EVOLUTION IN THE STAPHYLINID GENUS *PRIOCHIRUS* (COLEOPTERA)

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In previous papers I have dealt with the taxonomy of the primarily tropical, log-inhabiting genus *Priochirus* and with some aspects of the geographical distribution and ecology of species occurring in the Solomon Islands (Greenslade, 1971, 1972). The present paper gives an account of the evolutionary history of taxa within the genus. It depends on deriving evolutionary relationships of subgenera and groups of species from their morphology, a procedure that may be open to criticism, in particular for circularity of argument, if used alone. In this case, however, there is additional information which corroborates the results if it can be assumed, following Rensch (1959), that major evolutionary events are brought about by the same factors that are responsible for speciation. In this context major evolutionary events are the development of characters defining groups above the level of species; observations relating to speciation were made in the Solomon Islands. Here species' patterns of distribution were interpreted in terms of cyclic expansion and contraction of geographical range, accompanied by shifts of habitat (Greenslade, 1972). Taxonomic differentiation, which takes place concurrently, includes gross changes of structure. Together with data on the habitat ecology of species, these observations indicate both the direction of evolutionary change in morphology and the selective processes involved.

MORPHOLOGICAL RELATIONSHIPS AND DERIVATION OF TAXA

Strictly the two topics should be taken separately but as the taxa comprising the genus are described in detail elsewhere (Greenslade, 1971) a combined account is more convenient here. The classification is summarised in Table 1 and all the morphological types, and most of the species mentioned, are illustrated (Figs. 2, 4–7).[1]

Priochirus adults are robust, shining black beetles, 5–20 mm in length, elongate and parallel-sided. Typically, the head carries an array of teeth on the front margin and its upper surface is sulcate and impressed (Fig. 1). These features provide the most important taxonomic characters in the genus and, in addition, appear to have functional significance in the usual habitat, amongst humic material under bark of logs. Here movement is assisted by forward thrusts of the head in which the mandibles and sculptured structures on the anterior margin and dorsum are used to obtain purchase in the medium and to loosen it. Species differ in body size and convexity as well as head structure. At one extreme 'high relief' species, with the head boldly sculptured and the body convex, sometimes almost cylindrical, are found under loose bark and in soft, readily penetrated wood. At the other extreme 'low relief' forms, more compressed, with the head feebly sculptured, are adapted to constricted spaces under tightly adhering bark.

Subgenus Exochirus

This subgenus covers a wide range of head structure but all types can be derived, through intermediates, from a stock very close to, and for simplicity assumed to include, members of the present *beccarii* section (Figs. 2a, 3). The *conicicollis* section

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[1] Figures 1, 2, 4–7 are redrawn from Greenslade (1971) with permission of the Royal Entomological Society of London.

TABLE 1. *Subgenera and sections in* Priochirus.

Subgenera	Sections	Number of species		Figures
Exochirus	*beccarii*	15	54	2 a
	conicicollis	9		2 b, c
	sororculus	4		2 d
	deceptor	5		4 b
	parvus	2		2 e, f
	spinosulus	19		2 g–j
Syncampsochirus	*lorquini*	4	32	4 c
	adjacens	15		4 d, e
	miles	13		4 a, f
Eutriacanthus	Sections not distinguished		43	5 a
Cephalomerus			35	5 d–g
Barychirus	—		3	5 b, c
Peucodontus	—		1	6 a
Stigmatochirus	—		3	6 b
Euleptarthrus	*japonicus*	5	10	6 d
	malayanus	1		6 e
	longicornis	4		6 f
Leiochirus	—		1	6 c
Plastus	*drescheri*	2	94	7 a
	eucerus	28		7 b, c
	associatus	15		7 d
	monilicornis	18		7 e–g
	philippinus	17		7 j
	novaeguineae	4		7 h
	simplex	5		7 i
	unplaced species	5		–
Priochirus s. str.	—		11	7 k
Incertae sedis			1	–

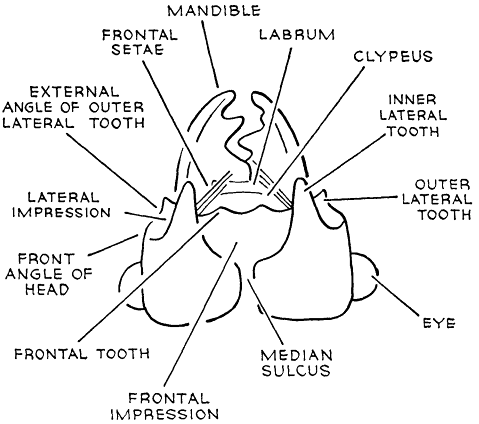

FIG. 1. Typical head structure in the beetle *Priochirus*.

is a progression of increasing relief through *P. valens* and related species (Fig. 2b) to *P. divisifrons* (Fig. 2c). In contrast the *sororculus* section (Fig. 2d) contains low relief species but again readily obtained from a morphology resembling *P. beccarii.* The *parvus* section (Fig. 2e, f) would be derived in the same way but by more extreme compression. While *P. conicicollis* illustrates a correlation between convexity and large teeth on the head, *P. brunneipes* in the *parvus* section (Fig. 2f) shows how compression can lead to reduction in size and number of teeth. Indeed the characters of the two members of this section are reduced so much as to obscure their origin.

