FIGURE 55.—SEM micrographs of posteromedial portion of buccal floor and pharynx in dorsal view for *Crossodactylus* species (left) and *Crinia tasmaniensis* (right). Scale lines = 400 μm and 100 μm, respectively. Note variation in amount of papillation on buccal floor. *Crossodactylus* is unusual in having a fringe on posterior ventral velum. *Crinia* (and *Pseudophryne*) are exceptional among tadpoles examined in medial convergence of their 4th filter plates.

stream or flowing-water tadpoles—*Crossodactylus, Hylodes, Megaelosia, Paratelmatobius, Proceratophrys appendiculata, Pseudopaludicola;* macrophagous carnivores—*Ceratophrys, Lepidobatrachus;* subaerial tadpoles—*Cycloramphus izeck-sohni, Thoropa;* non-feeding tadpoles—*Adenomera, Cycloramphus stejnegeri, Eleutherodactylus. Rhinoderma darwinii* may be included in this last group although its tadpoles could conceivably receive some nutrition from the ingestion of mucus secreted by the brooding adult.

Not all larvae show such a good match between predicted habitat/ecology based on morphological features with actual habitat preferences. Larvae of *Mixophyes* and *Taudactylus* are stream dwellers, but do not show all the internal oral features predicted for stream forms. In contrast, *Crinia* and *Pseudophryne* larvae are reported to live in ponds, but have morphological features more suggestive of stream forms. The *Heleophryne* tadpole is internally quite unlike most stream-associated neobatrachian larvae. However, it closely resembles, internally and externally, the torrent-adapted *Ascaphus* larva and shares some features, such as reduced buccal papillation, with the neobatrachian torrent-adapted *Amolops* (Ranidae).

The suite of features observed in *Crossodactylodes* was

understandable only by knowing that the tadpoles lived in bromeliads. We would not have predicted that habitat based on the internal oral anatomy alone. Other arboreal tadpoles however, do have morphological features indicative of dietary specialization, most commonly macrophagy (Lannoo et al., in press).

Within *Leptodactylus, L. knudseni* and *pentadactylus* were notably distinct from the other typical pond larval *Leptodactylus* examined (e.g., Figure 53a,b). Apparently, the more specialized morphologies of *knudseni* and *pentadactylus* correlate with facultative carnivory (Heyer et al., 1975); but again, this dietary capability was not predictable to us based on larval anatomy that we examined.

Pleurodema nebulosa stood out in the morphological analysis as being very different from other *Pleurodema* or, for that matter, leptodactyloid pond larvae in general. For example, secretory ridges on the ventral surface of the ventral velum are absent in this species (Figure 60). When the specimens were being examined, we did not recall the larval habitat or diet of *P. nebulosa* and were unable to predict where the larvae might live or what they might eat, aside from the observation that it did not seem to be a typical pond tadpole. Mares et al., (1977)
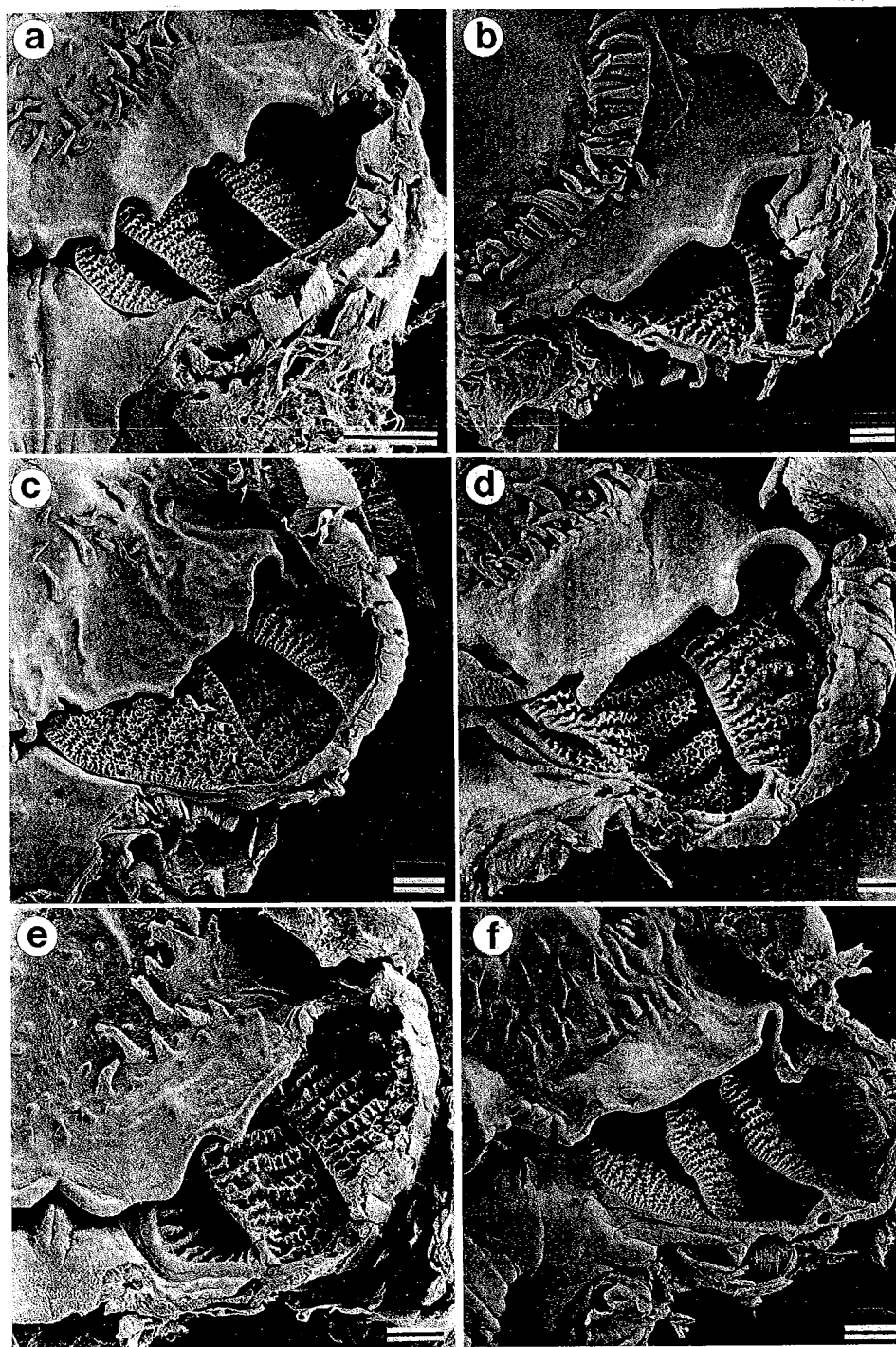
FIGURE 56.—SEM micrographs of branchial baskets in dorsal view for selected leptodactyloid larvae: (a) *Atelognathus reverberii* (scale line = 1 mm); (b) *Paratelmatobius* (scale line = 200 μm); (c) *Pleurodema brachyops* (scale line = 400 μm); (d) *Pleurodema cinerea* (scale line = 200 μm); (e) *Heleioporus* species (scale line = 400 μm); (f) *Platyplectron ornatus* (scale line = 400 μm). All are right branchial basket except for b, which is a left basket printed in reverse to orient with other figures. Note that tadpoles vary in height and orientation of filter plates and filter-mesh density. There may be two (e.g., b,c,d) or three (e.g., a,e,f) major filter cavities visible in this view. Interspecific variation in *Pleurodema* branchial morphology is great (e.g., c,d) compared to species in other genera.
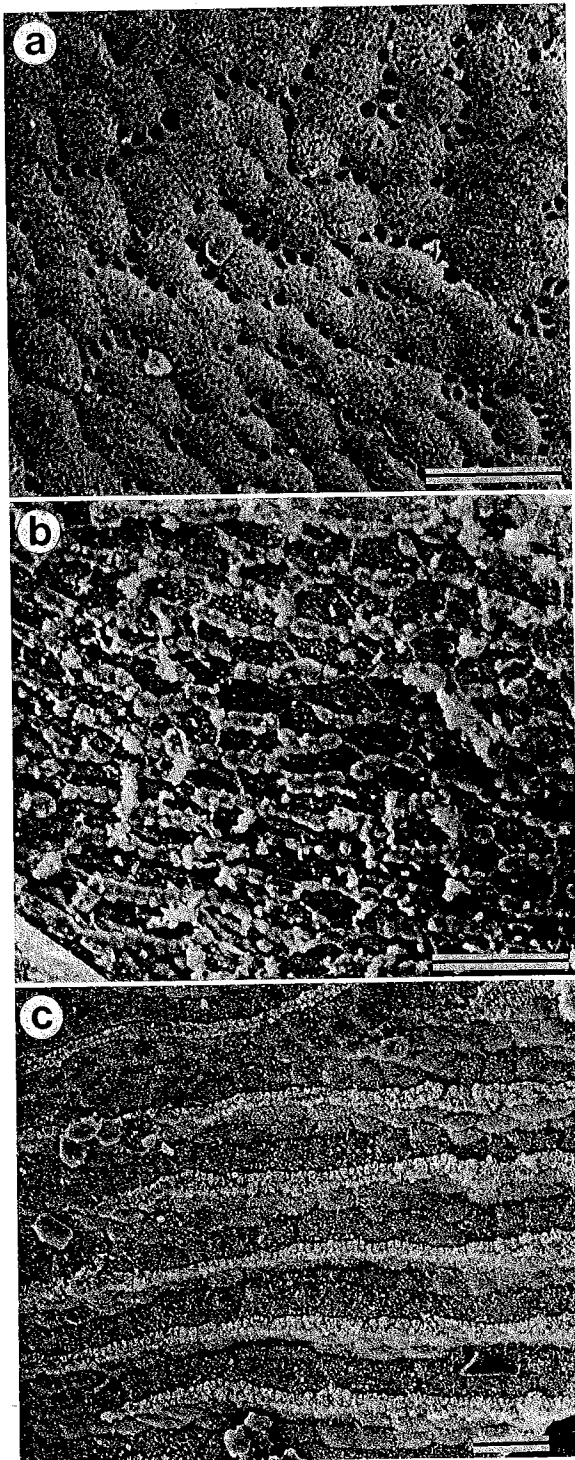
FIGURE 57.—SEM micrographs of secretory tissue in branchial food traps: (a) *Heleophryne natalensis;* (b) *Crinia tasmaniensis* and (c) *Hylorina sylvatica.* All scale lines = 20 µm. Note that secretory cells are numerous in all three species but are not organized into ridges in *Heleophryne.* Absence of ridges is a feature that *Heleophryne* shares with most archeobatrachian genera; however, whether it is a primitive feature in this leptodactyloid genus is not known. *Crinia* and *Hylorina,* as representative tadpoles of Australian and American leptodactyloid radiations, both show the ridged pattern.

