a result of the relative sizes and numbers of eggs produced per reproductive effort. For example, the lamprey is semelparous and produces a large number of small eggs (Ballinger, 1978), and its ovary is a vast lobed structure filling the entire body cavity at maturity, thus enabling the animal to produce thousands of eggs. In contrast, the hagfish ovary is little more than a string of oocytes, as these animals produce relatively few large eggs with copious yolk (Ballinger, 1978). Like lampreys, most teleosts are oviparous, producing vast numbers of small eggs (Ballinger, 1978), and the ovaries are massive structures which may distend the abdominal cavity when mature. In contrast, the simple nature of the caecilian ovary reflects their relatively low fecundities (4-15 enlarged oocytes per ovary in some species; Wake, 1968) associated with considerable parental care, and ovoviviparity and viviparity in some species.

With the evolution of the amniote egg in reptiles, reproductive patterns became considerably modified in comparison with those of the non-amniote groups (Ballinger, 1978). In particular, reptiles produce large, yolky eggs, and fecundity is greatly reduced, with the largest clutches probably those recorded for marine turtles - for example, about 100 eggs per clutch in the Loggerhead and Green Turtles (Cogger, 1983). Thus their ovaries are compact and ovoid or elongate, and apparently never massive and lobed. The ovaries of birds are also relatively small, compact and unlobed, as again the number of eggs produced per clutch is small (one or two to a dozen, rarely more; Lack, 1968), although gross seasonal enlargement of the ovaries is seen due to the immensely yolky nature of the eggs produced. The ovaries of mammals are compact and smaller relative to body size than in non-mammalian vertebrates (Dodd, 1977), reflecting the production of a small number of very small almost yolkless eggs, at most up to 20 in rodents (Ballinger, 1978), with viviparous development of the

young and extended parental care.

In general, the vertebrates display some of the tendencies which I observed amongst the Anura, with regard to ovarian morphology in association with reproductive mode. For example the Mode I anuran ovary corresponds morphologically (large and lobed) with that of the lamprey. It is also comparable with the oviparous teleost ovary, except that I can find no published account of lobing in fish ovaries. Vertebrates which produce smaller numbers of larger, yolkier eggs possess ovaries similar to those of Modes II and III anurans - more compact with few or no lobes, and seasonally enlarged with mature oocytes. The only anuran possessing ovaries comparable with those of mammals and other viviparous vertebrates is the single known viviparous species *Nectophrynoides occidentalis*. In this species the ovaries are small, simple sacs (Angel and Lamotte, 1944), and are never grossly enlarged because the oocytes produced are invested with very little yolk.

Ovarian asymmetry apparently has arisen independently on numerous occasions among the vertebrates. In the lamprey the morphological arrangement is not strictly asymmetrical since both ovaries fuse and contribute to oogenesis. In these semelparous animals ovarian fusion may help to maximise reproductive effort as the entire body cavity becomes an egg chamber prior to spawning and death. Functional asymmetry has occurred by the lack of development of one ovary in viviparous teleosts, of the left ovary in hagfish, viviparous sharks and some bats, and of the right ovary in viviparous rays, most birds, the platypus, and some toothed whales. No satisfactory explanation has been proposed for any of these examples of ovarian asymmetry. The suggestion that a single functional ovary in birds reduces the possibility of the large eggs occluding following ovulation is negated by the presence of two functional ovaries in the

Kiwi, which lays the largest eggs known, relative to its body weight (Harrison, 1978). Spatial asymmetry of the ovaries occurs in snakes and lizards, but in every case both ovaries are functional.

Functional ovarian asymmetry is not known to occur in oviparous species which produce large numbers of small eggs. It is the province of viviparous species or those which produce a small number of relatively large, yolky eggs. Perhaps a reduction in the number of eggs produced per reproductive effort predisposes the species to ovarian asymmetry, with one ovary capable of producing all of the eggs. The only example that I encountered of ovarian asymmetry among anurans was likewise in a species which produces a small number of large eggs: the Mode III species *Rheobatrachus silus*. In this frog both ovaries are functional, but I found a significant trend towards reduction of the left ovary in terms of number of lobes and number of vitellogenic oocytes. Perhaps this species is an indication that functional ovarian asymmetry might eventually evolve in the Anura, as it has in so many other vertebrate groups.