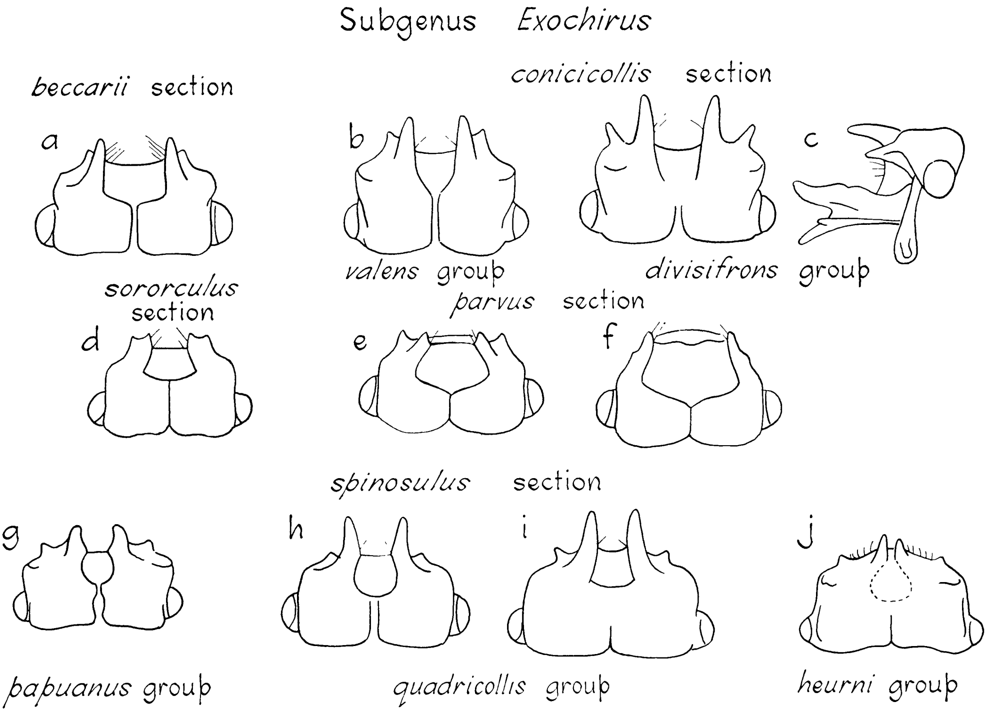

FIG. 2. Range of head structure in subgenus *Exochirus*: a) *P. beccarii*; b) *P. valens*; c) *P. divisifrons*; d) *P. sororculus*; e) *P. parvus*; f) *P. brunneipes*; g) *P. albertisi*; h) *P. spinosulus*; i) *P. quadricollis*; j) *P. heurni*.

Although geographical distributions suggest that this may differ from that of the rest of the subgenus (*parvus* section, Borneo, remainder of *Exochirus*, Moluccas eastwards (Fig. 12)), in the absence of any other grounds for erecting a separate subgenus the two *parvus* section species are placed in *Exochirus*. Here they illustrate a possible, final product of trends seen in the *sororculus* section. The *deceptor* section (Fig. 4b) is morphologically close to *sororculus* and *beccarii* sections, differing from the former by smaller teeth and from the latter by greater convexity. Finally, the *spinosulus* section, linked to the *beccarii* section by intermediate species (Fig. 3), contains three lines of development: *papuanus* species group (Fig. 2g), massive, high relief forms; *quadricollis* group (Fig. 2h, i), compressed with erect, rather centrally placed inner lateral teeth; *heurni* group (Fig. 2j), high relief, inner lateral teeth more strongly convergent than *quadricollis* group so that the head is acuminate.

On the evidence of morphological variation in this subgenus alone Figure 3 could be presented to show any group or section in the supposed ancestral position. However *Exochirus* is most easily obtained from a head structure typical of subgenus *Plastus* (Fig. 7, see following account of Evolutionary trends) and the *beccarii* section forms the best link. Subgenus *Exochirus* would result if the prominent subsidiary lateral teeth (Fig. 1) of many *Plastus* species (Fig. 7b–d) were to move laterally and upwards. *Priochirus* (*Plastus*) *pannosus* (Fig. 7e) suggests an intermediate stage (although almost certainly one arising independently).

In *Exochirus* there has been exploitation of the head structure of the *beccarii* section in that this section contains a number of closely related species, (Table 1) differing

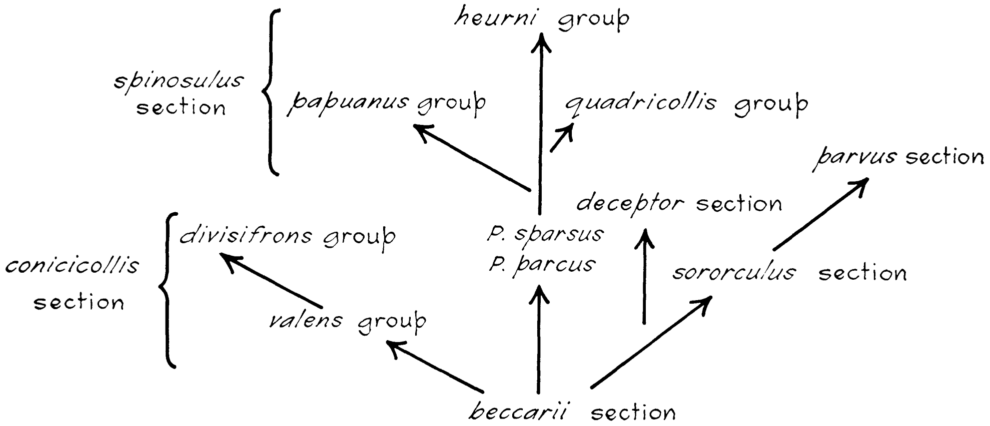

FIG. 3. Morphological relationships and most likely derivations of groups within subgenus *Exochirus*: high relief groups to the left, low relief to the right; members showing the greatest structural differences from the *beccarii* section are placed furthest from it.

in size, relief and other characters but sharing the same essential head structure (Fig. 2a) with one pair of moderately prominent teeth. In addition four other types of head have developed and they recur in other subgenera: inner and outer lateral teeth small, about equal in size, front of head almost serrate (Figs. 2d, 4b); one pair of teeth large and erect (Fig. 2h, i); head deeply divided by an excavate frontal impression, teeth prominent (Fig. 2c); head acuminate (Fig. 2j).