commented at length on the convergence of *P. nebulosa* with *Scaphiopus* of the North American deserts. Both have very short larval periods, breed in very ephemeral desert ponds, are carnivorous, and if stressed, cannibalistic. *Pleurodema nebulosa* clearly is not an obligate carnivore like *Lepidobatrachus,* since it retains most of the suspension feeding structures (such as gill filters) seen in generalized tadpoles. On the other hand, the absence of secretory pits and secretory ridges on the branchial food traps certainly correlates with a macrophagy. Presumably, *P. nebulosa* and *Scaphiopus,* compared to other pond larvae, have specialized in terms of being able to feed on large, individual food items at the expense of efficiency in entrapping small, microscopic particles. Interestingly, besides lacking secretory ridges in the branchial food traps, both *P. nebulosa* and *Scaphiopus* (Wassersug, 1980) share a peculiar feature: a convex shape to the free lateral margins of the ventral velum. While both *P. nebulosa* and *Scaphiopus* have a rather well-developed filter-mesh apparatus, the mesh is much finer in *Scaphiopus.* Buccal papillation differs as well in these two taxa.

Heleioporus has too low a filter-mesh density for typical microphagous pond tadpoles. Although *Heleioporus* larvae occur in ponds, their natural diet is unknown; thus, we do not consider *Heleioporus* a typical pond tadpole.

The tadpoles of *Megistolotis* have been associated with both streams and ponds (rocky pools) in nature, yet can be cannibalistic in the laboratory. Nevertheless, we found that the internal oral anatomy is typical of pond larvae.

Leptodactyloid larvae collectively seem to embrace most specializations for habitat and diet found in anurans. However, this diversity does not hold up when considered on a continental basis. Africa has but one genus of leptodactyloid and all species have stream-adapted larvae. The American leptodactyloids lack at least two major tadpole types that were identified previously: oophagous arboreal larva (Lannoo et al., in press); and the obligate, microphagous suspension feeder (Wassersug, 1980). Concerning the former type, arboreal dendrobatids and hylids seem to have filled this niche in Central and South America. Concerning the latter, American leptodactyloids generally co-occur with pipids and microhylids, most of which have specialized microphagous larvae. Phyllomedusine hylids also are common in the Neotropics in association with leptodactylids and they also have tadpoles particularly adapted for midwater microphagy (Wassersug, 1980). Pipids and phyllomedusine treefrogs are absent in Australia, and microhylids are a minor part of the Australian herpetofauna, both in terms of numbers of species and geographic distribution. It is puzzling that *Taudactylus,* which occurs in stream habitats, has the extremely narrow secretory ridges in the branchial food traps that typically characterize obligate, microphagous, suspension feeders (Wassersug and Rosenberg, 1979). As we have examined only a small portion of the myobatrachids, we do not know the full extent of the
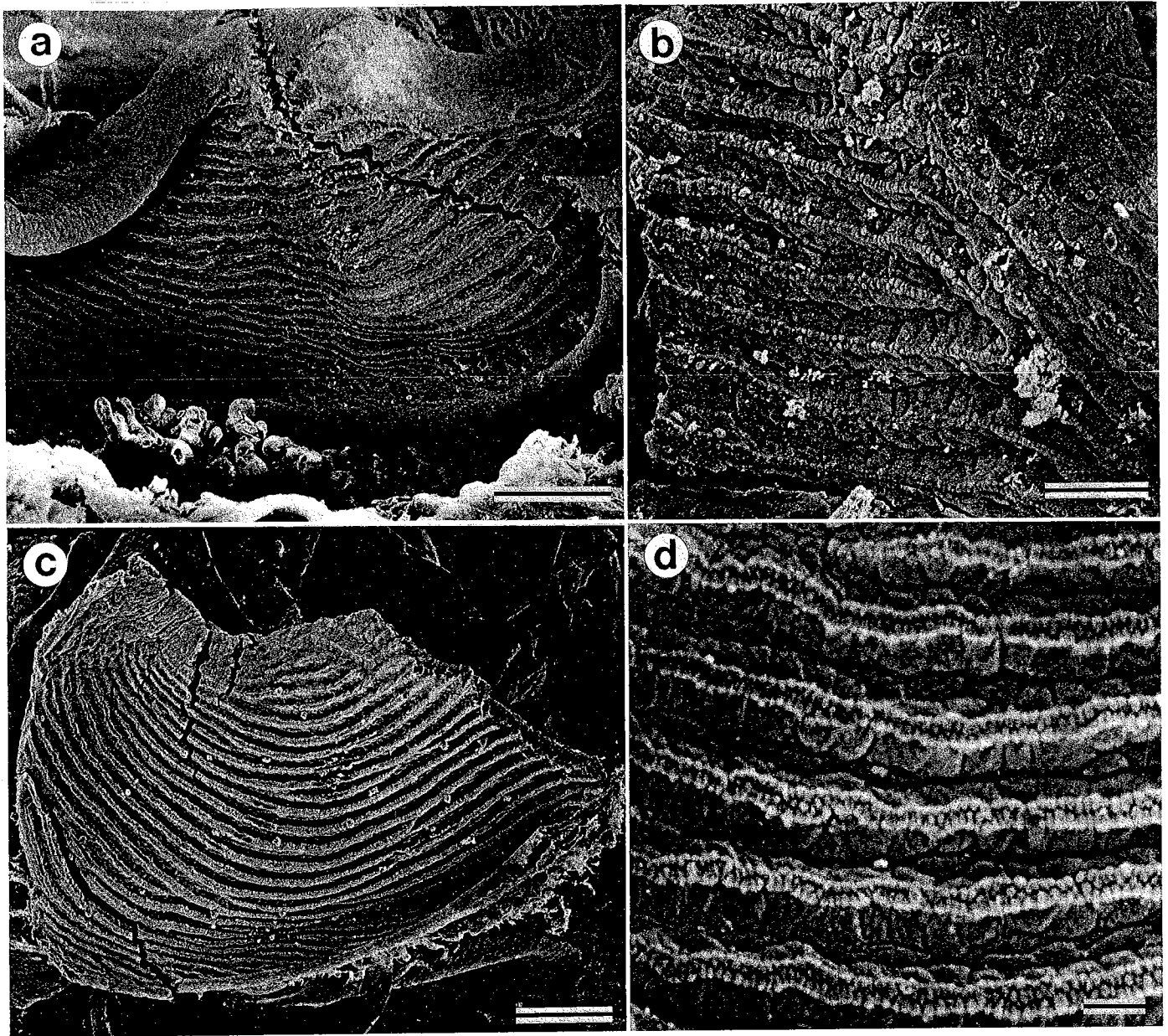
FIGURE 58.—SEM micrographs of branchial food traps (left) and secretory ridges at higher magnification (right) of *Proceratophrys appendiculata* (*a* and *b*) and *Megistolotis lignarius* (*c* and *d*). From *a* to *d* scale lines = 100 μm, 40 μm, 100 μm, and 20 μm, respectively. Since both of these tadpoles and other stream associated leptodactyloid larvae have secretory ridges in branchial food traps, it is unlikely that absence of such ridges in *Heleophryne* (Figure 57a) is an adaptation to flowing water.

