The Skeletal Characters of *Leiopelma hamiltoni* McCulloch,
With Particular Reference to the Effects of Heterochrony on
the Genus

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Abstract

Comparison of the main skeletal features of the three species of *Leiopelma* Fitzinger
is made, the greater part of the skeleton of *L. hamiltoni* being described and illustrated
for the first time. The suggestion is made that *L. archeyi* Turbott is a genetically
neotenic form of *L. hamiltoni* McCulloch. The skeletal features of sexually mature
specimens of *L. archeyi* resemble those of immature stages of *L. hamiltoni*. As far as
external features are concerned, it appears that the only important difference between
*L. archeyi* and *L. hamiltoni* is that of maximum size.

Introduction

During earlier work (E. M. Stephenson, 1951, 1952), skeletal material of *L. hamiltoni*
McCulloch was not obtainable, and descriptions were confined to *L. hochstetteri*
Fitzinger and *L. archeyi* Turbott. Shortly afterwards, a single specimen of
*L. hamiltoni* from Stephens Is. in Cook Strait was made available through the
courtesy of the Hon. Minister for Internal Affairs, Wellington, and Mr. W. H.
Dawbin, then of the Victoria University of Wellington. The head of this frog was
sectioned and a brief comparison was made between it and the heads of the other
two species (E. M. Stephenson, 1955).

At the time of publication of the results of recent field studies on *L. archeyi*
and *L. hochstetteri* (E. M. and N. G. Stephenson, 1957), the distribution of
*L. hamiltoni* was thought to be confined to a small area on Stephens Is. Because
of this rarity of occurrence, the gift of a second specimen of *L. hamiltoni*, a male
of apparently advanced age, by Mr. W. H. Dawbin, was of particular value. The
specimen in question had been kept in captivity by Mr. Dawbin for some time. After
preparation of the frog as an alizarin transparency, a general comparative survey
of the skeletons of the three species was begun. Obviously, the material of *L. hamiltoni*
was far too limited to be satisfactory, but it was thought unlikely that more
would be available.

In 1957, an unexpected and extremely important discovery occurred. Mr. B.
Bell, of the Wild Life Branch of the Department of Internal Affairs, reported to
the Department that frogs of *L. hamiltoni* type had been discovered on Maud Is.
in Pelorus Sound. One of these specimens was sent to me at the request of the
Secretary for Internal Affairs in an endeavour to ascertain whether the Maud Is.
frogs should be assigned to a new species. Two more frogs were later supplied at
my request. In addition, Mr. Bell carried out an extensive series of measurements
of frogs on Maud Is. and these were compared with the measurements of a specimen
of *L. hamiltoni* in the Dominion Museum and one in the Canterbury Museum.

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As far as could be judged from all the evidence available, no justification for a change in the specific status of the Maud Is. frogs existed, but the discovery of a new and more favourable locality than Stephens Is. for *L. hamiltoni* was, of course, of very great importance. A key to the species and a discussion of the name for the family are to be found in a recent publication (E. M. Stephenson, 1960).

**Acknowledgments**

I wish to acknowledge with thanks the help afforded by the following:

The Hon. Minister for Internal Affairs, Wellington, for permission to collect specimens of *Leiopelma* on various occasions, and particularly for permission to study specimens of *L. hamiltoni*.

Mr. B. Bell, Senior Field Officer of the Wild Life Branch of the Department of Internal Affairs, Wellington, for collecting three specimens of *L. hamiltoni* from Maud Is. and for carrying out a tedious series of measurements in the field at my request.

Mr. W. H. Dawbin, Department of Zoology, University of Sydney, for providing two specimens of *L. hamiltoni* from Stephens Is.

My husband, Dr. N. G. Stephenson, Department of Zoology, University of Sydney, for help in collecting and studying frogs in the Coromandel and other regions, and for reading the present manuscript.

Dr. J. Ruthven Lang and Mr. S. Lang, of Auckland, Mr. R. Bartley and Mrs. H. Smith, of Port Charles, for assistance during field work on Mt. Moehau.

**Material and Methods**

Details of the specimens illustrated or examined are provided below for each part of the skeleton described.