Subgenus Syncampsochirus

This subgenus can be derived also from a *Plastus*-like ancestor, but this time by development of the frontal teeth (Fig. 1), and not, as in *Exochirus*, of the subsidiary laterals. This gives the series: *Plastus*-like form → *Syncampsochirus*, *lorquini* section (Fig. 4c) → *adjacens* section (Fig. 4d, e) → *miles* section (Fig. 4a, f). In this sequence the frontal teeth have moved up from the horizontal plane of the frontal impression (Fig. 1) to that of the lateral teeth, and in so doing have eliminated the antero-lateral part of the frontal impression on each side so that it has become contracted towards the front (Fig. 4c, d). The frontal teeth have then increased in size, displacing the lateral teeth outwards (Fig. 4a, e, f) and deforming the lateral impression (Fig. 1) whose shape is therefore distinct from that found in *Exochirus* (Fig. 4a, compare 4b). Agreeing with this interpretation of head structure in *Syncampsochirus* there is a subsidiary tooth below each outer lateral tooth (Fig. 4a) in all members of the subgenus except for a few strongly compressed species in which it is very indistinct or has been lost. It should be homologous with the subsidiary, lower lateral tooth of many *Plastus* species (Fig. 7b–e), which, in *Exochirus*, becomes the outer lateral tooth. Consequently *Exochirus* differs consistently from *Syncampsochirus* in that the outer lateral tooth is always simple, without a subsidiary tooth (Fig. 4b, compare 4a).

Within *Syncampsochirus* there are further differences between sections in the structure of the frontal impression and of the first antennal joint. The latter is simple throughout the genus *Priochirus* apart from most *Syncampsochirus* species; here the upper surface is sulcate in most members of *adjacens* and *miles* sections but remains simple in all but one species in the *lorquini* section. The frontal impression is generally contracted towards the front in *Syncampsochirus* but is parallel-sided or even slightly divergent anteriorly in some

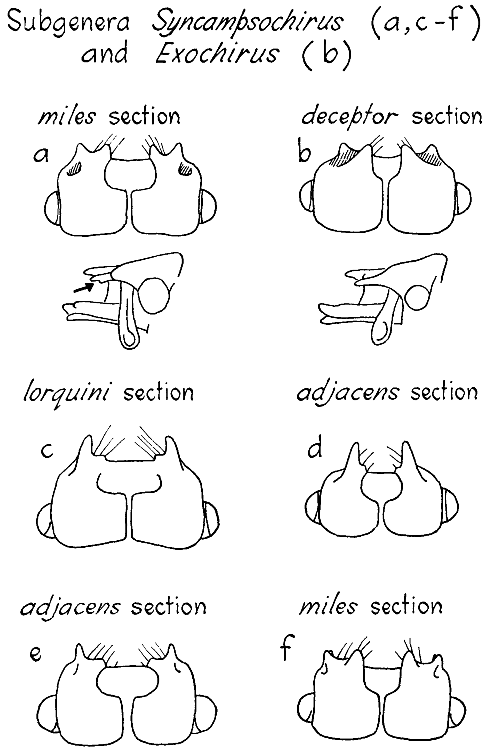

FIG. 4. Head structure in subgenera *Syncampsochirus* (4a, c–f) and *Exochirus* (4b): a) *P. samoensis*; b) *P. rastri*; c) *P. lorquini*; d) *P. armatus*; e) *P. browni*; f) *P. austeni*. Note convergence in subgenera *Exochirus* and *Syncampsochirus* in the outline of the anterior margin of the head (Fig. 4a, b) but differences in the form of the lateral impression (hatched, Fig. 4a, b) and the presence (*Syncampsochirus*) or absence (*Exochirus*) of a subsidiary denticle (arrowed, Fig. 4a) on the outer lateral tooth. These differences can be related to the mode of origin of the two subgenera from a stock with only one pair of lateral teeth. In *Exochirus* an additional pair seem to have developed from subsidiary laterals while in *Syncampsochirus* they appear to have been aquired by development and lateral movement of frontal teeth, *P. lorquini* (Fig. 4c) representing an early stage in the process.

miles section species (Fig. 4f). This appears to be a secondary development from the contracted form and so, in terms of these two characters, most *lorquini* section species represent a primitive condition for the subgenus and most members of *samoensis* section an advanced one with the *adjacens* section intermediate.

Subgenera *Syncampsochirus* and *Exochirus* show how similar basic head structures can be arrived at by quite different routes and they converge in several species in which the outline of the front of the head is almost identical when seen from above (Fig. 4a, b). But, in contrast to *Exochirus*, there is little variety of head structure in *Syncampsochirus* beyond the development sequence. The *miles* section is equivalent to the serrate type in *Exochirus* with teeth small, equal and regularly spaced while some members of the *adjacens* section (Fig. 4d) resemble the type with two prominent teeth.

Subgenus Eutriacanthus

This subgenus (Fig. 5a) characterised by a central frontal tooth, was not studied in detail. It includes high and low relief species in which either the frontal tooth or the laterals may be large or very small. Therefore it covers all the head shapes found in *Exochirus* apart from the excavate type. The simplest derivation would be from a *Plastus*-like form through the appearance of a single median frontal tooth and suppression of other subsidiary teeth.

Subgenus Cephalomerus

Again no formal groups were distinguished in this subgenus but many species resemble *P. selangorensis* (Fig. 5d) and this morphology can be taken as typical and equivalent to the basic *beccarii* section head type of subgenus *Exochirus*. There are three morphological trends away from this structure. The inner lateral teeth may increase in size so that species between *P. selangorensis* and *P. borolinoides* (Fig. 5e) represent the acuminate head type and that with one pair of prominent lateral teeth. Species near *P. persimilis* (Fig. 5f) have small obscure teeth so that the front of the head is bluntly serrate, while *P. bilobatus* (Fig. 5g) and others resemble the excavate type.

