The Vertebral Column of the Anura: Its Bearing on the Classification.

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SINCE the publication of my article on "The Vertebral Column of the Anura,"[1] I have come across some contributions on the subject, published later to Nicholls' work[2] and really too important to be overlooked in a general résumé in this connection. It is only fair to indicate briefly, how this later investigation adds to our knowledge of the vertebral column of this group, and to bring the matter of my article to date.

Apparently, for five or six years, Nicholls' work (1916), an extremely valuable piece of pioneering research though it was, passed off practically neglected. Then in 1922 appeared Noble's masterly study[3] on the Phylogeny of the group, a paper in which a careful scrutiny was made of all the bases of Salientian classification and new myological data were brought forward in order to help to make the classification natural. As far as the vertebral column is concerned, Noble followed Nicholls in essentials, and pointed out that Nicholls' four divisions of the Anura (*viz.*, *Opisthocœla*, *Anomocœla*, *Procœla* and *Diplasiocœla*) "group the frogs and toads into natural categories".[4] According to him, "of all the characters which have been fully investigated, those of the vertebral column seem · · · the most important"[5] in a natural system of classification.

Noble examined 113 skeletons, prepared by a modification of Schultze corrosive technique, combined with a staining process. Of this number, fifty specimens belonging to the following species formed exceptions to the conclusions reached by Nicholls; the rest agreed:—

(*a*) *Procœlous Vertebral Column* (instead of a diplasiocœlous one):

Arthroleptis pœcilonotus; *A. variabilis*; *Atelopus elegans*; *A. ignescens*; *A. varius*; *Brachycephalus ephippium*; *Cardioglossa elegans*; *Dendrobates parvulus*; *D. trivittatus*; *D. tinctorius*; *Geobatrachus walkeri*; *Hyloxalus collaris*; *Phyllobates boulengeri*; *P. infraguttatus*; *P. trinitatus*; *Rhinoderma darwinii*; *Sminthillus limbatus*; and *S. peruvianus*.

(*b*) *Other deviations*:

Dendrobates typographus, and *D. tinctorius* fusion of the II + III and VIII + IX.

Phrynobatrachus dendrobates: VIII opisthocœlous; VII biconcave.

Rana cœruleopunctata, *R. christyi* and *R. pipiens* (?) VIII + IX (sacral) fused.

All these exceptions refer to Nicholls' tribe[6] *Diplasiocœla*; and while there can be no doubt that some of them at any rate were abnormalities, the others show that this subdivision is really not strictly circumscribed from the *Procœla*. As a result of these observations, coupled with the nature of the pectoral girdle[7] and the presence of bufonid-like thigh muscles, Noble felt it necessary to create a new family (*Brachycephalidæ*) within the suborder *Procœla*, in order to accommodate the neotropical toads with procœlous vertebræ, and thereby to relieve the families *Ranidæ* and *Brevicipitidæ* (= *Engystomatidæ*)[8] of a great many exceptions[9] to their characteristic, diplasiocœlous type of vertebral column. One should like to mention, however, the following anomalous cases, definitely known still to remain in the suborder *Diplasiocœla* and to point out that a careful scrutiny of the remaining genera would probably add to such cases:

Ranidæ ..	*Micrixalus*
	Nannobatrachus
	Rhacophorus[10]
	Ixalus
	Arthroleptis
	Cardioglossa
Brevicipitidæ:	*Rhombophryne*
	Asterophrys[11]

It is hardly necessary to state that a thorough anatomical examination of such exceptional genera alone can bring forward the data, required for deciding whether the suborder *Diplasiocœla*, as at present constituted, should be regarded as a natural group, with some persisting, procœlous forms reminiscent of its origin from procœlous ancestors (Fig. 1), or it should be made homogeneous (as far as the vertebral