Five specimens of *L. hamiltoni* were available, two from Stephens Is. and three from Maud Is. One of the former had been partly sectioned for previous examination of the head (E. M. Stephenson, 1955). The other specimen from Stephens Is. and two of the specimens from Maud Is. were used to prepare alizarin transparencies, following examination with special reference to the condition of the gonads. The head of the third and obviously youngest specimen from Maud Is. was sectioned, and the hyoid reconstructed, the rest of the body being used for an alizarin transparency.

Specimens of *L. archeyi* and *L. hochstetteri*, collected under previous permits and prepared as alizarin or toluidine blue transparencies, included as far as possible a representative series, although of course the actual age of any specimen was not known.

Where necessary, reference was made to previously prepared slides of heads of all three species (E. M. Stephenson, 1951, 1955).

**The Skull** (Text-fig. 1)

Descriptions or comments on the whole or parts of the adult skull of *Leiopelma* include those of Wagner (1934a, 1934b), de Beer (1937), E. M. Stephenson (1951), van Eeden (1951), E. M. Stephenson (1955).

My first investigations (1951) dealt with the heads of *L. archeyi* and *L. hochstetteri*. When a specimen of *L. hamiltoni* became available, a brief description of the head was published (1955), including photographs and reconstructions of certain regions, but a reconstruction of the entire skull was not provided. In the light of evidence arising from the present studies, it is probable that explanations for the differences between the head of the specimen of *L. hamiltoni* in question and those of *L. archeyi* can be provided on neotenic grounds. In the present discussion, however, attention is focused exclusively on skeletal structures.
Figure 1A illustrates the condition of the skull of a mature female specimen of *L. archeyi*, while Figure 1B shows the condition in an old male specimen of *L. hamiltoni*. Although basically similar to each other and to the skull of *L. hochstetteri*, certain points of difference are obvious as far as the bony structures are concerned. In view of the previous descriptions already referred to, no attempt at a comprehensive description is made here. Certain bones, the development of which is variable with respect to time and species, are selected for discussion.

1. **The exoccipital and prootic.**

The exoccipital and prootic of each side tend to be widely separated by uncalcified cartilage in all specimens of *L. archeyi* so far examined. Only in one specimen of *L. archeyi*, of obviously advanced maturity, is any evidence of intervening calcification present. The specimen in question, TA, came from a Tokatea Ridge population. Wide separation of the prootic and exoccipital is the case in smaller (and undoubtedly fairly young) specimens of *L. hamiltoni*. As shown in Figure 1B, however, ultimate fusion of these bones occurs. This condition has been recorded also for *L. hochstetteri* (E. M. Stephenson, 1951, 278).

2. **The quadrate and articular.**

In *L. archeyi*, the quadrate and articular are cartilaginous and uncalcified in all specimens so far examined. In *L. hamiltoni*, with increasing age, they become ossified, but the rate of bone development seems to be relatively slower than in *L. hochstetteri* (E. M. Stephenson, 1951, 279). In fact, in a female *L. hamiltoni* of 44 mm body length, the quadrate and articular are still largely cartilaginous although ossification centres are visible. In a specimen of *L. hochstetteri* of body length 36 mm, ossification of the quadrate and articular is already fairly well advanced.

3. **The sphenethmoid.**

The differential rate of development of this bone has already been pointed out (E. M. Stephenson, 1951, 278). It is rare to find any trace of a sphenethmoid ossification in *L. archeyi*, except in occasional large and relatively old specimens—e.g., TA from Tokatea Ridge.