The typically large, inner lateral teeth of *Cephalomerus* (Fig. 5d) and the shape of the faint lateral impression (Fig. 5e)

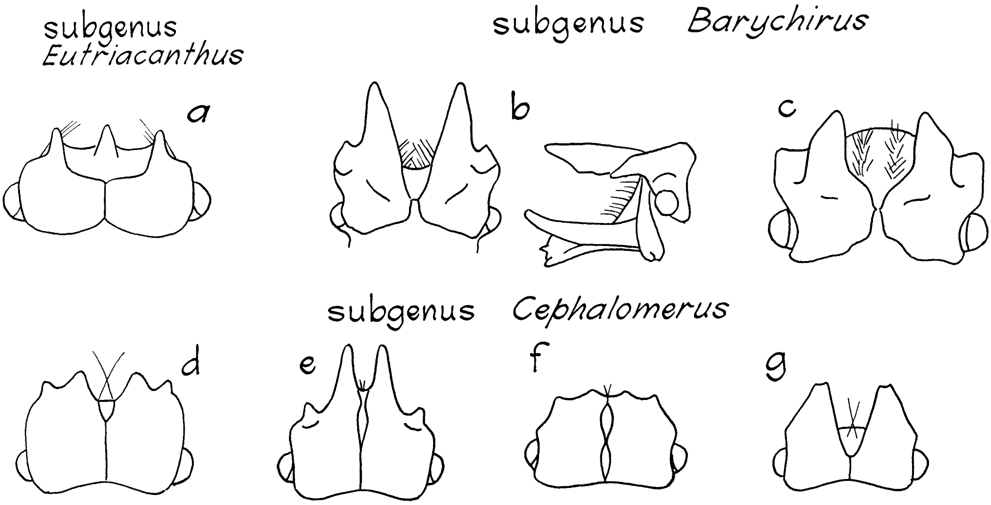

FIG. 5. Head structure in subgenera *Eutriacanthus*, *Barychirus* and *Cephalomerus*: a) *P. immarginatus*; b) *P. arrowi*; c) *P. annamensis*; d) *P. selangorensis*; e) *P. borolinoides*; f) *P. persimilis*; g) *P. bilobatus*.

are reminiscent of subgenus *Exochirus* suggesting an origin from a *Plastus*-like form by development of subsidiary lateral teeth.

Subgenus Barychirus

All the species in *Cephalomerus* are of low or moderate relief and the strongly convex members of *Barychirus* can be regarded as high relief analogues. They would be obtained by inflation of *Cephalomerus*-like species, *P. arrowi* (Fig. 5b) from one such as *P. borolinoides* (Fig. 5e) and *P. annamensis* (Fig. 5c) from one between *P. selangorensis* and *P. bilobatus* (Fig. 5d, g). There is of course, no intention to suggest that *Barychirus* is directly or even closely related to *Cephalomerus*; instead its species are likely to be the survivors of an earlier radiation along similar lines. Vertical expansion of moderate relief morphology would lengthen the clypeus and in *Barychirus* this appears to have drawn out the frontal setae (Fig. 1) into irregular elongate rows (Fig. 5b, c); this is to be seen also, though to a lesser extent, in the *conicicollis* section of *Exochirus* (Fig. 2c). A further similarity between these two groups, associated with extreme high relief, is an erect dorsal blade on the mandibles (Figs. 2c, 5b).

Subgenera Euleptarthrus, Leiochirus, Peucodontus *and* Stigmatochirus

The head structures of these subgenera are all very different and differ from those found in the rest of the genus. All species are large and most of them strongly convex, and in all except the single member of *Peucodontus* with head dentition greatly reduced (Fig. 6a), there are at least traces of two pairs of lateral teeth.

Euleptarthrus contains three sections of which the *japonicus* section (Fig. 6f) is composed of convex species with an upward projecting dorsal blade to the mandible while species in *longicornis* section (Fig. 6d) are more compressed with a dull, coriaceous integument and no erect, mandibular tooth. The single *malayanus* section species (Fig. 6e) is intermediate both structurally and in texture of the integument.

Even the most aberrant of these subgenera, *Peucodontus* (Fig. 6a) and *Stigmatochirus*, in which the foreparts are clothed in setae (omitted from Fig. 6b), can be traced to a *Plastus*-like ancestor if it is assumed that intermediate forms no