B. THE REPRODUCTIVE TRACT

i) Morphology of the Oviduct Among Vertebrates

a) Cyclostomes: There are no ducts leading from the gonads of cyclostomes; the eggs are shed into the coelom and then into the aquatic environment via abdominal pores (Wake, 1979).

b) Elasmobranchs: The oviducts of elasmobranchs are fused anteriorly so that a single opening to the coelom is present. Each oviduct has an anterior enlargement, the shell gland. It is best developed in oviparous forms and secretes the horny egg case that protects the egg. The

posterior one-third to one-half of each oviduct is enlarged to form a uterus, which joins the cloaca separately from that of the other side. The uteri are best developed in ovoviviparous and viviparous forms (Wake, 1979). Among the viviparous rays the right oviduct undergoes varying degrees of reduction or loss (Wourms, 1981). Wake (1979) gives an illustration of the female reproductive system of a viviparous shark, the spiny dogfish, which shows that the oviduct is unconvoluted.

c) Teleosts: The oviduct, or gonoduct, of teleosts is a posterior continuation of the ovarian tunic, thus the ova are not discharged into the peritoneal cavity following ovulation (Hoar, 1969). The duct terminates in a genital pore or urinogenital papilla (Wake, 1979). Even though it serves the same function, the teleost gonoduct is not homologous with the oviduct of other fishes and other vertebrates in which the oviduct is a modified Müllerian duct, i.e. renal in origin (Wourms, 1981). According to Wake (1979), teleost oviducts are often fused for most of their lengths. In certain teleosts - Salmonidae, Galaxidae and a few other families - the oviducts degenerate in whole or part so that the ova pass into the peritoneal cavity and thence through pores or funnels, depending on the degree of degeneration, to the exterior (Hoar, 1969). The teleost oviduct is apparently not convoluted nor differentiated into externally distinguishable regions.

d) Amphibians (caudates and caecilians): In the caudates the oviducts remain separate, and they become expanded and coiled in the breeding season (Wake, 1979); an illustration given by Wake (1979) of the female reproductive system of *Necturus* shows about 70 convolutions of the oviduct. Harrison Matthews and Marshall (1956) noted that in *Triturus viridescens* the oviducts become narrower and less convoluted with the shedding of eggs in early summer. The posterior ends of urodele oviducts

are often slightly enlarged and act primarily to store ova before egg-laying (Wake, 1979). In caecilians the oviducts also remain separate (Wake, 1970), but they are usually straight tubes; they enlarge but do not become convoluted in the breeding season (Wake, 1979). Caecilian oviducts are extremely elongate, extending from their anterior opening near the heart posteriorly to the cloaca (Wake, 1970).

e) Reptiles: The oviducts of reptiles remain separate and join the cloaca independently (Wake, 1979). The oviducts enlarge and coil as the breeding season approaches (Wake, 1979); an illustration given by Wake (1979) of the female reproductive system of a turtle shows about 45 convolutions of the oviduct. Fox (1977) quoted examples of lizard species in which the oviducts become highly convoluted and thick-walled in the breeding season but return to a straight, thin-walled condition afterwards, and of other species in which the oviducts remain highly convoluted once developed, regardless of the season. Lizards in general have paired oviducts, each comprising an anterior infundibulum, a thin-walled fallopian tube, a thicker-walled uterus incorporating shell glands, and a short, narrow, posterior vagina (Cuellar, 1966; Fox, 1977). The oviducts of adult alligators are convoluted anteriorly but straighten at a position ventral to the kidneys (Fox, 1977). Loss of the left oviduct (either total absence or reduction to a vestige) is known in a) six snake genera and one legless lizard genus (*Anniella*), all burrowing species with no specific latitudinal limitations in their distributions, and b) 13 species of four skink genera, all of which are fully limbed and tropical in distribution (Greer, 1977). Impaction of eggs descending both oviducts in a narrow abdomen, or an undesirable increase in girth, may have led to the loss of an oviduct in members of the first group. Members of the second group may have lost an oviduct in conjunction with a reduction in brood size to one only and as part of a life history found in many tropical lizards - of maturity at an

early age and frequent brood production (Greer, 1977); in these animals a second oviduct may be superfluous. In all of these taxa it is the left oviduct which has been lost, perhaps because in squamates it is the shorter of the two oviducts, hence its loss is less likely to be disruptive to development (Greer, 1977).