In *L. hamiltoni*, development of a bony sphenethmoid is associated with advancing age. In the two youngest specimens examined, the specimen of *L. hamiltoni* previously described (1955) and an obviously young female from Maud Is. (26 mm body length), no trace of a sphenethmoid is visible. In two mature females from Maud Is. it shows transitional stages. In the first specimen (39 mm body length), the orbitosphenoid extension is clearly ossified on one side and scarcely at all on the other. In the region of the nasal septum, fairly heavy staining can be seen in an alizarin transparency. In the second specimen (44 mm body length), the whole sphenethmoid is formed of bone, with perhaps a small amount of calcified cartilage. In the male specimen from Stephens Is., of slightly smaller size but of apparently greater age than the previous frog, the sphenethmoid has the condition illustrated in Figure 1B. In the same frog, in addition to the clear ossification in the region of the nasal septum and the orbitosphenoids, patches of somewhat irregular ossification occur further forward than normally in the nasal region, and also in the cartilage of the lamina orbitonasalis. A similar condition has not so far been recorded in any other specimen of *Leiopelma*. The ossified areas probably illustrate the tendency of the sphenethmoid to develop further with increasing age. It might even be possible to find a specimen of *Leiopelma* in which the sphenethmoid is of sufficient extent to incorporate lateral ethmoid ossifications as well as a more extensive ossification in the anterior nasal region. Such a condition is apparently not uncommon in certain anurans, as reference to a number of diagrams in Parker's monumental work (1881) will show. It is, however, obviously unwise to draw too many conclusions from the isolated specimen of *L. hamiltoni* illustrated in Figure 1B.
The condition of the sphenethmoid in *L. hochstetteri* has previously been illustrated (E. M. Stephenson, 1951, 277). It approximates to the condition in *L. hamiltoni*, but again probably ossifies at a relatively faster rate. It is recognisable in at least one specimen of *L. hochstetteri* of 27 mm body length.

**THE HYOID APPARATUS (Text-fig. 2)**

In 1951, I recorded that certain differences in the hyoid skeleton appeared to have a specific basis, as follows:

<table>
<thead>
<tr>
<th><em>L. hochstetteri</em></th>
<th><em>L. archeyi</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Definite anterior process present.</td>
<td>1. No definite process. Sometimes a slight expansion of the ceratohyal.</td>
</tr>
<tr>
<td>2. A clearly defined alary process present.</td>
<td>2. Alary process absent. (Except in one case (Trewavas, 1933) in which a small and unexpanded process was recorded.)</td>
</tr>
<tr>
<td>3. Ceratohyal relatively narrow.</td>
<td>3. Ceratohyal relatively wide.</td>
</tr>
</tbody>
</table>

In 1954, a head of *L. hamiltoni* was sectioned. The hyoid, unfortunately, was extremely buckled and a good reconstruction was impracticable. It could be seen, however, that an anterior process was absent, an alary process of simple type was present, and that the ceratohyal was relatively wider than in *L. hochstetteri*. Unfortunately, through an oversight, the reverse condition with regard to alary and anterior processes was recorded—i.e., it was stated that an anterior process was present and an alary process was absent (E. M. Stephenson, 1955, 799).

Fortunately, further material of *L. hamiltoni* has since become available. Figure 2F illustrates the hyoid of an old male specimen of *L. hamiltoni* from Stephens Is. An anterior process is absent and a slightly expanded alary process is present. The condition of the latter is not nearly so definite as in *L. hochstetteri* (Fig. 2B). The hyoid cornu is of no greater relative width than in *L. hochstetteri*.

Figures 2C and 2D illustrate the hyoids of female specimens of *L. hamiltoni* from Maud Is. In C, a small but definite anterior process is present, but in D a process of this kind is completely lacking. In a third specimen (not illustrated), the ceratohyal is expanded in the region in question. All three specimens show a slight though variable degree of expansion to form what can be called an alary process, but again this does not approach the condition of the same process in *L. hochstetteri*.

The hyoids of two specimens of *L. archeyi* are also illustrated (Figs. 2A and 2E). Neither provides any indication of an anterior process, but A shows a slight expansion to form an alary process. In both, the hyoid cornu is relatively wider than in the specimens of *L. hamiltoni* examined, though in neither A nor E is the condition so apparent as in the specimen illustrated previously (E. M. Stephenson, 1951, Fig. 15B).