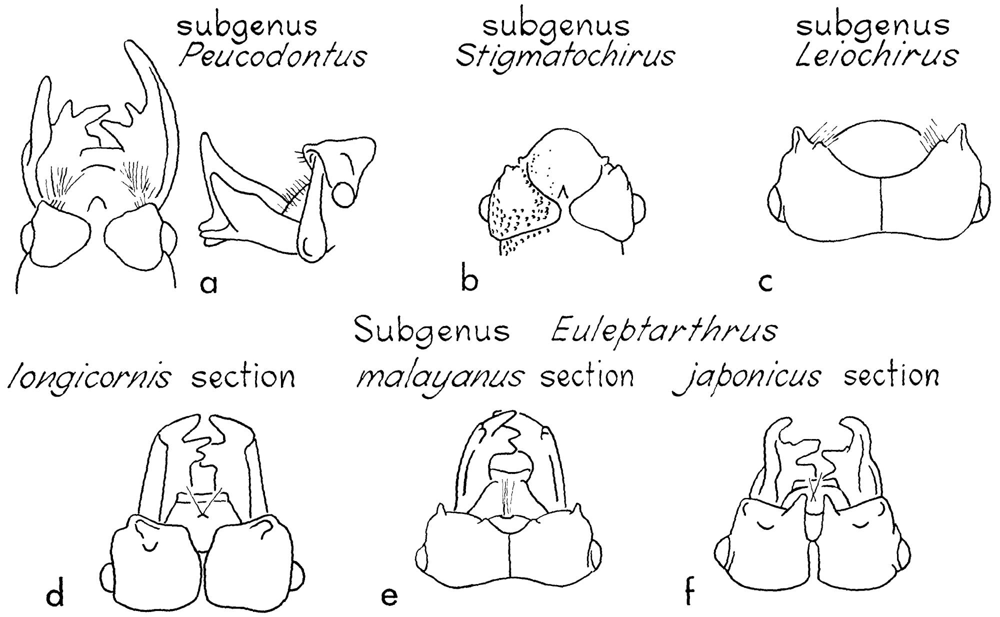

FIG. 6. Head structure in subgenera *Peucodontus*, *Stigmatochirus*, and *Euleptarthrus*: a) *P. mandibularis*; b) *P. chapmani* (omitting setae); c) *P. latifrons*; d) *P. longicornis*; e) *P. malayanus*; f) *P. japonicus*.

longer exist. In *Exochirus* for example some members of the *conicicollis* section and the *heurni* species group in the *spinosulus* section (Fig. 2c, j) would seem to be far from *Plastus* were it not for intermediates. Moreover there are signs of the most bizarre features of *Peucodontus* and *Stigmatochirus* in other subgenera. The hypertrophy of the mandibles in the former is foreshadowed by the dorsal mandibular blade in other convex species (Fig. 2c, 5b, 6f) while the extension of the frontal setae in *Barychirus* (Fig. 5b, c) and other high relief forms could lead to the densely setose clypeus of *Stigmatochirus*.

Subgenera Plastus *and* Priochirus

Although *Plastus* still requires further study seven sections can be recognized: *drescheri* section (Fig. 7a), convex, frontal impression deep, quadrate or elongate; *eucerus* section (Fig. 7b, c) convex, often with numerous subsidiary teeth; *associatus* section (Fig. 7d), convex, frontal impression continuous with clypeus; *monilicornis* section (Fig. 7e–g), frontal teeth present and asymmetrical, relief variable; *philippinus* section (Fig. 7h) with a complex of characters especially upright or divergent lateral teeth, frontal impression never small and quadrate or elongate, confined to the Philippines, relief variable; *novaeguineae* section (Fig. 7i), small, often compressed, frontal teeth present and symmetrical; *simplex* section (Fig. 7j), small, moderately compressed, frontal teeth absent.

Plastus, together with subgenus *Priochirus* (Fig. 7k)to which it is morphologically very close, embraces the whole range of head structures seen in *Exochirus*. The types with one pair of teeth moderately or very prominent occur throughout the two subgenera, the excavate type is represented by several members of the *eucerus* section of *Plastus*, the acuminate type by extreme examples of the *monilicornis* section (Fig. 7f) and the serrate type by *associatus* section (Fig. 7d) and species such as *P. lawrencei* (Fig. 7i).

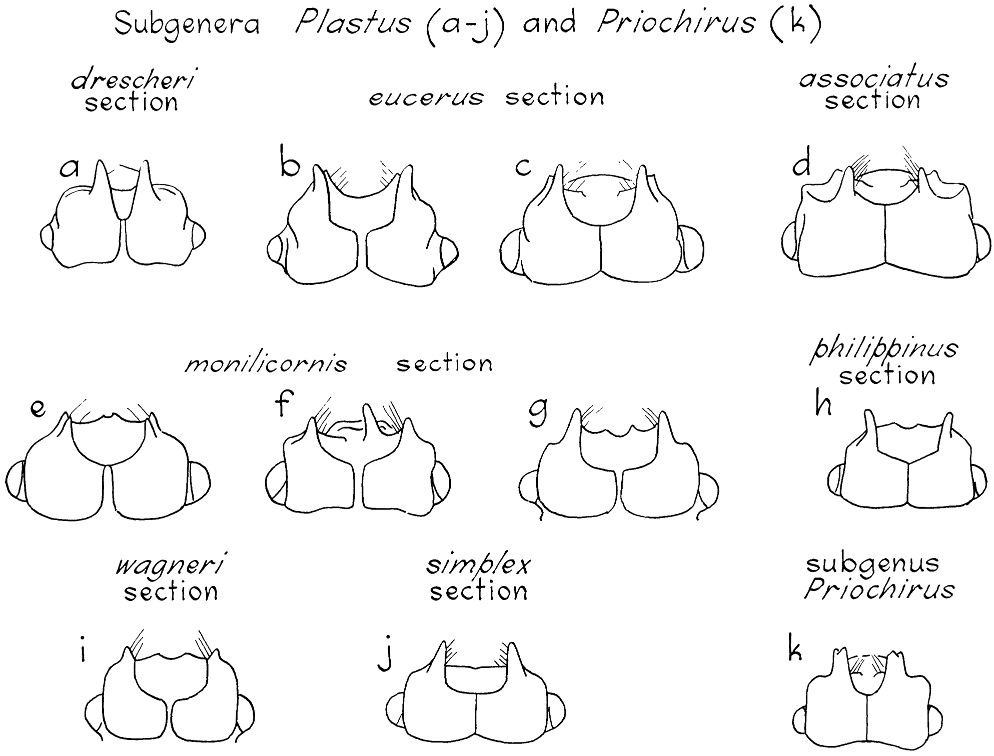

FIG. 7. Head structure in subgenera *Plastus* and *Priochirus*: a) *P. drescheri*; b) *P. sikkimensis*; c) *P. olthofi*; d) *P. cilifrons*; e) *P. pannosus*; f) *P. monstrosus*; g) *P. yalomis*; h) *P. schultzei*; i) *P. simplex*; j) *P. lawrencei*; k) *P. salvini.*

The sections within *Plastus* and its separation from subgenus *Priochirus* are poorly defined and these groups show a web of similarities. The *drescheri* section is most isolated but comes nearest to *eucerus* section species with a deep frontal impression such as *P. olthofi* (Fig. 7c). The *eucerus* section also converges on the *associatus* section again by way of *P. olthofi,* and other species, in which the anterior margin of the frontal impression is indistinct between the frontal teeth. In some *associatus* section species there is a pair of small, asymmetrical frontal teeth, so leading to the *monilicornis* section. This, in turn grades into the *novaeguineae* section with frontal teeth equal since the asymmetry may be very slight as in *P. yalomis* (Fig. 7g). The *novaeguineae* section is also close to the *philippinus* and *simplex* sections (Fig. 7h, j).

