A NEW SPECIES OF *LECHRIODUS* (ANURA: LEPTODACTYLIDAE) FROM THE TERTIARY OF QUEENSLAND, WITH A REDEFINITION OF THE ILIAL CHARACTERISTICS OF THE GENUS

by MICHAEL J. TYLER*

Summary

TYLER, M. J. (1989) A new species of *Lechriodus* (Anura: Leptodactylidae) from the Tertiary of Queensland, with a redefinition of the ilial characteristics of the genus. *Trans. R. Soc. S. Aust.* 113, 15–21, 31 May, 1989.

A large collection of frog ilia from the Tertiary site of Riversleigh Station in northwestern Queensland, includes 190 specimens of *Lechriodus intergerivus* sp. nov. The new species is described, compared with the four extant congeners, and shown to be the smallest member of the genus. A revised definition of the ilium of *Lechriodus* is provided, and the significance of the find as a link between the geographically isolated extant species is discussed. The rainforest habitat preferences of all extant species suggest a similar environment at Riversleigh Station in the Late Oligocene to Mid-Miocene.

KEY WORDS: *Lechriodus*, ilia, Leptodactylidae, Tertiary, Queensland.

Introduction

Lechriodus Boulenger comprises a group of ground-dwelling leptodactylid frogs confined to the Australian Geographical Region. In addition to the morphological attributes that support its recognition, it is unique in the nature of its distribution: of the five leptodactylid genera that have been reported to occur both in Australia and New Guinea, it is the only one which is represented by more species in New Guinea than in Australia (Zweifel 1972).

McDonald & Miller (1982) clarified the geographic distribution of *Lechriodus* in Australia, demonstrated that a previous record from north Queensland was in error, and confirmed that there is a major disjunction between the Australian and New Guinea populations. Thus, whereas other shared genera occupy the Cape York Peninsula of north Queensland (Tyler 1972), *Lechriodus* does not, and in Australia it is confined to the eastern seaboard along the Great Dividing Range between Ourimbah, N.S.W. and Brisbane, Qld. All that can be interpreted about such allopatry is that at some time in the past *Lechriodus* must have occurred in the intermediate area.

Here I report a new species of *Lechriodus* from the Tertiary. The material comes from Riversleigh Station in northwest Queensland, which is intermediate between the distribution of the extant species. The finding is significant for several reasons: it constitutes the link in the distribution of the extant species; it is the first record of fossil *Lechriodus*, and it is the first occasion on which an Australian frog fossil has been reported from a site that is beyond the modern geographic range of its genus.

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Material and Methods

The material is deposited in museums and other collections abbreviated in the text as follows: Australian Museum, Sydney – AM; Department of Zoology, University of Adelaide – AUZ; Queensland Museum, Brisbane – QM; South Australian Museum, Adelaide – SAM, and American Museum of Natural History, New York — AMNH. Letters following the abbreviations are departmental identifications.

Comparative studies were based on the osteological collections of the Department of Zoology, University of Adelaide, supplemented by skeletal material of New Guinea taxa borrowed from the American Museum of Natural History.

Osteological nomenclature follows Tyler (1976). The following measurements were taken with dial callipers: ilial length – measured from the superior extremity of the dorsal acetabular expansion to the distal end of the shaft; dorsal acetabular expansion to ventral acetabular expansion (DAE–VAE) measured as the distance between their extremities, and acetabular fossa diameter measured at the proximal, external edge of the peripheral acetabular rim.

Fig. 1. Orientation of ilium to horizontal plane during preparation of descriptions.

All measurements and descriptive features are derived from the lateral surface. Expressions of relative extent of features are obtained with the ilium positioned in such a way that the proximal edge of the bone is maintained at 45° to the horizontal (Fig. 1). Concepts of relative size of

component features to one another are perceived with regard to their proportional size in other anuran taxa.

Scanning electron micrographs were taken on an ETEC Autoscan SEM at 20 Kv.

Systematics

Family: Leptodactylidae Werner, 1896.

Sub-family: Limnodynastinae Lynch, 1971

Genus: *Lechriodus* Boulenger, 1882

The definition of the generic characteristics of the ilium by Tyler (1976) was based solely on *L. melanopyga* (Doria). Now that representatives of all extant species and the fossil species have become available, the definition requires modification and expansion:

Ilial shaft slightly to moderately curved, bearing large, fanlike dorsal crest extending along at least three-quarters its length. Maximum depth of dorsal crest approximately one-third from proximal end. Crest concave to varying extents proximally, flattened distally.