Australian diversity of larval types.

It is worth emphasizing the very high degree of correlation of internal oral features with larval habitat and diet, and that leptodactyloid larvae in general show the same patterns found in other anuran families (e.g., see Inger, 1985). Most of the exceptions observed involve larvae specialized for living in extreme habitats, such as the desert pond-dwelling *Pleurodema nebulosa* (Figure 60a,b) or the bromeliad inhabiting *Crossodactylodes*. Few larvae that inhabitat these specialized environments have been examined to date (but see Lannoo et al., in press). Study of more species of desert-pond larvae and arboreal larvae may result in recognition of morphological features that can characterize each of these as another major larval type.

Formas (1981a) reported the results of a phenetic analysis comparing external larval morphologies and ecological characteristics for the leptodactylid larvae inhabiting the temperate forests of Chile. He found a good correlation between external
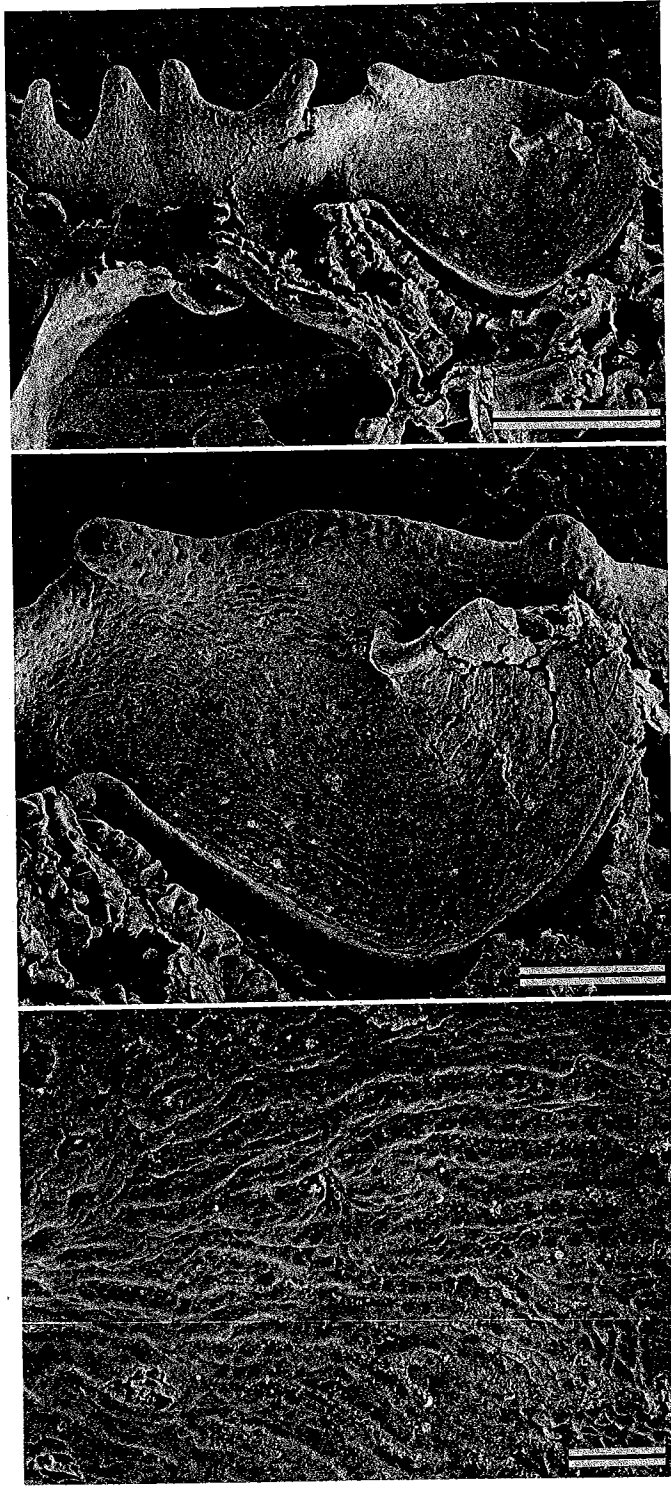
FIGURE 59.—SEM micrographs of branchial food traps and secretory ridges of *Alsodes monticola* larva at three different magnifications. From top to bottom scale lines = 1 mm, 400 μm, and 100 μm. *Alsodes,* like all other telmatobiine tadpoles examined, has secretory ridges in the branchial food traps (contra Sokol, 1981).
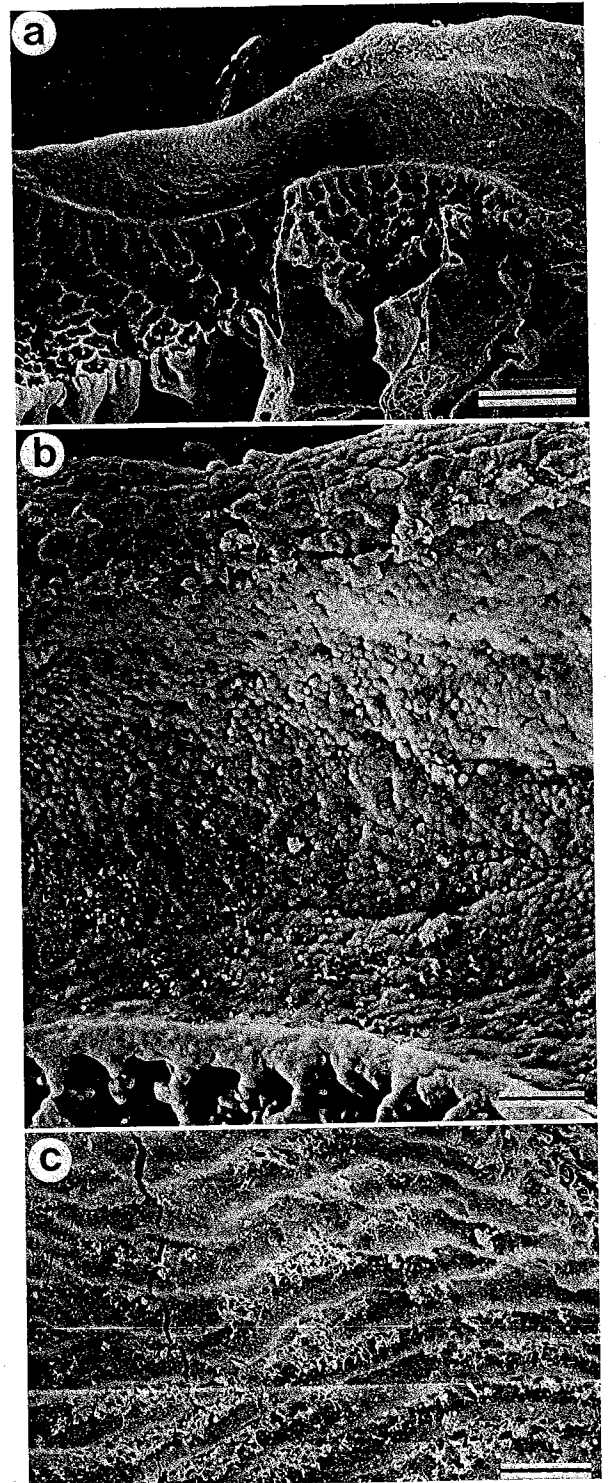
FIGURE 60.—SEM micrographs of branchial food traps of: (a) *Pleurodema nebulosa;* (b) secretory tissue of that food trap at higher magnification compared to; (c) secretory tissue of branchial food traps of *Pleurodema brachyops.* Scale lines = 200 μm, 40 μm, and 40 μm respectively. Of the *Pleurodema* examined, *P. nebulosa* is unique in lacking secretory ridges in branchial food traps. In this and other features *P. nebulosa* appears to be convergent with desert-adapted *Scaphiopus,* and distinct from other *Pleurodema.*