The *drescheri* and *simplex* sections together contain only four described species and they differ from the vast majority of species in subgenera *Plastus* and *Priochirus* in the absence of all subsidiary lateral and frontal teeth, and this is, probably, a derived condition. Tooth structure is relatively simple in the *novaeguineae* group as well, and as the species are discontinuously distributed in Sumatra and the New Guinea—Solomons area may well have resulted from two or more independent reductions from other groups. The *eucerus* section occupies a central position in *Plastus* and all other sections can be derived from it, or from a less convex form of similar head structure. In tooth arrangement this section also resembles subgenus *Priochirus.*

EVOLUTIONARY TRENDS

A heavily sculptured head usually including teeth or other structures on the anterior margin, a frontal impression and median sulcus, are features common to *Priochirus* and its most closely allied genera, *Leptochirus*, *Borolinus* and *Thoracochirus*. Although *Priochirus* is formally diagnosed by the structure of the mouth parts and the ventral surface (Cameron, 1930) it is also distinguished by the above head characters and additional frontal and lateral teeth. This combination, shown in Figure 1, is therefore basic to *Priochirus* and the account of the morphological relationships of groups within the genus shows that they can all be derived from it. With the exception of *Exochirus* containing the two *parvus* section species of uncertain affinities all the subgenera in *Priochirus* appear to be natural and monophyletic. Therefore the simplest interpretation of evolution in the genus is that it has consisted of a series of radiations, each comprising departures from the original head structure involving changes in the number and arrangement of teeth with accompanying changes in size and convexity. Generally an extra pair of lateral teeth has been gained or an additional frontal tooth and similar arrangements have been acquired independently in several cases. Examples are the four-tooth arrangement of *Cephalomerus*, *Syncampsochirus* and *Exochirus* and the central frontal tooth of *Eutriacanthus* and some species in *monilicornis* section of *Plastus*. Within subgenera further variation has led to the excavate or acuminate types or to a head with two prominent teeth or a serrate front margin. This is the simplest way in which the morphology of groups within the genus can be accounted for and although other explanations may be possible they would require additional steps. Whether the original ancestor carried the full complement of teeth shown in Figure 1, or not, is immaterial since, ultimately, this line presumably developed from Staphylinidae without or with fewer teeth.

The relation between size and convexity on one hand and the strength of sculpturing of the head and the amount of elaboration of its structure on the other is often allometric. In very high relief forms tooth development tends to increase disproportionately in relation to the increase in size and convexity, hence the excessive, luxuriant structures of the head and mandibles in subgenera *Peucondontus* and *Barychirus* and the *conicicollis* section of *Exochirus* (Figs. 2c, 5b, c, 6a). In compressed species, density and length of setae are usually reduced, presumably adaptively, in response to constricted existence under tight bark. Conversely the habitat of convex species allows greater development of setae and this reaches its maximum in the hirsute forebody of members of the high relief subgenus *Stigmatochirus*. High relief species, therefore, show the greatest departure from the morphology of the bulk of the genus, while in low relief forms there may be a return to a simple tooth condition with a moderately prominent main pair of teeth and a pair of subsidiary teeth. This was seen in *Exochirus* in the series *beccarii-sororculus-parvus* sections (Fig. 2) and in the loss of subsidiary lateral teeth in very low relief *Syncampsochirus* species.

In Figure 8 these evolutionary trends are divided into four grades of which D represents the greatest departure from the supposed ancestral morphology. That changes in head shape, grade C, do follow changes in tooth arrangement in grade B, is indicated by *Syncampsochirus* where a characteristic dentition has been acquired but there is little additional variation in the structure of the head. In contrast the subgenera *Cephalomerus*, *Eutriacanthus* and *Exochirus* exhibit a wide range of head types, but, in each subgenus, it is based on a single tooth arrangement. Figure 9 shows the evolutionary status of the different subgenera with each one placed according to the morphology of the majority of its species. *Plastus*, with only one main pair of teeth must be placed in grade A and is taken to include the ancestral stem

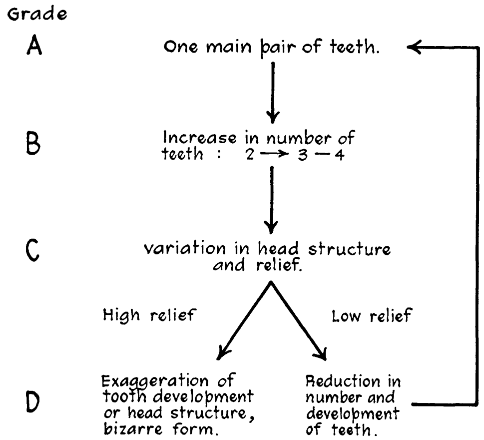

FIG. 8. Evolutionary steps in *Priochirus* radiation.