Acetabular fossa diameter varies with size of individual from which it is derived: proportionally larger in larger species. Acetabular fossa bordered by rim in large species; rim confined to inferior half in smaller species. Location of dorsal margin of acetabulum ranges from base of ilial shaft to midway up shaft.

Pre-acetabular zone narrow, meeting inferior border of ilial shaft in gentle curvature, commonly forming quadrant. Ventral acetabular expansion moderately developed, commonly truncate inferiorly.

Dorsal prominence small, extending superiorly above superior margin of ilium, or not. Dorsal prominence moderately to well developed, oval and horizontal or vertical.

Dorsal acetabular expansion acutely angled, its superior margin on a level with or above the maximum extent of the dorsal crest.

Lechriodus intergerivus sp. nov.

FIG. 2

Holotype: QM F16614. An almost entire left ilium collected at C.S. Site, Riversleigh Station, Queensland.

Description of holotype: Ilial shaft slightly curved and bears enlarged, fanlike dorsal crest whose maximum depth is at position approximately one-third from proximal end of shaft. Proximal one-half of crest concave on lateral surface, progressively becoming less pronounced distally. Distal half of crest flat.

Acetabular fossa small, deep and with prominent rim bounding inferior half. Dorsal margin of acetabular fossa situated slightly superior to inferior margin of ilial shaft.

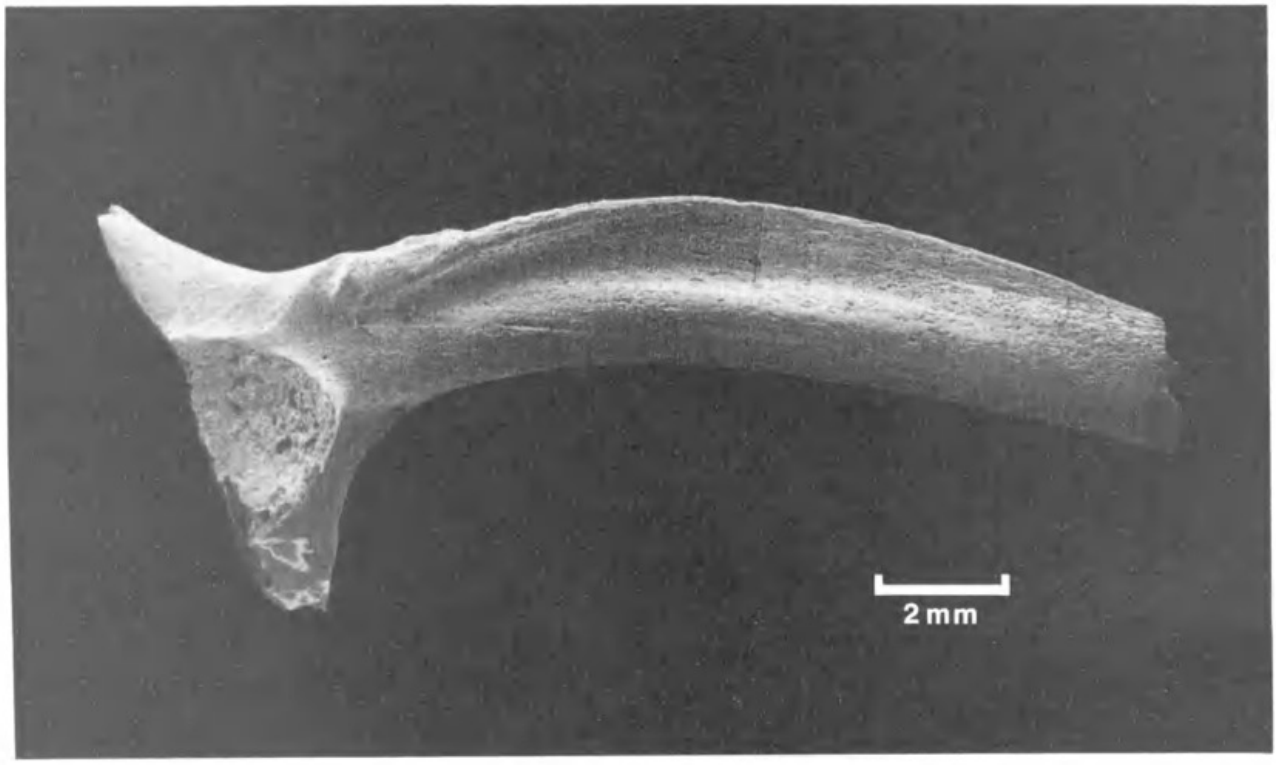

Fig. 2. S.E.M. of *Lechriodus intergerivus* (SAM P29771). A left ilium, but image reversed to aid comparison with Fig. 3.