FIGURE 61.—SEM micrographs of front of roof of mouth in ventral view for selected leptodactyloid larvae: (*a*) *Leptodactylus fuscus;* (*b*) *Leptodactylus knudseni;* (*c*) *Megaelosia goeldii;* and (*d*) *Odontophrynus americanus.* Scale lines = 400 μm for *a* and *b*, 1 mm for *c* and *d*. Note the differences in postnarial papillae, median ridge, and lateral-ridge papillae in *L. fuscus* vs. *L. knudseni.*
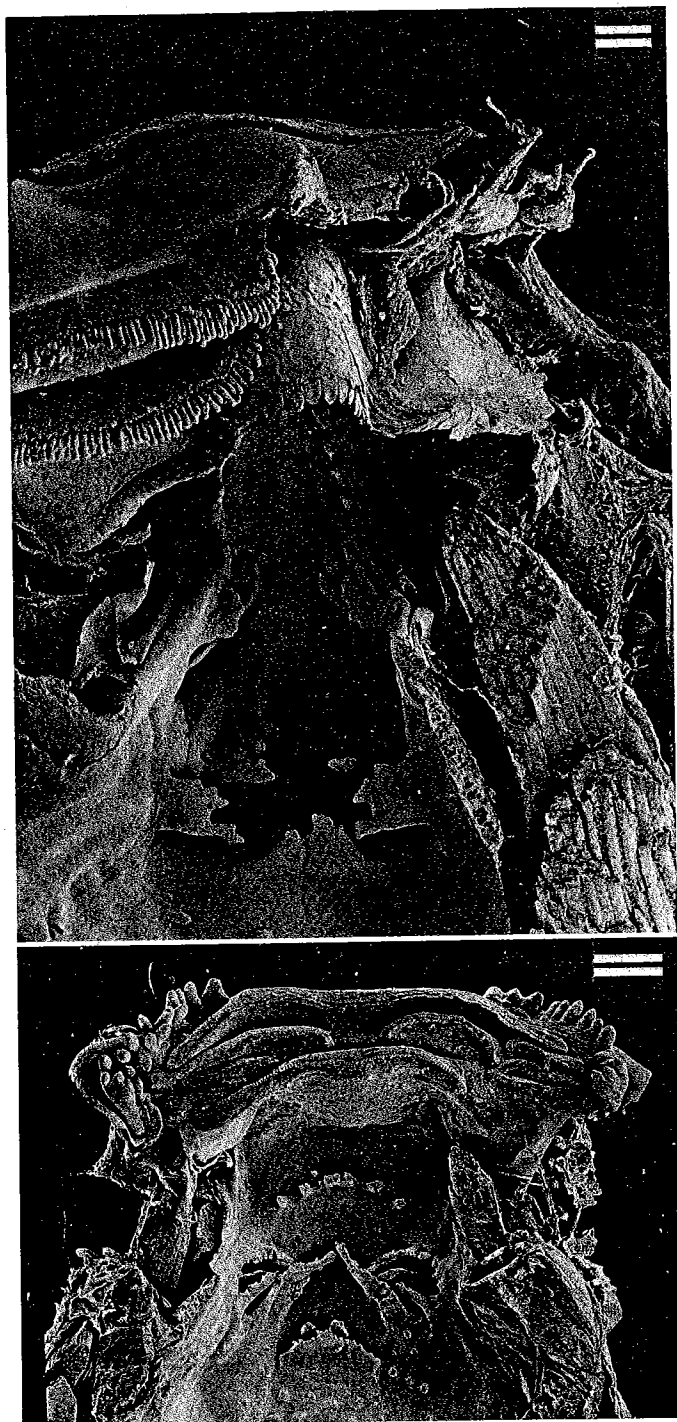
FIGURE 62.—SEM micrographs of front of roof of mouth in ventral view of *Thoropa miliaris* (above) and *Platyplectron ornatus* (below). Scale lines = 200 and 400 μm respectively.

larval morphology and the ecological conditions. Both external and internal features are necessary to understand the ecological correlates, however. For example, Formas (1981a) found that externally, *Eupsophus* tadpoles are distinctive from *Alsodes*,

Batrachyla, and *Caudiverbera.* The distinctive external *Eupsophus* morphology correlates with a habitat of living in crevices or small caves under rocks. Internally, we find no distinctive differences within this group. Alternatively, the larvae of *Proceratophrys appendiculata* and *boiei* are externally almost identical. Internally, they demonstrate differences that correlate with differences in standing- versus flowing-water habitats.

PHYLOGENETIC CORRELATES

Any phylogenetic inferences must be proposed within the framework of the preceding discussions on ontogenetic, individual, and intraspecific variation. The most difficult factors to separate in this study are ecological and phylogenetic. The clearest correlation of internal oral anatomy for leptodactyloid larvae is with larval ecology. Because of this correlation, parallelism and convergence are common in larval evolution, making phylogenetic interpretation difficult. For example, two species that have features characteristic of stream larvae may have those features because they shared a common stream-dwelling ancestor, but it may be just as likely that the features were independently derived due to convergent adaptations to stream life. In too many cases, information is inadequate to resolve the question of whether morphological similarities are due to convergence or to common ancestry.

Another limitation of these data for phylogenetic analysis is the central and common occurrence of the typical pond tadpole in leptodactyloid evolution. We infer that the primitive leptodactyloid tadpole was a typical pond larval type (see below). If this is true, one would not expect to find much, if any, phylogenetic information within the larvae of taxa that retain this generalized larval type.

Within these constraints, internal oral anatomical features do suggest some phylogenetic patterns.