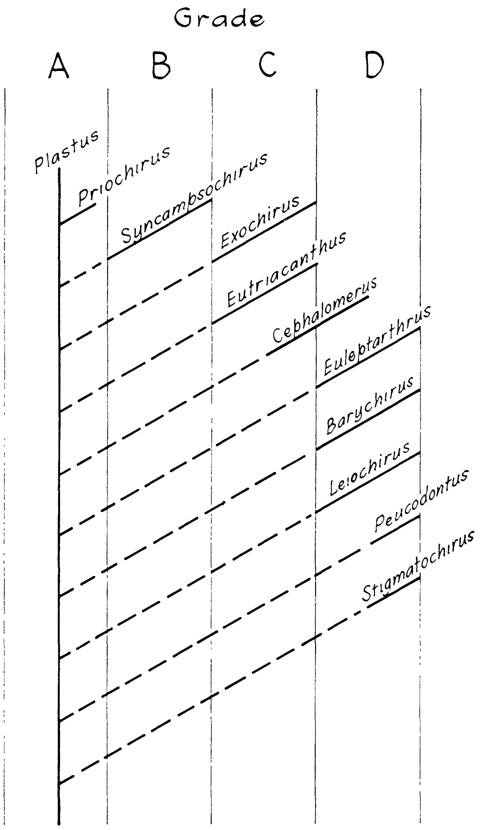

FIG. 9. Evolutionary relationships of *Priochirus* subgenera. All are treated as deviants from *Plastus* or a *Plastus*-like stem and those which have progressed furthest through the grades A–D (Fig. 8) are considered the oldest. Solid lines indicate parts of the sequence with existing species while broken lines show previous stages that are no longer represented.

from which the other subgenera have diverged. However the sections within *Plastus* are evidence of another series of radiations within the framework of the grade A tooth arrangement. These sections can be graded, as were the subgenera, according to the individuality and diversity of the head structures they include. If the characteristic structure of the *philippinus* section stands for grade B, then the *novaeguineae* and *simplex* sections are at an earlier stage, grade A. The *monilicornis, eucerus* and *associatus* sections can be taken as successively later stages between grades B and D so that the convex, morphologically isolated species forming the *drescheri* section represent grade D.

According to Figure 10 the numbers of species in each subgenus, and in the constitutent sections of *Plastus,* depend on the grade of evolutionary development reached, with the maximum achieved in grade C. In grade B high numbers result from variation in size and relief once a new tooth arrangement has been acquired, and then, in grade C, there is further radiation in which the various possibilities inherent in diversification of head structure are exploited, high relief forms persisting and comprising grade D. The curves are skewed to the right but if it were possible to substitute a time scale for grade on the abscissa the peak might well be shifted to the left, with a period of relatively rapid increase in species (grades B, early C) following a lag phase (grade A) and tailing off into prolonged declining and persistent phases (late grade C and grade D) (Zeuner, 1958).

GEOGRAPHICAL DISTRIBITIONS

These confirm the position of subgenera *Plastus* and *Priochirus* as most likely to be near the stock from which the whole sub-

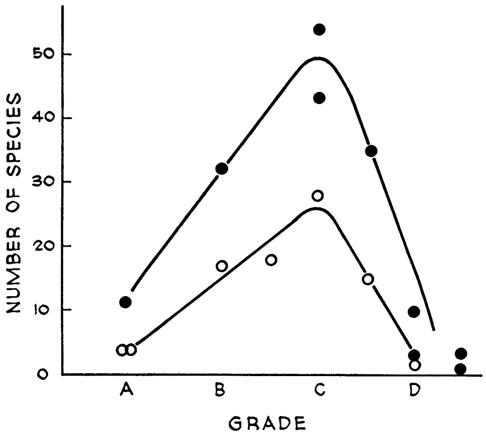

FIG. 10. Number of species in subgenera (excluding *Plastus*) and sections (*Plastus*) according to grade: O, sections within *Plastus*; ● other subgenera.

genus evolved (Fig. 11, Table 2). In *Plastus* the most generalised forms, in the *eucerus* section, are distributed from Madagascar through the Oriental region as far east as New Guinea while the closely related subgenus *Priochirus* extends the joint distribution to Central America. Of the other subgenera, those which are most advanced in the sequence A–D are restricted to continental Asia and large, adjacent islands (Fig. 11, Table 2). Many of the species occur outside the tropics, often on mountains, especially in the eastern Himalaya, and of the few representatives in tropical rain-forest at least one, *P.* (*Euleptarthrus*) *malayanus*, is a mountain species. *Cephalomerus* is intermediate between these and the other subgenera in both distribution and grade (Figs. 9, 11, Table 2); there are several Formosan species and it is the typical subgenus of peninsula India. Further east less advanced subgenera predominate; although *Eutriacanthus* overlaps extensively with *Cephalomerus* (Fig. 11, Table 2) its distribution is centered on the East Indies rather than continental Asia and *Syncampsochirus* and *Exochirus* are centered on New Guinea (Fig. 11, Table 2).

TABLE 2. *Distribution of subgenera and numbers of species of* Priochirus *in major geographical regions.*

Subgenus	Grade (Fig. 8)	1 Madagascar	2 Continental Asia and adjacent large islands	3 East Indies	4 New Guinea and Pacific	5 Central America
Peucodontus	D	–	1	–	–	–
Stigmatochirus	D	–	3	1	–	–
Barychirus	D	–	3	–	–	–
Euleptarthrus	D	–	10	–	–	–
Leiochirus	D	–	–	1	–	–
Total, Grade D subgenera		–	17	2	–	–
Cephalomerus	C–D	–	24	15	–	–
Eutriacanthus	C	–	16	31	5	–
Exochirus	C	–	–	2	52	–
Syncampsochirus	B	–	–	1	32	–
Plastus	–	3	13	43	35	–
Priochirus s. str.	A	–	–	–	–	11
Total species		3	87	96	124	11

Territories included: 1, Madagascar and Comoros; 2, Ceylon, India (with Sikkim), Southwest China, Japan, Formosa, Hainan, Burma, Indochina, Malaya (with Singapore); 3, Sumatra, Java, Lesser Sunda Islands, Borneo, Celebes, Philippines; 4, Moluccas, New Guinea (with associated small islands), Micronesia, Australia (Queensland), Bismarcks, Solomons (with S. Cruz group), New Hebrides, Samoa and Fiji; 5, Mexico to Venezuela.