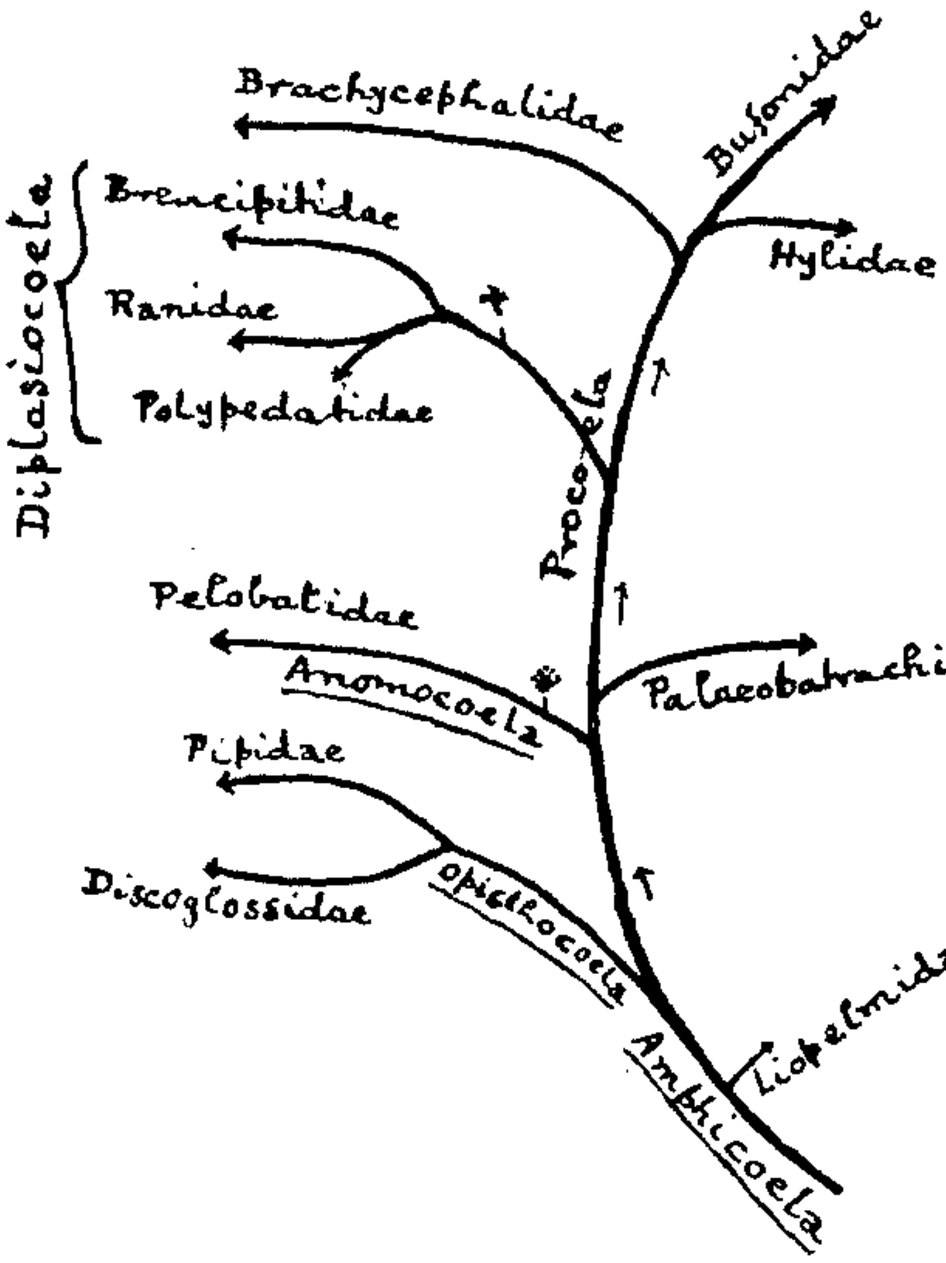

Fig. 1. Phylogenetic relationships of the Anura (after Noble, 1931, with slight modifications).
* Probable position of *Megalophrys*.
† Position of procœlous ' diplasiocœla '.

character is concerned) by shifting the exceptions to the suborder *Procœla*. A student of mine is undertaking such a scrutiny of pertinent oriental genera, and I hope that his studies will have much taxonomic importance in this connection.

Of the two exceptions to the suborder *Anomocœla*, recorded by Nicholls, one (*Asterophrys*) is shifted on by Noble in a later work (1931)[12] to the family *Brevicipitidæ*, and the other (*Megalophrys*) still remains within the family *Pelobatidæ*, a case perhaps to be accounted for as retaining the primitive ancestral type of vertebral column.