From the data provided above, an amended table can be drawn up as follows:

<table>
<thead>
<tr>
<th><em>L. hochstetteri</em></th>
<th><em>L. archeyi</em></th>
<th><em>L. hamiltoni</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1. A very clearly defined anterior process present.</td>
<td>1. Anterior process absent. Sometimes a slight expansion of the ceratohyal (Trewavas, 1933).</td>
<td>Anterior process highly variable, embracing any of the following conditions:—</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(a) Completely absent.</td>
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<tr>
<td></td>
<td></td>
<td>(b) Represented by a slight expansion of the ceratohyal.</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(c) Present and clearly defined, though small.</td>
</tr>
<tr>
<td>2. Clearly defined alary process present.</td>
<td>2. Alary process completely absent or slightly developed.</td>
<td>2. Alary process recognisable but not developed to the extent found in <em>L. hochstetteri</em>.</td>
</tr>
</tbody>
</table>
As far as the relative width of the ceratohyal is concerned, this is greater in *L. archeyi* than in *L. hamiltoni*. If, in fact, *L. archeyi* is comparable to a juvenile stage of *L. hamiltoni*, this is to be expected. It is probable that the specimen of *L. hamiltoni* described previously (E. M. Stephenson, 1955) was younger than any of the members of the same species described in the present account.

From the data supplied above it is clear that the hyoids of *L. archeyi* and *L. hamiltoni* have a much closer resemblance to each other than either of them does to the hyoid of *L. hochstetteri*.

A parahyoid bone is normally present in all three species. Its absence has been recorded in one specimen of *L. archeyi* (Fig. 2E).

*Ascaphus truei* has an anterior process but lacks an alary process (de Villiers, 1934a, and personal observation).
THE VERTEBRAL COLUMN (Text-fig. 3)

The vertebral column of *L. hochstetteri* has already been described in some detail (E. M. Stephenson, 1952). Further illustrations are included here for the sake of completeness as far as the genus is concerned. At the time of publication of the previous description, the vertebral column of *L. hamiltoni* had not been examined.

Ritland (1955) has provided a full description of the vertebral column of *Ascaphus*, with supplementary remarks concerning that of *Leiopelma*. He includes a discussion relating to the failure of the term "amphicoelous" alone to cover adequately the vertebral condition of *Leiopelma* and *Ascaphus*. However, as no completely satisfactory single term has yet been devised to replace "amphicoelous" it seems necessary to retain the latter in order to place the vertebrae of these two genera in a category separate from those of other anurans.

The vertebral column of *L. hamiltoni* (Fig. 3A) exhibits the essential characteristics already described for *L. hochstetteri*. The pattern of the vertical column of *L. archeyi* is also similar except that typically the whole series has a more delicate appearance, with a relatively greater amount of uncalcified cartilage in evidence.

In the vertebral column of the old male specimen of *L. hamiltoni* illustrated (Figs. 3A, 3C, and 3F), considerable calcification of cartilage and certain bony fusions have occurred. The ribs are partly fused with the transverse processes of the vertebrae concerned, while the characteristic forked and flattened expansions of the lateral extremities of the second pair of ribs, though visible dorsally, are largely fused together.

In all three species, nine presacral vertebrae are present except in occasional cases where fusion of two adjacent vertebrae is obvious. The urostyle has usually at least one pair of well-defined transverse processes developed on the first post-sacral vertebra. Of these vertebrae, portions of three may sometimes be distinguished from the dorsal aspect of the urostyle.

The sacral vertebra, as already reported for *L. hochstetteri* (E. M. Stephenson, 1952), consists of two separate bony halves joined dorsally and ventrally by units of cartilage. This condition, which is not found in *Ascaphus*, is possibly unique among anurans. In the vertebral column of the specimen of *L. hamiltoni* illustrated in Figs. 3A, 3C and 3F, the ventral cartilage of the sacral region has remained uncalcified, but the dorsal portion, forming what is in effect the highest point of the neural arch, is seen to be heavily calcified, with possibly some development of bone. It still remains, however, as a discrete element and has been pushed slightly out of position by partial fusion of the two bony halves of the vertebra. Dorsal views of the same region in a mature specimen of *L. archeyi* and a young *L. hochstetteri* are provided (Figs. 3B and 3E).