f) Birds: The oviducts of birds arise in the embryo as paired structures, but in most species only the left develops and differentiates fully into a functional adult organ (Gilbert, 1979). Paired oviducts in adult birds are rarer than paired ovaries. As with the ovaries, paired oviducts predominate in the Falconiformes although they have also been found in several other orders; however, the evidence for a functional right oviduct is almost non-existent (Gilbert, 1979). In Kiwis, in which paired ovaries occur consistently, only the left oviduct is functional, and is placed so as to admit ova from either side; vestigial right oviducts occur only rarely (Kinsky, 1971). The regions of the oviduct in birds are more specialized than in reptiles, for the secretion of various layers around the egg (Wake, 1979). Interspecific differences in the oviducts of birds, where they exist, are often of minor nature and their functional significance is largely unknown (Gilbert, 1979). The avian oviduct is divided into five regions: an infundibulum, a long and highly distensible magnum, an isthmus, a shell gland or "uterus" where the calcareous outer shell is deposited, and a short vagina (Gilbert, 1979; Wake, 1979). In the breeding state the oviduct is greatly enlarged - it lengthens, broadens, and is thrown into folds. The number of oviducal convolutions formed in the breeding season is relatively small, in the region of about 5-15, and the folds are very loose (pers. obs.). In the non-breeding condition the adult oviduct is similar to that of the juvenile: a narrow tube, i.e. it regresses following laying (Gilbert, 1979).

g) Mammals: As in all other vertebrates, the oviducts of mammals form in the embryo as paired and entirely separate structures (Eckstein and Zuckerman, 1956). In monotremes the ducts remain separate in adult life. The infundibular funnels lead into relatively long but poorly convoluted fallopian tubes. The paired, thicker-walled uteri enter separately into a long unpaired median urinogenital sinus, there being no vagina in monotremes (Hughes and Carrick, 1978). Although in the platypus the right ovary is universally rudimentary, both right fallopian tube and right uterus are only marginally less developed than on the left side (Hughes and Carrick, 1978); however, only the left oviduct is functional (Griffiths, 1978). In the echidna, both oviducts are functional (Griffiths, 1978).

In marsupials the oviducts consist of a short fallopian tube, uterus, and vagina; as in monotremes they remain separate in adult life, and the vaginae open into a median urinogenital sinus (Frye, 1977). The ureters of marsupials run ventro-medially from the kidneys to drain directly into the bladder, and in doing so pass medially between the two lateral vaginae which are thereby unable to unite (Tyndale-Biscoe, 1973). In fact the two lateral vaginae do become united anterior to the ureters, at the base of the two uteri, and a median vaginal cul-de-sac is formed. At parturition a birth canal forms in the connective tissue between the cul-de-sac and the urinogenital sinus, through which the foetus passes. In most marsupials this state is a transient one and reforms at each birth, but in most kangaroos and wallabies, and in the honey possum *Tarsipes rostratus*, it becomes lined by epithelium and remains patent after the first birth, so that a condition very similar to the eutherian (*q.v.*) is seen (Tyndale-Biscoe, 1973).

Among the eutherian mammals there is a marked tendency for the oviducts to fuse in a caudo-cranial direction (Eckstein and Zuckerman, 1956). Each oviduct consists of a fallopian tube, uterus, cervix and vagina.