As the bearing of vertebral characters on the classification of the Anura is at present recognised, we may recapitulate the main points in which Noble's classification (Fig. 2, B) marks an advance over the older, more prevalent[13] one (Fig. 2, A). In the first place, Noble disregards the subdivision of the Anura on the basis of the presence or the absence of the tongue (*Aglossa* and *Phaneroglossa*), and of the *Phaneroglossa* on the character of the pectoral girdle (*Arcifera* and *Firmisternia*); his primary

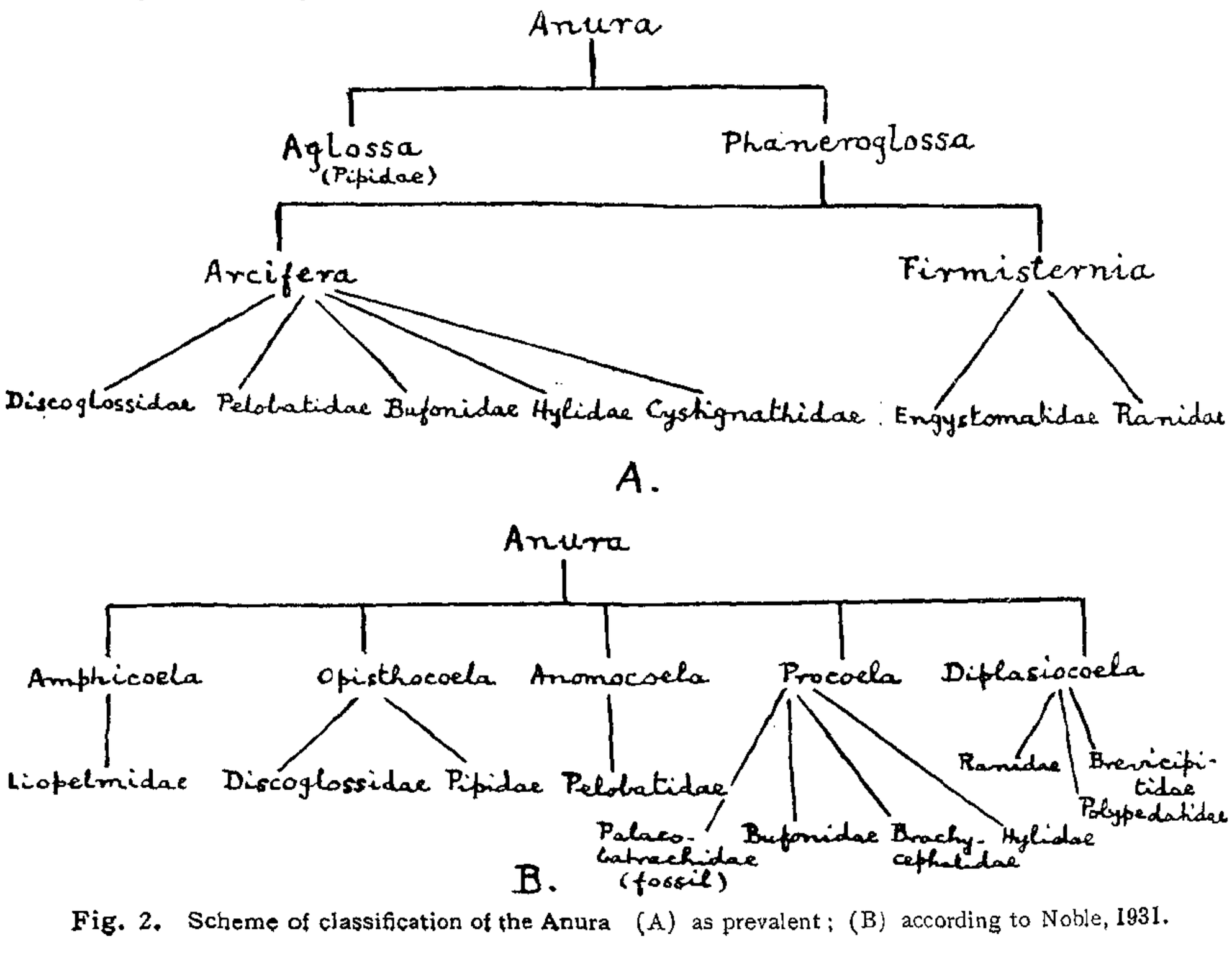

Fig. 2. Scheme of classification of the Anura (A) as prevalent; (B) according to Noble, 1931.

subdivisions rest on the characters shown by the vertebral centra, in accordance with the findings of Nicholls. To the four main divisions of Nicholls, however, he adds[14] a fifth suborder *Amphicœla*, consisting of a single family, *Liopelmidæ* with the two remarkable genera, *Liopelma*[15] of New Zealand and *Ascaphus*[16] of the North-Western United States. These genera, besides showing many apparently primitive features, are unique amongst the tailless Batrachia in possessing two tail-wagging muscles, the *pyriformis* and the *caudalipuboischiotibialis*, even though neither of them has a tail.