Inter-Continental Leptodactyloid Relationships

Taxonomically, the leptodactyloids have been treated at one extreme as a single family (e.g., Tyler, 1979) and at the other extreme as three separate families (e.g., Savage, 1973), each occurring in a separate continent. One of our initial interests in undertaking this project was to determine if there were any internal oral features of larvae that would resolve the relationships among the African, South American, and Australian leptodactyloids. Zoogeography suggests a Mesozoic Gondwanan origin for the leptodactyloids, but the fossil record is of little help in establishing the time of origin. In a recently proposed phylogeny for the Anura based on sixteen characters (Duellman and Trueb, 1986) the Australian forms clustered with the African leptodactyloid (*Heleophryne*), whereas the South American forms were more derived. These authors (p. 475) noted, however, unresolved polytomies: depending on
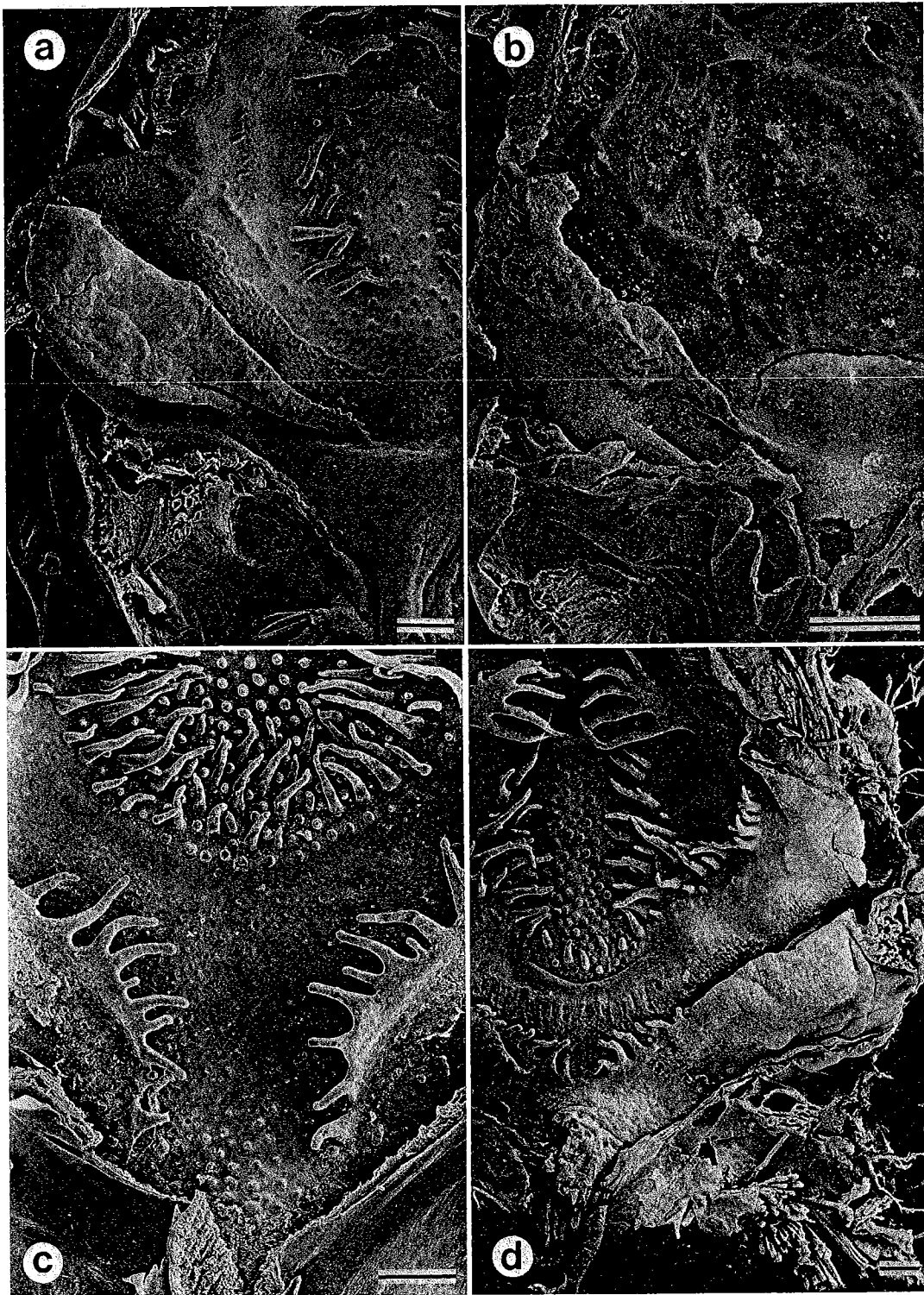
FIGURE 63.—SEM micrographs of posterior portion of buccal roof and pharynx in ventral view for selected leptodactyloid larvae: (a) *Alsodes monticola*, right side; (b) *Heleioporus* species, right side; (c) *Crossodactylus* species, midline; (d) *Hylodes* species, left side. All scale lines = 400 μm. Tadpoles vary in having few (e.g., *Heleioporus*) to many (e.g., *Crossodactylus*) buccal-roof papillae. Dorsal velum is unfringed in *Heleioporus* and heavily fringed in *Crossodactylus* and *Hylodes*. Other differences include size and distinctness of secretory zone in front of dorsal velum, and breadth of ciliary groove behind dorsal velum.
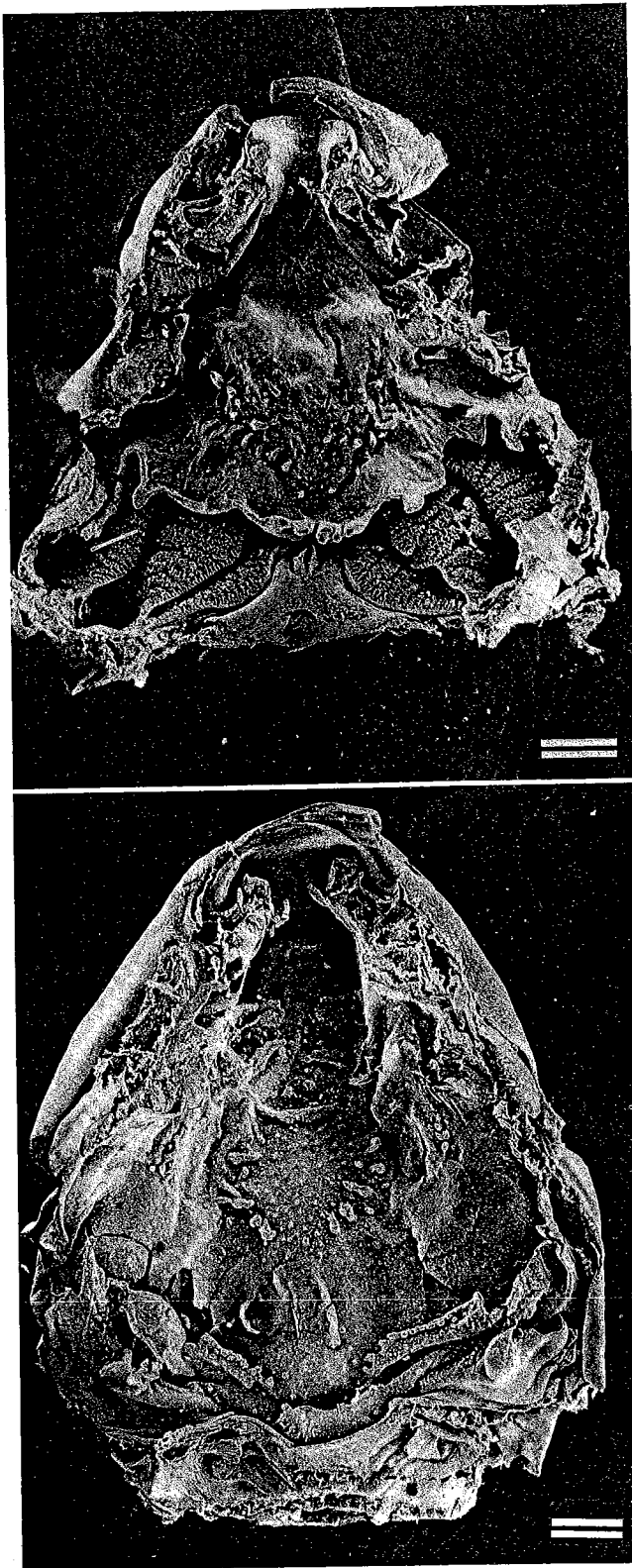
FIGURE 64.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Litoria alboguttata;* scale lines = 1 mm.

how one interpreted a single character (amplectic position) certain South American leptodactylids, e.g., *Batrachyla* and *Pleurodema,* fell in with the myobatrachids of Australia and the Australian forms overall could cluster with the Leptodactylidae rather than the Heleophrynidae. Regrettably, we do not find any single, derived, larval character-state that defines any one of these three groups.

Heleophryne presents a special problem, as there is but a single genus with a clearly specialized, stream larval type. Features unique to *Heleophryne* larvae include the longitudinal orientation of the internal nares, and the pair of ridges on each side in the area of the buccal roof where lateral-ridge papillae occur in other tadpoles. It is not clear, however, whether these features indicate a separate origin at the familial level or are specializations for stream life within the genus. The absence of secretory ridges in the branchial food traps (Figure 57*a*) is a feature that distinguishes *Heleophryne* from other stream-adapted leptodactyloid larvae and is similar to the pattern common, but not unique, to archaeobatrachian frogs (Wassersug and Rosenberg, 1979). *Heleophryne* tadpoles are, in fact, quite similar to *Ascaphus* tadpoles. *Heleophryne* shares with *Ascaphus* the following internal features: a V-shaped BFA with the BFA papillae arising from a common ridge, reduced buccal-roof papillation, cup-like structures in the infralabial region, and no secretory ridges in the branchial food traps. Both of these tadpoles externally have large oral disks specialized for holding onto rocks in torrential streams. Most of these features are clearly convergent. Some, for example, the reduced buccal papillation and cup-like structures in the infralabial region, also characterize other torrent-adapted tadpoles such as those of *Amolops* (Inger, 1985). Whether the absence of secretory ridges in the branchial food traps is due to convergence or retention of a primitive pattern in *Heleophryne* cannot be determined, but the somewhat similar *Amolops* clearly has the ridges (Wassersug, pers. obs.). Overall internal oral anatomy of the larvae argues neither for nor against a close relationship of *Heleophryne* with the South American and Australian leptodactyloids.