Almost all eutherian mammals, with the possible exception of certain Xenarthra, e.g. sloths, possess a single median vagina formed by fusion of the pair, but they differ among each other in the degree of development and fusion of the uterine and cervical segments (Eckstein and Zuckerman, 1956). The most primitive arrangement, of two separate uteri and cervical canals, is found in the rabbit, aardvark, elephant, some bats and many rodents. A slightly more advanced degree of fusion is represented by the guinea pig, in which more caudal parts of the cervical segment are fused to form one lumen. In other species the process of fusion extends even further and leads to the formation of a common uterine cavity. The two uteri fuse posteriorly and enter the vagina via a common cervix in the bipartite uterus of most carnivores, lagomorphs, some bats and rodents, and some ungulates. A greater degree of fusion is found in the bicornuate uterus of most ungulates, some carnivores and bats, insectivores and whales. In the Xenarthra (with a few exceptions) and primates, fusion is complete to form a single median uterus with no lateral horns: the simplex uterus (Eckstein and Zuckerman, 1956; Wake, 1979).

Beck and Boots (1974) discussed the nature of the fallopian tube (which they referred to as the oviduct) among mammals. They described four main regions of the fallopian tube: the infundibulum, the ampulla, which forms the anterior two-thirds of the tube, the isthmus, narrower than the ampulla, and posteriorly the uterotubal junction. They then described eight different types of fallopian tube found in mammals. In types 1 and 2 (found in primates) the tube is relatively straight except for a small bend at the anterior end. In types 3 and 4 (found in ungulates, lagomorphs, the opossum and pig) the tube is loosely coiled and forms a large bend at the anterior end. In type 5 (found in carnivores and the elephant) the tube is tightly coiled and follows a tortuous course around the ovary. In type 6 (mustelids, some squirrels) the tube is highly

convoluted and describes almost a complete circle around the ovary. In type 7 (rodents) the ampulla and isthmus lie in a coiled mass around one side of the ovary, and in type 8 (bat, shrew) the tube is extremely short and large in diameter and is relatively unconvoluted (Beck and Boots, 1974).

ii) Trends in the Form of the Vertebrate Oviduct and a Comparison With Anurans

As with the ovary, the reproductive tract of vertebrates is liable to alter drastically in form apparently influenced by environmental factors and the reproductive state of the individual. In oviparous species with eggs which are invested with thick protective layers, the oviducts enlarge greatly prior to ovulation as glands in the walls store substances to be secreted around each ovum. Regions of the viviparous mammalian oviduct undergo well-documented cyclical changes according to reproductive state, although changes to gross morphology are probably not as dramatic as in oviparous vertebrates. Body form does not appear to have such a significant effect on the oviducts as on the ovaries, as by and large the oviducts are elongate tubes in all vertebrates, except in some groups in which they are highly modified according to reproductive strategy. Undoubtedly though, extreme body form does bear some influence, as for example in the caecilians in which the oviducts are extremely elongate.

The major factor influencing oviduct morphology among vertebrates is reproductive mode, and its effect is dramatic. There is a strong trend for increased specialization and regionalization of the oviduct from lower to higher vertebrates. To begin with, among the cyclostomes there is no oviduct at all and eggs are simply shed into the coelom, to be squeezed out through abdominal pores which become patent at oviposition. In jawed fishes a seemingly less haphazard arrangement has evolved, with the appearance of oviducts to convey eggs to the external environment. They are relatively

simple structures in the teleosts, but somewhat more complex in the elasmobranchs in which they are involved in the deposition of horny cases around the eggs, or in gestation of the young in ovoviviparous and viviparous species. The elasmobranchs display a unique feature among vertebrates with two functional oviducts, and that is of anterior fusion of the pair to form a single ostium. With the relatively low fecundities of even oviparous elasmobranchs (Ballinger, 1978) it is clear that a single ostium is adequate to accomodate all ova following oviposition. The involvement of the ovary in gestation of the embryos in viviparous teleosts probably explains the lack of specialization of the oviduct in these species. Caudates display a more distinctive oviducal form than the teleosts; the oviduct becomes thick-walled and convoluted, i.e. highly glandular, prior to ovulation, following which it secretes layers of gelatinous material around the eggs, and there is often a slightly enlarged area at the posterior end to accommodate the eggs prior to oviposition. Unlike the oviducts of caudates those of caecilians do not become convoluted in the breeding season; many species retain the developing young in the oviducts (Wake, 1979), so it is not necessary for the oviduct to be a massive glandular structure capable of secreting thick protective layers around each egg.