Figure 3D illustrates the condition found in an immature female *L. hochstetteri*. This should be compared with the photograph of the vertebral column of an adult specimen of *L. hochstetteri* previously published (E. M. Stephenson, 1955, 610). It is of some interest to note that the uncinate processes typically seen on the most anterior pair of ribs are seen on the second pair in Fig. 3D.

As has already been reported (E. M. Stephenson, 1952, 606), fusion of two adjacent vertebrae is occasionally seen. It seems unlikely that this feature, as far as *Leiopelma* is concerned, is of any particular phylogenetic significance or that it provides evidence of a tendency towards specialisation. More probably, it indicates the fact that in the populations concerned, such occurrences are of little selective importance.

THE PECTORAL GIRDLE (Text-fig. 4)

An outline diagram of the pectoral girdle of *L. hamiltoni* was provided with McCulloch's first description of the species (1919). De Vos (1938a) was the first
TEXT-FIG. 4.—Pectoral Girdle. (Sternum omitted. All girdles flattened out into one plane.)
to provide a description and a reconstruction of the pectoral girdle of any species of *Leiopelma*. A further outline description (E. M. Stephenson, 1952) was discussed by Ritland (1955) and two corrections, involving the position of the cleithrum and the shape of the suprascapula, were made by him. Ritland also described in more detail than previous authors the pectoral girdle of *Asaphus*.

Pectoral girdles of the three species of *Leiopelma* are illustrated in Fig. 4. Comparing these with the diagrams of the pectoral girdle of *Asaphus* (Ritland, 1955, 146), it is clear that in *Leiopelma* the clavicle does not extend so far laterally, relative to the scapula, as it does in *Asaphus*.

The extent to which a procoracoid element can be identified varies with the species and from specimen to specimen within a species. It appears to develop and to ossify at a relatively faster rate in *L. hochstetteri* than it does in the other two species, in fact it seems probable that in *L. archeyi* and *L. hamiltoni* it does not ossify at all.

Fig. 4C illustrates the pectoral girdle of a mature male specimen of *L. hochstetteri*, in which the procoracoid is seen as an obvious bony element. A similar condition, seen in external view, is illustrated in Fig. 3 in a previous publication (E. M. Stephenson, 1952, 607). No specimen of *L. archeyi* so far examined by the author has shown any trace of a procoracoid ossification and alizarin transparencies show no differential staining of the area in question (Fig. 4D). In specimens of *L. hamiltoni* examined, alizarin transparencies of two mature females and one old male show pink staining in the region where a procoracoid would be expected, but it has not been found as a discrete bony element.

**The Abdominal Ribs**

These structures have previously been described and illustrated (E. M. Stephenson, 1952, 608). In general, these elements and the styles of the sternum remain cartilaginous and uncalcified in *L. archeyi* but tend to become heavily calcified and even ossified in mature specimens of *L. hochstetteri*. In mature specimens of *L. hamiltoni*, it is quite common to find completely cartilaginous abdominal ribs, but calcification and ossification have been noted in this species.

**The Pelvic Girdle (Text-fig. 5)**

Description or discussions of the pelvic girdle of *Leiopelma* include those of de Villiers (1934b), E. M. Stephenson (1952), Ritland (1955), and van Dijk (1955).

In general, in *L. archeyi*, the pubis remains cartilaginous throughout life. It is typically unstained in alizarin transparencies (Fig. 5A).

In *L. hochstetteri*, at least in some of the more mature specimens examined, the pubis shows a lateral and somewhat superficial development of bone and/or calcified cartilage which tends to extend as a strip towards the ilium or ischium or both. The whole arrangement is somewhat irregular, but the general position is constant. The epipubis typically shows extensive calcification or ossification (Fig. 5B).

The old male specimen of *L. hochstetteri* illustrated in Fig. 5B shows essentially the condition described above for *L. hochstetteri*, but the pubic ossification is complicated by irregular development of calcified cartilage, producing fusion with the ischium. The epipubis also shows irregular calcification. Mature female specimens of *L. hamiltoni* (Fig. 5C and another specimen not illustrated) show deep pink staining in the lateral region of the pubis, but the latter is quite clearly cartilaginous. The epipubis is unstained in both cases.