Secondly, as a result of the above-mentioned change, Noble includes the aglossid family *Pipidæ*—along with the family *Discoglossidæ* (*Phaneroglossa*), to which it is apparently allied—in one and the same suborder *Opisthocœla*. Such an arrangement was already proposed by Lataste[17] in 1879 and by Blanchard[18] in 1885.

Thirdly, Noble deletes[19] the family *Cystignathidæ* (*Leptodactylidæ*) and adds the genera of toothed toads to the family *Bufonidæ*. According to him, the toothed forms are more primitive than the toothless ones, but "as they have given rise to toothless bufonids in different parts of the world, it makes a more natural system to group toothed and toothless genera together as a single family."[20]

Fourthly, as already mentioned above, he creates a new family, *Brachycephalidæ*, within the suborder *Procœla* and thus removes the procœlous, neotropical toads from the suborder *Diplasiocœla*.

Fifthly, he distinguishes the diplasiocœlous frogs with intercalary cartilages as a separate family (*Polypedatidæ*)[21] from those in which the digits lack them (*Ranidæ*).

In the end, we must add that Noble's classification, superior though it undoubtedly is to the time-honoured old one, has not so far met with the publicity and acceptance which it deserves. Nieden and Ahl (1923, 1926, 1931),[22] Goodrich (1930),[23] Versluys (1931)[24] and the text-book writers are either not aware of it or are inclined to disregard it. Werner's statement (1931) that "Bikonkave (amphizöle), vorn ausgehöhlte (prozöle) und hinten vertiefte (opisthozöle) Wirbel kommen in nahe verwandten Gruppen vor, sind daher von geringerer klassifikatorischer Bedeutung, als man früher annahm"[25] is apparently in agreement with Gadow's view (1901) that "the systematic value of this pro- or opisthocœlous character has been much exaggerated"[26] and with Boulenger's verdict: "It is therefore clear that this character, however important it may appear at first, is worthless even as a specific character in these[27] Batrachians."[28]

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[1] *Curr. Sci.*, 1936, **4**, No. 10, 744.

[2] Nicholls, G. E., *Proc. Linn. Soc. Lond.*, 1915–16, Session 128, 80–92.

[3] Noble, G. K., *Bull. Amer. Mus. Nat. Hist.*, 1922, **46**, 1–88.

[4] Noble, G. K., *op. cit.*, 13.

[5] Noble, G. K., *op. cit.*, 21.

[6] Noble calls these subdivisions *suborders* not *tribes*.

[7] Arcifero-fermisternal or fermisternal.

[8] It is not intended to make out the exact equivalence of these family names, as conceived by different authors. The family *Engystomatidæ*, as generally understood (Gadow in *Camb. Nat. Hist.*, 1901; Nieden in *Das Tierreich*, Lief. 49, Anura II; Versluys in *Handwörterbuch der Naturwissenschaften*, 1931, article on "Amphibia", etc.), is equivalent to Boulenger's two families, *Engystomatidæ* and *Dyscophidæ* (*Cat. Batr. sal. Brit. Mus.*, 1882; *Enc. Sci., Batr.*, 1910); and to Cope's six families—*Hemicidæ Brevicipitidæ*, *Engystomidæ*, *Phryniscidæ*, *Cophylidæ* and *Dyscophidæ* (*Bull. U. S. Mus.*, 1889, **34**).

[9] *Atelopus*, *Brachycephalus*, *Dendrobates*, *Geobatrachus*, *Hyloxalus*, *Phyllobates*, *Rhinoderma*, *Sminthillus*.

[10] This genus is called *Polypedates* by many workers. However, Ahl (*Das Tierreich Anura III*, 1931) prefers the name *Rhacophorus* Kuhl., and Smith (*Proc. Zool. Soc., London*, 1927) gives strong reasons for the name.

[11] *Asterophrys*, which has opisthocœlous vertebræ, originally belonged to the family *Pelobatidæ*, where it could be regarded, like *Megalophrys*, as showing persistent affinities to the *Discoglossidæ*. However, Noble (*Biology of the Amphibia*, 1931, p. 535) shifts it to the family, *Brevicipitidæ*, where it holds a still more anomalous place.

[12] Noble, G. K., *The Biology of the Amphibia*, McGraw-Hill Book Company, Inc., New York, 1931.

[13] This is the classification generally adopted in text-books. Gadow (*Camb. Nat. Hist.*, 1901), Sedgwick (1905), Nieden and Ahl (*Das Tierreich*, 1923–31), Versluys (1931), etc., all stick to it.