There are greater radiations of larval types in both South American and Australian leptodactyloids. At the generic level, our sample of South American leptodactyloids is good; our sample of Australian leptodactyloids is much poorer. The samples, however, are adequate to draw the following two conclusions. First, no single larval feature unequivocally defines either group in relation to the other. Second, two pieces of evidence suggest that the radiations have occurred independently in each continent. The number of lingual papillae have been used by other workers to delineate taxonomic groups; e.g., in Europe, brown frog and green frog larvae can be distinguished on this character (Viertel, 1982); in South America most hylids have two lingual papillae whereas *Gastrotheca* has four (Wassersug, 1980; Wassersug and Duellman, 1984). All of the Australian leptodactyloid larvae examined have two lingual papillae, whereas most of
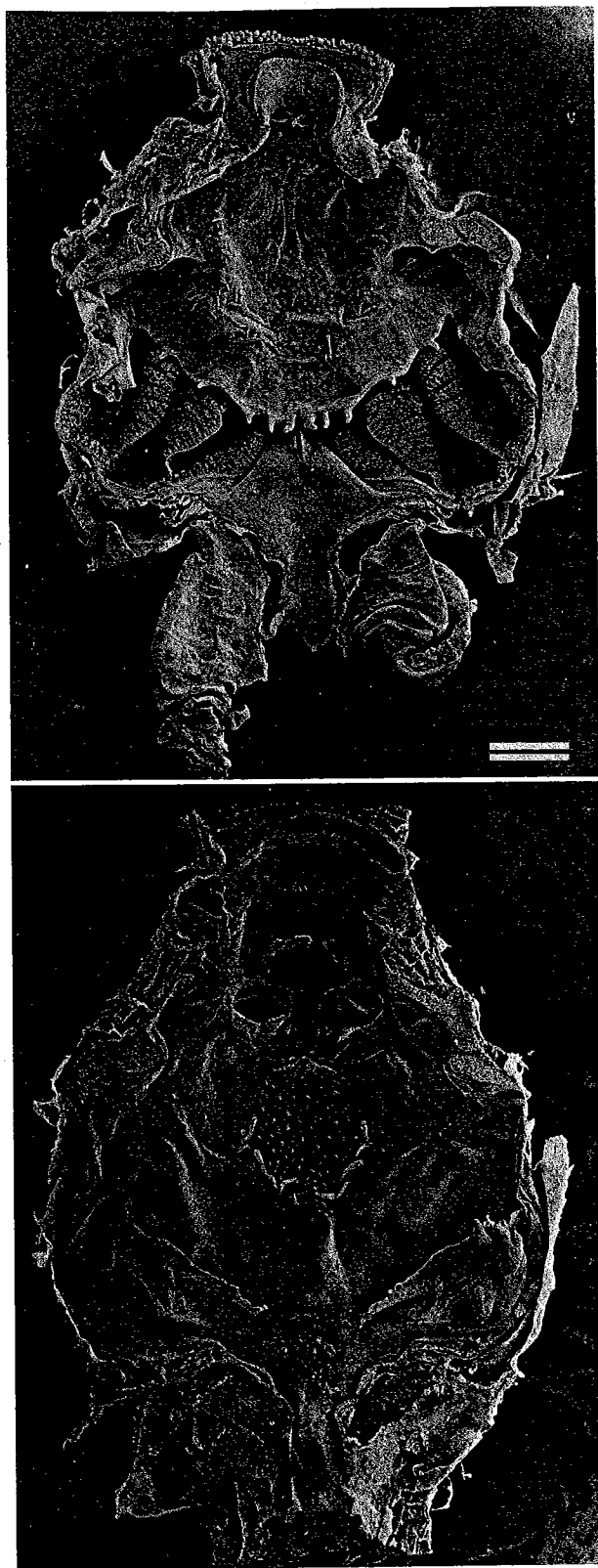
FIGURE 65.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Cyclorana australis;* scale line = 1 mm.
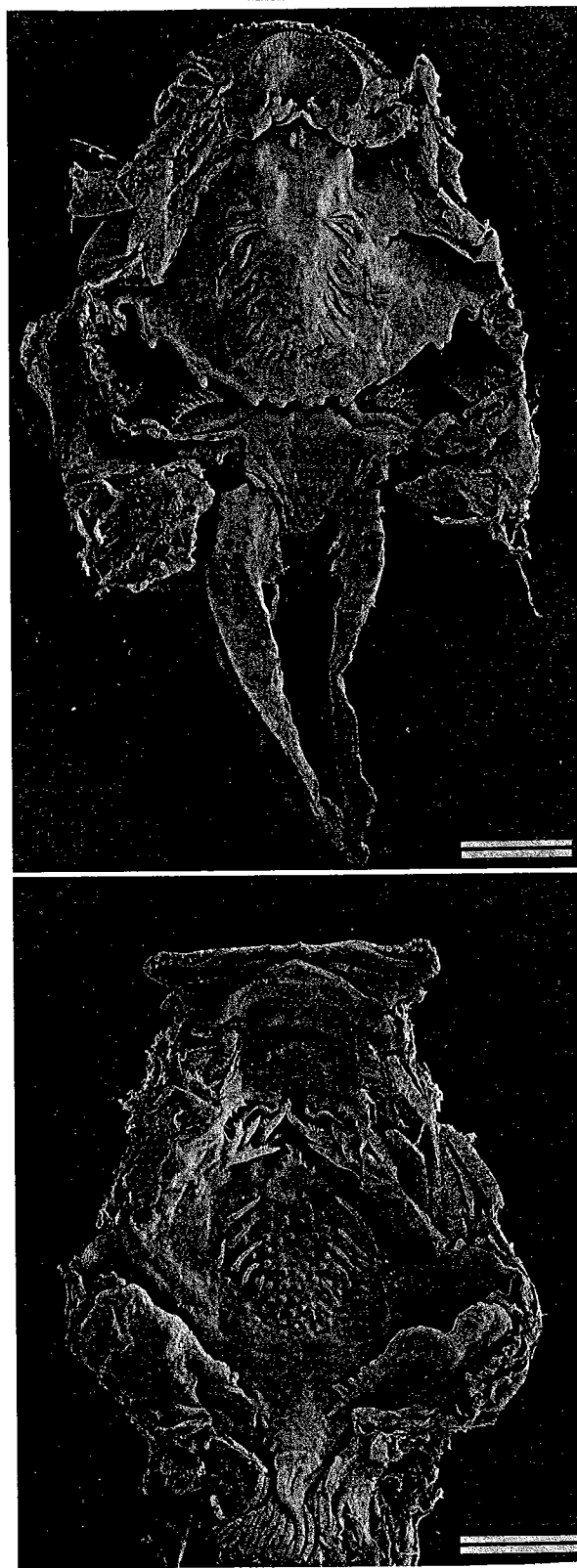
FIGURE 66.—SEM micrographs of floor (above) and roof (below) of oral cavity of *Colostethus whymperi;* scale lines = 1 mm.

the South American larvae have four (Figures 52–54). Whether two or four is the primitive pattern, the most parsimonious explanation for the variation seen in lingual papillae is that separate radiations have occurred in South America and Australia.

The South American stream larvae, for which we have the most data, show the same suites of morphological specializations · seen in other families. Similarly, South American leptodactyloids in general show the same extremes of morphology evidenced by carnivorous, subaerial, or non-feeding larvae in other families (Wassersug, 1980). The Australian larvae we examined do not fit nearly as well into these categories; of the tadpoles discussed in the ecological correlates section (above) that did not show easily interpretable congruence of habitat with internal oral anatomy, most were Australian. For example, the larva of *Mixophyes* is clearly an externally specialized stream-dwelling tadpole. Yet internally most of the features are not different from those characteristic of typical pond larvae. Similarly, *Taudactylus diurnus* larvae are reported (Liem, pers. comm.) from fast-flowing streams yet, except for slight expansion of the oral disc, they show little morphological specialization for life in currents, either externally or internally. This non-concordance of habitat, external morphology, and internal oral morphology suggests a different evolutionary pattern or a shorter period of evolutionary response.

Relationships Involving the Australian Leptodactyloids

The sample of Australian leptodactyloids is not extensive enough to adequately characterize the radiation in Australia. However, the sample does allow some comparisons and predictions.

Lynch (1973) suggested that certain pelobatids were closely related to cycloranine leptodactyloids among the Neobatrachia. The larval features examined herein argue against such relationships. The pelobatids (sensu lato) have a single-filter cavity per side and lack secretory ridges on the branchial food traps (Wassersug, 1980; Wassersug and Rosenberg, 1979). All of the Australian taxa examined (including both myobatrachines and cycloranines [= limnodynastines]) have well-developed secretory ridges in the branchial food traps and have either two or three filter cavities per side. The Australian leptodactyloids demonstrate less similarity to pelobatids than does either *Heleophryne* in South Africa or telmatobine leptodactylids in South America.

Historically, the genus *Cyclorana* has been included either in the Australian leptodactyloids or the Australian treefrogs (Hylidae or Pelodryadidae, depending on author). Currently, authorities agree that *Cyclorana* is a member of the Australian tree frog assemblage (for example, Maxson et al., 1982). We have examined one species of *Litoria*, *L. alboguttata* (Figure 64), and one species of *Cyclorana*, *C. australis* (Figure 65). Both of these larvae externally have a typical pond morphol-

ogy. The most striking feature that they share is 4–6 lingual papillae. This is unlike any of the myobatrachid larvae that we examined. It will be interesting to see if this difference in lingual papillae will hold up with additional sampling of pelodryadids and myobatrachids.

The few species examined support the two major groupings of Australian leptodactyloids recognized by all authors: the myobatrachines and limnodynastines (although the genus *Rheobatrachus* has been placed in a separate subfamily, the Rheobatrachinae, by some authors, e.g., Heyer and Liem (1976), others, such as Frost (1985), group this genus with the limnodynastines). *Crinia* and *Pseudophryne* have peculiar branchial basket morphologies with the fourth filter plates from each side almost in contact on the midline (Figure 55). This arrangement, unusual among all tadpoles examined, is associated with little lung development and is totally unexpected in pond larvae. More myobatrachines should be examined to determine whether this character defines the group.