Comparing the pelvic girdle of *Leiopelma* with that of *Asaphus*, it is found that the condition of *L. hochstetteri* resembles that of *Asaphus* more closely than does that of the other two species. However, examination of a male specimen of

Ascaphus prepared as an alizarin transparency shows that this specimen at least possesses a far more rigid and fused condition of the pelvic elements as a whole and a more definite lateral pubic ossification than any specimen of L. hochstetteri so far examined.

Limb Bones

The limb bones are not here described in detail but the same sort of comparative picture exists as for other parts of the skeleton. L. archeyi has a relatively greater degree of uncalcified cartilage and less fusion of elements in general than either of the other two species.

The Carpus (Text-fig. 6)

It will be seen from the representative series of distal carpal bones of all the species and both sexes as illustrated in Figure 6 that ossification and/or calcification is well advanced in mature specimens of L. hamiltoni and L. hochstetteri (Figs. 6A, J.
In L. archeyi, however, even in specimens which are apparently sexually mature, only a relatively slight degree of ossification occurs (Figs. 6B, 6C, 6D and 6H).

Individual variation in fusion of the distal elements is very pronounced. Typically, eight free carpal elements are observable, while the metacarpal of the prepollex is usually distinguishable. In Fig. 6C, however, this metacarpal is fused with the adjacent carpal element. In some cases, evidence has been noted of two apparent centres of ossification in the metacarpal of the prepollex, but in only one case, a specimen of L. hochstetteri, has a clear separation of a metacarpal element and a phalanx of the prepollex been noted. Unfortunately, this condition was illustrated by the author in a previous paper (E. M. Stephenson, 1952, 610) and gives the impression of being the normal condition for the genus. It would appear from all specimens examined recently that a condition involving a separate phalanx of the prepollex is an uncommon individual variation of little significance. If this is the case, Bombina alone (Ridewood and Howes, 1888) among the Discoglossidae and Ascaphidae commonly possess a phalangeal element of the prepollex.

The simple, relatively small, and usually cartilaginous metacarpal of the prepollex of Leiopelma is far removed from the corresponding enlarged and specialised bony element of Ascaphus (Figures of Ritland, 1955, and personal observations).

THE TARSUS (Text-fig. 7)

The tarsal elements of six different specimens representing the three species of Leiopelma are illustrated. Even in mature specimens of L. archeyi of both sexes (Figs. 7B, 7C and 7F) no alizarin staining of the distal tarsal elements occurs. Various ossification centres can be seen in the carpal elements figured for L. hamiltoni and L. hochstetteri, but it is difficult to generalize from these. In several specimens of L. hamiltoni from Maud Is., including two fully mature females, very few traces of staining of the distal tarsal elements could be seen. It would seem that the process of ossification of these elements occurs relatively more quickly in L. hochstetteri than in the other two species. The elements do not appear to ossify in any observable fixed order.

As with the carpus, variations occur in the fusions of the distal elements. In L. archeyi, in addition to the tibiale and fibulare, the most common pattern of tarsal elements appears to include five free distal elements. A small metatarsal of the prehallux is usually present. The specimen illustrated in Fig. 7B has an additional element on both sides. In Fig. 7F, the metatarsal of the prehallux is fused with the adjoining tarsal element although an indication of demarcation between them can be seen.

In one specimen of L. hamiltoni (Figs. 7D and 7G), an additional small element is present distally to the metatarsal of the prehallux. This presumably represents a phalanx of the prehallux, an element not represented in any adult Discoglossid or in Ascaphus. It has not been found in any other specimen of L. hamiltoni so far examined and probably it is merely an individual variation of little phylogenetic significance.