The evolution of the cleidoic egg has involved specialization and differentiation of successive regions of the oviduct in reptiles and birds (Gilbert, 1979). In both groups the oviduct is divided into a fallopian tube (itself divided into two regions in birds), a distinctive uterine region with shell glands, and a short vagina, not apparent in lower vertebrates. Again in both groups the oviducts convolute in the breeding season, as they become increasingly glandular and thicken and lengthen. Loss of one oviduct occurs in some reptiles, correlating either with their narrow, elongate body form and burrowing habit, or with a minimal fecundity

of one young per reproductive effort, in which case a single oviduct would suffice. A single functional oviduct is the usual state in most or all birds, as one would expect since most possess only one functional ovary. Clearly the solitary oviduct is capable of accommodating the small number of eggs produced by a female bird.

As a group the mammals show the most diverse array and the most specialized of oviducal structures. The egg-laying monotremes display the most primitive oviducal form, resembling that found in lower vertebrates, with not even a vagina apparent. The platypus parallels the situation in birds, with only one functional oviduct serving the one functional ovary. The oviducts of marsupials are somewhat more specialized, and exhibit some degree of fusion, although not of oviducal components themselves but of lateral offshoots from the vaginae due to the obstructive presence of the ureters. Such fusion permits the formation of a single birth canal for the few or solitary young. In eutherian mammals the ureters run laterally around the reproductive tract before draining into the bladder, so they do not hinder fusion of the vaginae, which are completely united in most if not all species. The fallopian tube is a relatively minor segment of the eutherian oviduct, and in general the further the uteri are united, the simpler and less convoluted are the fallopian tubes. It is the uterine portion of the oviduct which is the most prominent, in keeping with its role in long-term support and nutrition of the developing young. There is a trend for the uteri to unite to form a single chamber, and this trend correlates fairly closely with a reduction in the number of offspring produced in a single pregnancy (Frye, 1977).

Particular trends in oviducal form among vertebrates may be compared with those I found amongst the Anura. Perhaps the most striking vertebrate trend is that towards specialization and regionalization of the oviduct.

However, this is not seen within the Anura, members of which all possess an oviduct composed of similar regions: an ostium, pars recta, pars convoluta and ovisac, although these may be differently proportioned in different species. The only significant differentiation of the anuran oviduct that I observed was the gross enlargement of the posterior-most region of the pars convoluta in foam-nesting species. Another generalized trend among vertebrates is for a reduction in the degree of convolution of the oviduct from species producing many eggs to those producing few, and from oviparous to viviparous species. Thus for example there are numerous convolutions in the oviduct of a caudate which lays numerous, small eggs, but few in birds which produce only a few, large eggs, and none in ovoviviparous or viviparous caecilians, and viviparous sharks. This is a trend which I found to be quite distinctive amongst anurans, with numbers of convolutions ranging from more than 150 in species producing numerous small eggs to fewer than 10 in those producing a small number of large eggs, and few or no convolutions in the ovoviviparous and single viviparous species. As I suggest elsewhere in my thesis, this trend is probably associated with a decreasing need for vast quantities of glandular secretions to coat the eggs, either because there are fewer of them or because the eggs are retained within the oviducts for some or all of their development.

Reduction of the reproductive tract to one pathway has occurred a number of times in the vertebrates, particularly the more advanced groups, either by the functional loss of one oviduct, for example in birds, or by partial or complete fusion of the pair, for example in placental mammals. Such reduction also occurs in the Anura, as I detailed in my thesis, although the loss of one oviduct (except for the ovisac) occurs in only one species: *Sminthillus limbatus* (Griffiths, 1959). Fusion of the posterior ends of the oviducts in most anurans in which it occurs is not directly comparable with that in mammals, other than that in both groups

it is probably a response to greatly lowered fecundities. In anurans fusion probably serves simply to provide a single pathway for oviposition of the large eggs, whereas in mammals it provides a large chamber for development of the young, as well as a single, large birth canal. However, the mammalian situation is paralleled in the few ovoviviparous anurans and the single viviparous species; in these the ovisacs are either partly or completely united, and the resulting chamber functions as a uterus in protecting the developing young.

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Note: Those references already quoted in the main part of the thesis are not repeated here.

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