Relationships Involving the New World Leptodactyloids

Lynch (1973), among others, has proposed a close relationship between the family Dendrobatidae and the subfamily Elosiinae (*Crossodactylus*, *Hylodes*, *Megaelosia*) of the family Leptodactylidae, deriving the former from the latter. In addition to two species of *Colostethus* examined previously (Wassersug, 1980), we examined *Colostethus whymperi* (Figure 66). *Colostethus nubicola*, *subpunctatus*, and *whymperi* are very distinct from each other. *Colostethus subpunctatus* and *whymperi* are presumably pond-dwelling tadpoles, whereas *C. nubicola* is a funnel-mouthed tadpole that lives in shallow-stream pools. There are no larval features that argue for or against close relationships among the dendrobatids and elosiines. All of the elosiines have stream-adapted larvae; thus it is reasonable to assume that, if the dendrobatids were derived from elosiines, the ancestral dendrobatid had a stream larva. *Colostethus whymperi* shows some features associated with stream life, such as elongate BFA and BRA papillae, an elaboration of lateral-roof and postnarial papillae, and a papillate medial margin of the dorsal velum. Of these features, *C. subpunctatus* shares only the elongate BFA and BRA papillae; *C. nubicola* has none of these features. Thus, morphological traces of stream life are not evident in all dendrobatid tadpoles. Confirmation of whether dendrobatids are derived from elosiines must await a clearer understanding of phylogenetic relationships within the Dendrobatidae.

The genus *Rhinoderma* is often considered to be the only member of the family Rhinodermatidae (e.g., Duellman, 1975). The non-feeding larva of *R. darwinii* has lost some features of free-living, feeding larvae, but still retains many. We have been unable to examine *R. rufum* larvae, which are free-living pond forms (Formas et al., 1975). The data available for *R.*

darwinii neither support nor refute recognition of the family Rhinodermatidae.

Internal oral features do not provide any conclusive information of relationships among the New World leptodactylid genera. However, they argue against certain associations proposed on other, more limited, morphological features. For example, based on other characters, the genera *Ceratophrys* and *Lepidobatrachus* are considered to be closely related, as are the genera *Odontophrynus* and *Proceratophrys*. However, there is considerable difference of opinion on the relationships between these two lineages. Lynch (1971) recognized *Ceratophrys* and *Lepidobatrachus* in the subfamily Ceratophryninae and placed *Odontophrynus* and *Proceratophrys* in a separate subfamily, the Telmatobiinae. Heyer (1975) thought that these two lineages were closely related. The tadpoles of all four of these genera are much more distinctive from each other than they are similar. There are few features that link either *Ceratophrys* with *Lepidobatrachus* or *Odontophrynus* with *Proceratophrys*, let alone any features that support any close relationship between these two lineages within the Leptodactylidae. It is no surprise that *Odontophrynus* tadpoles, which are typical pond larvae, are different from *Proceratophrys* larvae, which show many adaptations to living in flowing water.

It is noteworthy that both *Ceratophrys* and *Lepidobatrachus* have macrophagous carnivorous tadpoles. Yet these larvae are so different, particularly in their head shape and jaw design, that they most likely have been independently derived. The features that they share, such as reduced branchial baskets, reduced gill filters, large buccal floor area, and reduced buccal papillation, are characteristic of tadpoles specialized for macrophagy regardless of family. Adults of the genera *Cycloramphus* and *Thoropa* are quite distinctive, yet the feeding larvae of both genera are remarkably similar and distinctive in external morphology. This paradox led Lynch (1971) to place these two genera in separate subfamilies by emphasizing the adult characters and Heyer (1975) to consider *Cycloramphus* and *Thoropa* much more closely related by utilizing larval characters, in part. The internal oral features of feeding *Cycloramphus* and *Thoropa* larvae are very similar, differing only in trivial ways. Yet the morphological features do not unambiguously support or reject either the hypothesis that the larvae are similar because of common ancestry, or that the larval morphologies are convergent as a result of similar adaptations to the subaerial way of life. These two examples are discussed in detail because they illustrate where internal larval anatomy might have been expected to shed light on phylogenetic relationships at the intergeneric level. Using external larval features, Diaz and Valencia (1985) concluded that "*Alsodes, Telmatobius* and *Hylorina* form a group united at a high level of phenetic similarity and that *Batrachyla, Caudiverbera, Insuetophrynus, Telmatobufo* and *Eupsophus* do not show sufficient similarity to justify formation of [subfamilial] groups [with the telmatobiine leptodactylids]." Based on the larger array of morphological features that we

have before us, we can neither support nor refute this suggestion. We find little evidence in the characters we examined for concluding that the first three genera are in any way closer phenetically or phylogenetically than are any of the latter genera.

A final example is the genus *Paratelmatobius*. The relationships based on adult morphology are enigmatic, as members of this genus have a peculiar mixture of primitive and derived character states (Heyer, 1975). The tadpole of *Paratelmatobius* is unique externally. The internal oral anatomy is as distinctive as any observed among leptodactyloids (Figure 28)—the tadpole data underscore the distinctiveness of *Paratelmatobius*, but provide no clue to its relationships with other genera of leptodactyloids.

In contrast to the little insight into suprageneric relationships given by the internal oral features of leptodactylid larvae, oral morphology does contain consistent phylogenetic information at the generic and specific levels. In almost all cases, there are similar features that unite members of the same genus. This subtle unity at the genus level is not easy to verbalize and is not always obvious within the standardized format of the written descriptions provided above. When either specimens, or good figures of specimens, are compared directly, it is easy in most cases to recognize members of the same genus. This is true, in the present sample, even for the two *Proceratophrys* examined, which occur in different habitats and apparently preferentially ingest different-sized particles.

The three exceptions to this general observation are instructive. Based on internal oral features, the larvae of *L. knudseni* and *L. pentadactylus* form a very distinctive grouping within the *Leptodactylus* species examined; the *L. wagneri* tadpole is distinctive, but somewhat similar to the tadpole of *L. chaquensis;* and the larvae of *L. fuscus, L. gracilis,* and *L. mystacinus* are very similar to each other (and are typical pond tadpoles). These groupings are identical to those proposed independently on other features (Heyer, 1969). Thus, larval features are useful for determining species groupings within the genus *Leptodactylus;* yet the total variation observed, while exceeding the variation seen in most other genera, is rather continuous and understandable within the context of a single genus.

The differences between the feeding and non-feeding larvae of *Cycloramphus* are striking, yet the non-feeding morphology is clearly derivable from the feeding morphology. In this case, based on only two species, a persuasive argument could be made that the relationships were at the generic, rather than specific level. Wassersug and Duellman (1984) described a morphocline in *Gastrotheca* ranging from the typical pond tadpole morphology to an extreme non-feeding tadpole morphology similar to that seen in *Eleutherodactylus*. Because of the example provided in *Gastrotheca*, we defer making any generic proposals for *Cycloramphus* based on larval morphology until the larvae of more species are studied.

Variation in the genus *Pleurodema*, based on species we

have examined, exceeds the degree of variation observed in all other leptodactyloid genera except *Cycloramphus*. The larvae of *P. nebulosa* are not only very different from the other *Pleurodema* species examined, but also distinctive among all leptodactyloid larvae. The distinctiveness of the internal oral features in part reflects the carnivorous feeding mode. *Pleurodema nebulosa* is a member of a species group that is distinctive within *Pleurodema* in lacking lumbar glands and living in desert regions (Cei, 1980; Duellman and Veloso, 1977). Based on the available tadpole data, we think that this species group should be elevated to the generic level. We refrain from formally proposing this action for two reasons. First, we have only examined five species of *Pleurodema*, only one of which is a member of the *P. nebulosa* species group. Second, a proposal should include members of the entire genus, especially considering the fact that the internal oral larval information for the other four species examined is at variance with relationships proposed on other characters. The internal oral anatomy of *P. cinerea* larvae differs from that seen in *P. borellii—bufonina—brachyops*. In the most recent treatment on relationships of *Pleurodema*, Duellman and Veloso (1977) indicated that *cinerea* and *borellii* were each other's closest relatives and that *brachyops* was a member of the same species group, but that *bufonina* was a member of a different species group. Clearly, more work is required to understand the relationships among the species currently placed in *Pleurodema*. *Pleurodema* is one case where examination of internal oral anatomy will provide useful phyletic information in determining relationships at the species group level.

Major Evolutionary Trends

The primitive leptodactyloid tadpole was a pond-dwelling, microphagous, suspension-feeding tadpole with keratinized mouthparts capable of substrate grazing. Evidence for this comes from outgroup comparisons with the sister-group families Bufonidae and Hylidae (Wassersug, 1980) and the fact that the primitive group of leptodactyloids in the New World, the Telmatobiines, are characterized by having generalized pond tadpoles.