DISCUSSION

The main fact emerging from a comparison of L. archeyi and L. hamiltoni is that a sexually mature specimen of L. archeyi is typically comparable with an immature form of L. hamiltoni as far as size and skeletal characters are concerned. Externally, the two species resemble each other closely, except for the maximum sizes attained (47 mm for L. hamiltoni and 41 mm, recorded once, for L. archeyi), and the fact that a green colour pattern, sometimes seen in L. archeyi, has not been

It seems evident that the skeletal and size differences referred to are due to the influence of the phenomenon of heterochrony or heterochronism, which involves essentially a departure from a typical ancestral sequence in the formation of certain organs. The implication here is that *L. archeyi* shows either a relative retardation in the rate of development of the body (soma) as compared with the gonads, or the development of precocious sexual maturity in a juvenile stage. Owing to complete absence of knowledge of rates of development in all except the very earliest post-hatching stages (Archey, 1922; N. G. Stephenson, 1951a, 1951b) in *L. archeyi*, and none at all in *L. hamiltoni*, the actual condition operating is difficult to determine.

Some discrepancies exist in the literature regarding the terminology for various conditions involving heterochrony, but an admirable discussion by de Beer (1958) elucidates most of the doubtful points. According to this authority, either of the conditions mentioned above can be included under the general term “neoteny”.

It seems a feasible suggestion that relative acceleration of sexual development compared with general somatic development could have had a favourable selective influence in permitting reproduction at an earlier age and even perhaps making possible a greater over-all breeding capacity. The last suggestion is, of course, pure surmise. The acceleration in question, however, could also be leading to the specialization apparently being shown in the skeleton of *L. archeyi*, with its tendency towards the loss of certain bony elements and the relative increase in the amount of cartilage. Noble (1931, 104) pointed out that among the various trends of evolution among amphibia is “the reduction in the number of skeletal elements and the increase in cartilage”. He further described this tendency as “progressive foetalization”.

An interesting point previously made (E. M. and N. G. Stephenson, 1957) is that the *L. archeyi* population on the slopes of Mt. Moehau and the population of the same species on the Tokatea Ridge appears to have different means and different maxima as far as body lengths are concerned. It has not been possible to carry out an extensive comparative survey of skeletal features of frogs in the two areas, but from the small amount of evidence available it seems reasonable to suggest that the typically smaller frogs of the Mt. Moehau area may show a more marked degree of neoteny than the relatively larger forms on the Tokatea Ridge.

*L. hochstetteri* is distinct from *L. archeyi* and *L. hamiltoni* as far as external features such as the presence of a half web and the absence of parotoid glands are concerned. It also shows a greater degree of external similarity to *Asaphus truei* Stejneger than do either of the other species. With regard to its skeletal features, particularly the relatively greater development of bony elements, *L. hochstetteri* appears to exhibit more primitive characteristics than either *L. archeyi* or *L. hamiltoni*. Evidence from the present investigation suggests that the cause of anatomical discrepancies of the kind indicated has been the operation of a process of neoteny.

**Key to the Lettering of the Text-Figures**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>ce</em>—centrum</td>
<td>fi—fibulare (calcaneum)</td>
</tr>
<tr>
<td><em>ch</em>—ceratohyal</td>
<td><em>fp</em>—frontoparietal</td>
</tr>
<tr>
<td><em>cl</em>—clavide</td>
<td><em>il</em>—ilium</td>
</tr>
<tr>
<td><em>clt</em>—cleithrum</td>
<td><em>is</em>—ischium</td>
</tr>
<tr>
<td><em>cor</em>—coracoid</td>
<td><em>lon</em>—lamina orbitonasalis</td>
</tr>
<tr>
<td><em>cpg</em>—paraglenoid cartilage</td>
<td><em>mpl</em>—metatarsal of prehallux</td>
</tr>
<tr>
<td><em>epb</em>—epiphysial bar</td>
<td><em>mpp</em>—metacarpal of prepollex</td>
</tr>
<tr>
<td><em>epc</em>—epicoracoid</td>
<td><em>ms</em>—maxilla</td>
</tr>
<tr>
<td><em>epu</em>—epipubis</td>
<td><em>na</em>—nasal</td>
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<tr>
<td><em>exac</em>—exoccipital</td>
<td><em>op</em>—operculum</td>
</tr>
<tr>
<td><em>fgl</em>—glenoid foramen</td>
<td><em>par</em>—parahyoid</td>
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REFERENCES


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