Pre-acetabular zone evenly rounded with narrow separation from acetabular fossa. Ventral acetabular expansion poorly developed and incomplete inferiorly.

Dorsal acetabular expansion narrow but well developed superiorly, extending to position approximately on a level with maximum extent of superior margin of ilial crest.

Dorsal prominence poorly developed and scarcely detectable: in profile visible as slight superior extension upon dorsal margin of ilium. Dorsal protuberance ovoid, lateral, well developed and projecting laterally. Anterior margin of dorsal prominence extends to position slightly anterior to anterior margin of acetabulum.

Length of ilium 13.6 mm; DAE–VAE 3.7 mm; acetabular fossa maximum diameter 1.4 mm.

Paratypes: Henk's Hollow Site: SAM P29742; Two Trees Site: AM F76951–52, AMNH 25351–53; Last Minute Site: SAM P29764–65; Gag Site: AM F76957, AMNH 25355–58, SAM P27968; Upper Site: AM F76953–54, 76958, AMNH 25354, QM F16640–50, 17036–39, SAM P29734, 29743–44, 29757–62; C.S. Site : AM F76955–56, 76959, AMNH 25359–60, QM F16615–18, 16674, 17031–32, SAM P29746–50; Wayne's Wok Site: AM F76960, QM F16636–39, 17034–35, 17040–47, SAM P29756, 29766–67; Outasite Site: SAM P27929, 29751–55; R.S.O. Site: QM F16619–35, 17033, SAM P29735–41, 29745, 29771 (subject of S.E.M.).

Variation: The complete ilia range in length from 5.3 mm to 14.4 mm. A paratype is shown in Fig. 2. There is minimal difference in overall shape, and variation is largely confined to the position of the dorsal prominence in relation to the acetabulum. Thus some specimens agree with the holotype in having the anterior margin of the prominence on a level with the anterior margin of the acetabulum, in others the anterior half of the prominence may project beyond the acetabulum.

The extent and degree of the curvature of the dorsal crest varies in terms of its elevation, proximal limit and medial protrusion.

Referred specimens: Small portions of an additional 79 specimens are sufficiently complete to permit identification, but so fragmentary that they do not contribute to an understanding of the nature or variability of the species. For those reasons they are considered here "referred specimens" rather than paratypes. All of the referred specimens are lodged in the Queensland Museum: Henk's Hollow Site: F16652; Two Trees Site: F16688–89; Last Minute Site: F16673, 16675, 16678–79, 16685; Gag Site: F16651, F16676–77, 16680–83, 16686–87, 16700–01; Upper Site: F16658–59, 16665–72, 17050–53; C.S. Site: F16660–64, 16684, 16690, 17048; R.S.O. Site: F16653–57, 16691–99, 17049; Wayne's Wok Site: F16702–14, 17054–63.

Comparison with other species: Ilia of all extant species have been examined: *L. fletcheri* (Boulenger) (AUZ 8 uncat.); *L. melanopyga* (Doria) (AMNH 81223, AUZ 2 uncat.); *L. aganoposis* Zweifel (AMNH 74646), *L. platyceps* Parker (AMNH 74178). Representatives are shown in Fig. 3.

The comparisons assume that the sample size of *L. intergerivus* is sufficient to reflect with reasonable confidence the size of ilia attained by the species. With that assumption it is relevant to note that the absolute sizes of the ilia examined of each of the adults of New Guinea species is substantially larger than any of the *L. intergerivus*.

The relationship between ilial length and snout to vent length of extant species is almost linear. Thus given ilial length alone it is possible to extrapolate snout to vent length. The longest ilium of *L. intergerivus* is 14.4 mm. The corresponding snout to vent length derived from the closely lineal relationship of congeners is approximately 37.5 mm (Fig. 4). This, the apparent maximum is less than two-thirds of the size of the smallest adult *L. aganoposis* and *L. platyceps*, and is slightly below the range of *L. melanopyga* and *L. fletcheri* (Table 1). Clearly *L. intergerivus* is the smallest member of the genus.