There have been two major trends in the evolution of oral anatomy of leptodactyloid larvae: either elaboration or simplification of surface structures. Elaboration of buccal papillae, usually as proliferation and/or elongation, is seen in the stream-dwelling larvae. Interestingly, in the leptodactyloids we have surveyed, there has been no major hypertrophy of the branchial baskets or the gill-filter system as seen in obligate, microphagous-feeding tadpoles.

The most common trend has been simplification, either general or structure-organ specific. Apparently, simplification is a result of altering the normal larval development of specific oral features at different stages. Most of the simplified larval structures seen are morphologically similar to embryonic or early ontogenetic stages of tadpoles with typical pond morphology. However, the simplification of larval anuran anatomy can be achieved through the modification of a developmental program along more than one evolutionary pathway (Wassersug, 1980). For example, a particular larval feature in one species may appear to be incompletely developed in comparison to that of a sister species because (1) either the onset of, or rate of, embryonic development is retarded in relation to other features, or (2) the onset of, or rate of, metamorphosis is accelerated in relation to other features (see also Alberch et al., 1979). In anurans it is sometimes actually possible to distinguish between evolutionary pathways because of what could be called "developmental hysteresis," i.e., metamorphosis is not a simple reversal of larval development. A larval feature may look quite different halfway through its embryonic development than it does halfway through its metamorphosis. To determine the actual evolutionary pathway taken requires both good developmental series and confidence in the inferred phyletic relationships of the species in question. Unfortunately, we lack both for leptodactyloids.

A general developmental simplification in larval oral surface features is seen in two feeding specialists: non-feeding tadpoles and macrophagous tadpoles. The loss is extreme in the direct-developing *Eleutherodactylus*. The non-feeding *Adenomera* larva is less extreme and, in comparison to *Eleutherodactylus* and direct-developing gastrothecine hylids (Wassersug and Duellman, 1984), appears to have arrived at its simplified morphology by modification of the early embryology of a generalized leptodactylid larva. Simplification of the branchial basket and food trap structure is seen to a lesser extreme in larvae that feed on larger food items, such as in the subaerial larvae of *Cycloramphus* and *Thoropa*, some stream larvae, such as *Heleophryne*, the bromeliad larvae of *Crossodactylodes*, and the carnivorous *Ceratophrys* and *Lepidobatrachus* larvae. The structural simplification seen in *Lepidobatrachus*, in contrast to *Adenomera*, apparently is the type involving early onset of or accelerated metamorphosis (compare Figures 2 and 17). The wider mouth, eroded ventral velum, and enlarged anteriorly directed glottis in *Lepidobatrachus* are all features more characteristic of leptodactylid larvae near metamorphosis than of leptodactylid embryos.

Leptodactyloids show the same discordance of larval and adult morphological specializations observed in other groups of frogs. Starrett's Rule (Savage, 1981) may be paraphrased: the plainest of adult frogs often have the most unusual tadpoles, whereas the most bizarre adult frogs usually have ordinary tadpoles. *Macrogenioglottus* has a bizarre adult morphology involving very specialized locomotor and feeding adaptations. *Macrogenioglottus* tadpoles are very ordinary pond tadpoles. *Proceratophrys* are striking frogs, and the external morphology of the tadpoles is very ordinary, but the internal oral features are distinctive and betray a stream way of life. Some leptodactyloids (certain *Leptodactylus*) are ordinary as both

adults and larvae; others (such as *Paratelmatobius* and *Rhinoderma*) are distinctive both as adults and larvae. Clearly, the adult and larval stages represent, at one level, discrete units of selection in the leptodactyloid life cycle. At another level, however, the two stages of the life cycle must be coadapted, for the larva and adult of any species share a single genome. Understanding the nature of these coadaptations remains one of the major unsolved problems in anuran biology.

Summary and Conclusions

(1) Ontogenetic variation in internal oral morphology is relatively slight once a tadpole has developed the external larval features characteristic of the species.

(2) Individual variation is remarkably low for tadpoles from the same collection series. However, tadpoles from a single collection may be siblings, reducing the amount of genetic and consequently phenotypic variation.

(3) Several oral features described by previous workers were found to be too affected by preservation and dissection artifact or otherwise too variable to be of systematic use.

(4) Among the features found to vary little within species but vary considerably among species—and consequently to be of systematic value—are the number, size, shape, and position of the infralabial, lingual, and buccal floor papillae; the shape of the ventral velum; the presence or absence of secretory ridges in the branchial food traps; the size and shape of the filter plates (and the filter cavities between them); the number of filter rows and the density of the filter ruffles on the filter plates; the size and shape of postnarial papillae, median ridge, and lateral-ridge papillae on the buccal roof; the shape of the medial portion of the dorsal velum; and the extent of lung development.

(5a) The ecology of most, but not all, tadpoles that live in ponds or streams may be predicted from internal oral morphology even when external morphology gives little evidence of tadpole habitat. The extent and complexity of buccal papillation and particularly the extent of lung development are the features that best predict the flow regime in which tadpoles live. Stream tadpoles typically have large, prolific buccal papillae and little lung development.

(b) Leptodactyloid larvae can be sorted into the following ecological categories: generalized suspension feeding, pond tadpole; tadpoles living in flowing water; macrophagous carnivorous tadpoles; subaerial tadpoles; and non-feeding tadpoles. Africa has but one adaptive type of tadpole—a highly specialized version of the type associated with flowing water.

Our limited sample of Australian leptodactyloid larvae contains generalized suspension feeding pond tadpoles; tadpoles living in flowing water; and perhaps an obligatorily microphagous tadpole. The correlation of morphology with ecology in the Australian larvae examined is not as robust as in the South American larvae examined. The South American leptodactylid larvae show all of the ecological/morphological types listed above, but lack at least two major types recognized from other studies: an obligatorily microphagous tadpole type and an oophagous arboreal larval type. These tadpole types do occur in other New World anurans among hylids, microhylids, and pipids.

(6) Morphological observations with systematic and phylogenetic implications include the following.

(a) *Heleophryne* shares several morphological features, such as the absence of secretory ridges in its branchial food traps, with *Ascaphus* and certain other archaeobatrachian anurans. These features, however, may be convergent.

(b) Australian leptodactyloid larvae do not share any unique, derived features with pelobatid larvae.

(c) All Australian leptodactyloid larvae have two or fewer lingual papillae whereas South American leptodactyloid larvae typically have four lingual papillae, suggesting that the Australian forms represent a single, separate radiation.

(d) *Cyclorana* has 4–6 lingual papillae, unlike the Australian leptodactyloids examined, supporting non-larval based arguments for a non-leptodactyloid assigment of the genus.

(e) Most South American leptodactylids have similar, generalized pond larvae; consequently, oral morphology gives limited insight into the phylogenetic relations among genera. However, the morphology suggests that *Lepidobatrachus* and *Ceratophrys* represent two independent evolutionary lines with macrophagous carnivorous larvae. *Paratelmatobius* larvae are extremely different from other leptodactylids and are not close to any other genus examined. *Leptodactylus knudseni* and *L. pentadactylus* are most similar to each other and differ from other *Leptodactylus; L. wagneri* is distinct, but most similar to *L. chaquensis. Leptodactylus fuscus, gracilis* and *mystacinus* form a natural group, in support of previous suggestions. *Pleurodema nebulosa* larvae lack secretory ridges in their branchial food traps and differ in a variety of ways from all other *Pleurodema* at a level consistent with generic differentiation. Interspecific variation in pharyngeal morphology in the genus *Pleurodema* is great, suggesting several distinct species groups.

(f) Except for *Pleurodema nebulosa*, all telmatobine tadpoles examined have secretory ridges in their branchial food traps, a feature that distinguishes them from all pelobatids examined to date.

(7) The major evolutionary trends in leptodactyloid larval internal oral anatomy have involved either elaboration or simplification of surface structures. Elaboration has been through proliferation and/or elongation of structures. Elaboration of buccal papillae and concomitant reduction in the size of the lungs and branchial baskets (and density of the gill filters) characterizes tadpoles associated with flowing water. Simplification has been a more common pattern that may have occurred through a variety of evolutionary pathways. Overall

simplification typifies carnivorous tadpoles and non-feeding larvae as well as species with direct-development. The simplification seen in the non-feeding *Adenomera* appears to be due to a truncation of the development of normal larval features, whereas the simplification seen in the carnivorous *Lepidobatrachus* appears to be the result of premature metamorphosis of normal larval features.

(8) No obvious correlation of the degree of specialization between larvae and adults of the same species exists across the leptodactyloids. This underscores, at one level, that natural selection acts independently at these two stages of the life cycle. At another level, the two stages of the life cycle must be coadapted; understanding the nature of this coadaptation remains a major challenge.

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