[14] Noble, G. K., *The Biology of the Amphibia*, 1931, 485–86.

[15] *Liopelma* was first described by Fitzinger in 1861 (*Verh. Ges. Wien.*, **11,** 218). Different views have been held about its affinities from time to time. Fitzinger regarded it as closely related to *Telmatobius peruvianus*; Boulenger (1882) placed it in the family *Discoglossidæ*; Nieden (1923) places it in *Cystignathidæ*; Noble, although at first agreeing with Boulenger, later (1924) institutes the family *Liopelmidæ* for its reception. Amongst the recent work on the genus, mention might be made of Wagner's "*Liopelma* studies Nos. 1 and 2" (*Anat. Anz.*, 1934, Bd. 79, Nr. 1/4, 5/6).

[16] Described first by Stejneger in 1899 (*Proc. U. S. Nat. Mus.*, **21,** 899); Regarded by Nieden (1923) as a member of the family *Discoglossidæ*. Its vertebral column is opisthocœlous (Noble, 1922). De Villiers' papers on this genus (*Nature*, 1933, 693; *Anat. Anz.*, 1934, etc.) are interesting contributions on its anatomy.

[17] Lataste, F., "Etude sur le Discoglosse," *Actes Soc. Linn. Bordeaux*, 1879, **33.**

[18] Blanchard, R., "Remarques sur la Classification des Batraciens Anoures," *Bull. Soc. Zool. France*, 1885.

[19] The other families deleted by Noble (1922) are: *Dendrobatidæ*, *Ceratobatrachidæ*, *Genyophrynidæ*, *Hemiphractidæ*, *Amphignathodontidæ*, *Dendrophryniscidæ* and *Dyscophidæ*.

[20] Noble, G. K., *The Biology of the Amphibia*, 1931, 496.

[21] Noble, G. K., "The value of life-history data in the study of the evolution of the Amphibia," *Ann. Acad. Sci., New York*, **30,** 111. The name *Polypedatidæ* is based on the genus *Polypedates*, which had better be called *Rhacophorus* (see foot-note 10, above). Perhap the family should be called *Rhacophoridæ*.

[22] Nieden, Fr., "Anura I and II", *Das Tierreich*, Lief. 46 (1926) and 49 (1926); Ahl, E., "Anura III," *Das Tierreich*, Lief. 55 (1931).

[23] Goodrich, E. S., *Studies on the Structure and Development of Vertebrates*, London, 1930, xxi.

[24] Versluys, J., "Amphibia" in *Handwörterbuch der Naturwissenschaften*, 1931, 296–97.

[25] Werner, Franz, "Dritte Klasse der Craniota. Dritte und zugleich letzte Klasse der Ichthyopsida. Amphibia Lurche." Kukenthal's *Handbuch der Zoologie*, Bd. 6, zweite Halfte; zweite lief., p. 20.

[26] Gadow, H., "Amphibia and Reptiles", *Camb. Nat. Hist.*, 1901, **8,** 19.

[27] He is referring to the species of the Genus *Megalophrys*.

[28] Boulenger, G. A., "A Revision of the Oriental Pelobatid Batrachians (Genus *Megalophrys*)," *Proc. Zool. Soc. London*, 1908, 408.

A Note on Section Cutting of Insects.

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IN Bolles Lee's (1928, p. 510) Microtomist's Vade-Mecum, it is stated that the sectioning of insects is a grim business. Numerous methods of microtomy of insects are reported but none can claim to have a wider range of application (Kennedy, 1932, p. 40), nor is suitable for routine work. It becomes therefore, increasingly, difficult for insect anatomist or histologist in selecting a fixative well suited for a particular material, without the laborious task of giving trial to several of the known methods. Eltringham (1930, p. 93) remarks that there is no satisfactory method of softening chitin without at the same time destroying the structure of the softer internal tissues.

The following fixative which I prepared, gave me satisfactory results in my investigations of the anatomy and histology of insects such as collembola, ants, beetles, etc., perfect sections of the entire insects being obtained as will be seen from photomicrographs given in some of my papers cited in the reference. To enable the beginners interested in the study of insect morphology, to do away with some of the common difficulties which generally hamper the progress of work, I give below the method which we have adopted in our laboratory.

1. Specimens are fixed in the following mixture overnight:

Saturated solution of picric acid in 90% alcohol	..	75 parts
Formalin ..	..	25 „
Strong nitric acid	..	5 „