As indicated by the generic definition, the ilium in this genus is conservative and interspecific variation is not pronounced. For that reason I am reluctant to ascribe differences in ilial characters greater significance than they may merit. However, given the data on size, the integrity of *L. intergerivus* is not in question.

Stratigraphy and lithology: The assumed stratigraphic sequence of the sites at Riversleigh is that followed in the list of paratypes. Of the sites named to date those containing *L. intergerivus* form an almost uninterrupted sequence. One of the fossil bearing sediments is described by Hand (1985) as fine-grained arenaceous freshwater limestones, and possibly a facies within the Carl Creek Limestone. The ages of the sediments containing *L. intergerivus* are currently understood to be between Late Oligocene and Middle Miocene (M. Archer pers. comm.).

Etymology: Latin for "placed between", so alluding to the geographic position of the fossil population between those of the extant species.

Phylogeny: Zweifel's (1972) proposed phylogenetic relationships is reproduced here as Fig. 5. Given the geographic location of *L. intergerivus* (Fig. 6), the age of the Riversleigh Station deposits, and the fact that the lower estimation of age is contemporaneous with the emergence and subsequent uplift of most

Fig. 3. Ilia of extant species with or without ischium and pubis: A. *Lechriodus fletcheri* (AUZ uncat.); B. *L. melanopyga* (AMNH 81223); c. *L. platyceps* (AMNH 74178); D. *L. aganoposis* (AMNH 74646).

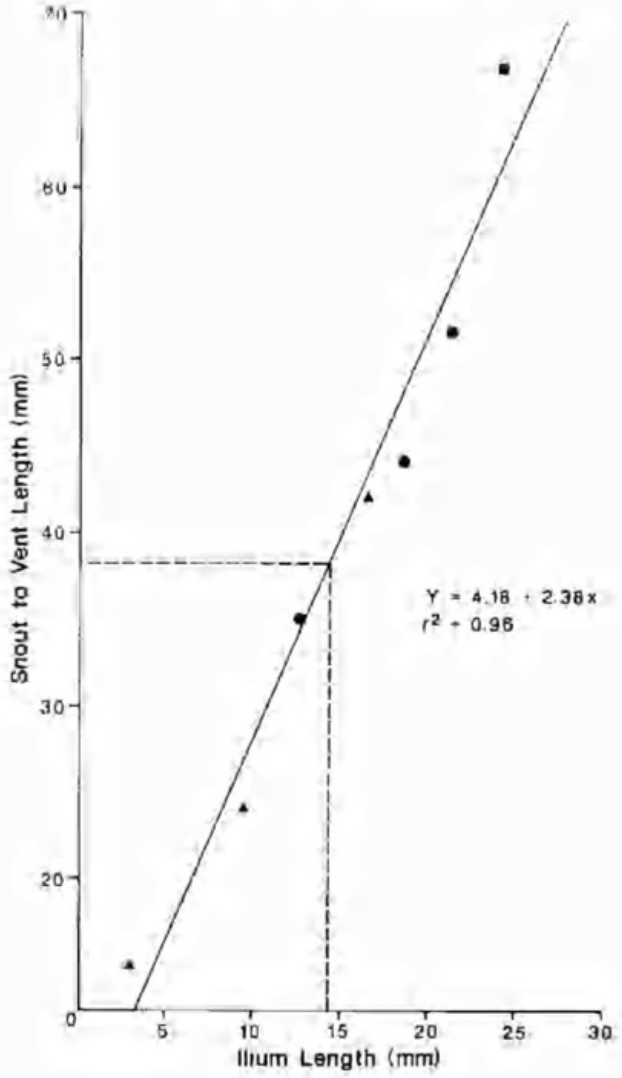

Fig. 4. Length of ilia of *Lechriodus* species plotted against snout to vent length. Assumed snout to vent length of fossil species indicated by broken lines. t-value for slope 10.891, $p < .001$. For $x = 14$, $y = 37.51$ (95% confidence limits = 33.75–41.25). Square = *L. platyceps*; circles = *L. melanopyga*; triangles = *L. fletcheri*.

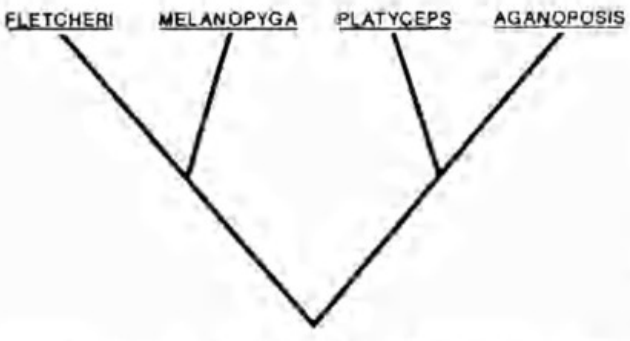

Fig. 5. Phylogenetic relationships of extant species of *Lechriodus* as postulated by Zweifel (1972).

of New Guinea, *L. intergerivus* is a candidate as the ancestral stock from which the extant species evolved.

With the existence of *L. intergerivus*, Zweifel's phenetic scheme would require two invasions into New Guinea: one deriving *L. melanopyga* from an intermediate ancestor that also gave rise to *L. fletcheri*, and the other leading to *L. platyceps* and *L. aganoposis*. A slightly simpler scenario would derive *L. fletcheri* directly from *L. intergerivus*, with a second stock giving rise to the three New Guinea species. Further systematic studies are required to test the validity of that option.

Discussion

The fossil frog fauna of Australia includes 22 species and nine genera from 10 sites of Quaternary or Tertiary age (Tyler 1989). Riversleigh Station appears likely to be the richest fossil frog site yet discovered, in terms of the number and diversity of species. This trend is common to other vertebrate classes, and Archer, Hand & Godthelp (1988) state that more than 200 new species have been recovered there. The frog fauna will increase the total.

Amongst the frog material from Riversleigh Station now available, *L. intergerivus* is the predominant species. Of 379 ilia now known from the site 190 (50%) represent that species.

Extant *Lechriodus* are predominantly inhabitants of temperate and sub-tropical rainforest and, in the absence of any data to the contrary, it can be inferred that the habitat of *L. intergerivus* would have been rainforest. A second point relevant to interpreting the mid-Miocene environment is the fact that a high proportion of the ilia of other frog species found in Riversleigh Station deposits are from small creatures. Because frogs lose water readily through the skin, the body mass/surface area ratio is such that small frogs are particularly vulnerable to dehydration. In consequence they are predominant only in areas which are moist throughout the year. In communities of frogs in Australia high frequency of small frogs occurs only in areas of high and seasonally reliable rainfall, such as the extreme southwest of Western Australia and the northern periphery of Arnhem Land in the Northern Territory (Tyler 1989).

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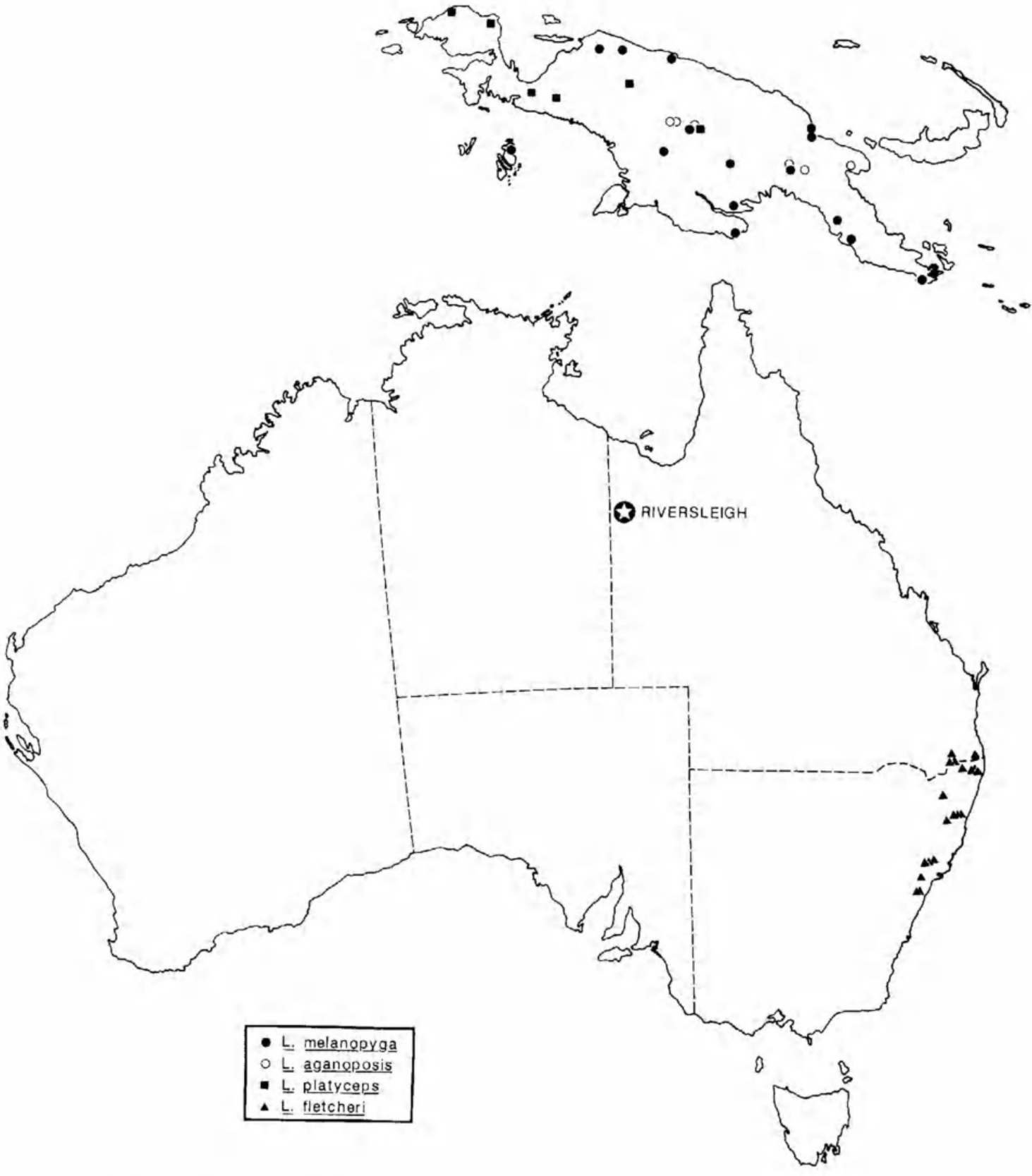

Fig. 6. Geographic distribution of *Lechriodus*.

TABLE I. *Size of* Lechriodus *species in millimetres.* Snout to vent length data mostly obtained from Zweifel (1972). Snout to vent length of donor *L. aganoposis* unknown, and maximum length of *L. intergerivus* extrapolated from Fig. 4.

species	snout-vent length		largest ilium examined			
	♂♂	♀♀	size of donor	ilium length	DAE-VAE	acet. fossa diam.
aganoposis	64–73	66–77	–	24.2	8.1	3.5
fletcheri	42–48	45–54	42	16.3	4.2	1.9
intergerivus	max. 41		?37.5	14.4	4.0	1.7
melanopyga	38–47	46–60	52	20.7	6.0	2.6
platyceps	64–78	72–95	67	24.0	7.8	3.8

played a vital role in that she undertook the cataloguing and initial sorting of material, and prepared Figures 1–2 and 4–6.

Dr R. G. Zweifel and Dr C. W. Myers (American Museum of Natural History) lent ilia of extant species and provided data about them, and Mr J. I. Menzies (National Museum & Art Gallery, Konedobu) provided distribution records from Papua New Guinea. Mr P. Kempster prepared Figure 3.

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OVER-SUMMERING REFUGES OF AQUATIC MACROINVERTEBMTES IN TWO INTERMITTENT STREAMS IN CENTRAL VICTORIA

*BY A. J. BOULTON**

Summary

Eight potential refuges for macroinvertebrates were sampled in two intermittent streams in central Victoria, Australia, during summer 1982-83 and summer 1983-84. Ninety-one aquatic taxa, mostly insects, were recorded. Receding pools harboured nearly three-quarters of these taxa; comparatively few were collected from the hyporheos or the water in crayfish burrows. Almost half the taxa were from refuges that did not hold free water. Macroinvertebrates persisted as desiccation-tolerant eggs (mayflies), larvae (chironomids and some beetles) or adults (beetles).

There was remarkable similarity between the broad taxonomic representation in these refuges and those described for intermittent streams in Ontario, Canada.

KEY WORDS: Intermittent streams, over-summering refuges, aquatic macroinvertebrates, Victoria, Australia, pholeteros, hyporheos.