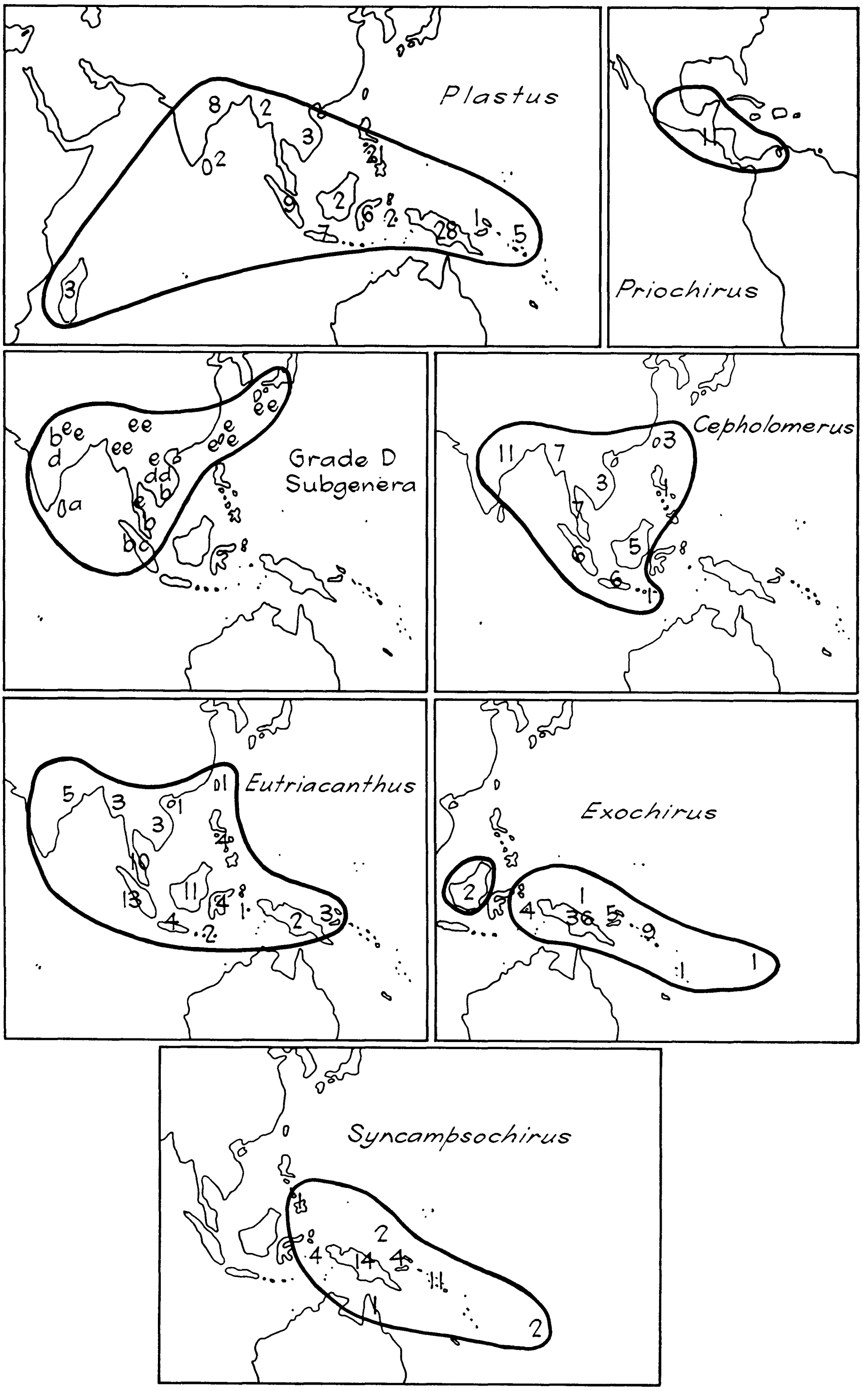

FIG. 11. Geographical distribution of subgenera showing numbers of species in each of the areas listed in table 2. Grade D subgenera: a, *Peucodontus*; b, *Stigmatochirus*; c, *Leiochirus*; d, *Barychirus*; e, *Euleptarthrus*.

These patterns are reflected in regional differences in density of species and subgeneric diversity. Despite unevenness of collecting there are indications of a positive species-area relationship on the islands and archipelagoes from Sumatra to the Pacific. The largest islands, Borneo, New Guinea and Sumatra, carry more species than smaller ones such as Celebes and islands of the lesser Sundas and Moluccas (Fig. 11). Although there are island groups with many species, notably the Philippines and Solomons, these are complex archipelagoes in which there appears to be island endemism. However, the rate of increase of species with area is greater in Melanesia than the East Indies with 80 species recorded from New Guinea (Fig. 11) compared with less than 30 on either Borneo or Sumatra. On continental Asia there are even fewer species for the area concerned as only about 30 are known from the subcontinent of India and less than this from Indochina plus Burma. Passing from west to east there is an opposing gradient of decreasing subgeneric diversity. Seven subgenera occur in continental Asia and nearby islands (Table 2), seven amongst the more numerous species of the East Indies and only four on New Guinea.

RADIATION AND EXPANSION IN THE PACIFIC

The small number of New Guinea subgenera have radiated extensively so that, in respect to the Oriental Region, the New Guinea *Priochirus* behave as a peripheral fauna. This radiation and the expansion of some of its products to other island groups can be considered in detail which is not possible for areas to the West where there are more large islands and exchange of species is likely to be complex. Allowing for probable cases of radiation within an archipelago from one original colonisation it is possible to make a first estimate of total faunal movement by members of this genus between island groups in the Southwest Pacific. In Figure 12 it is assumed that any hiatus in a stock's known distribution indicates that a species is present but uncollected on the intervening island or archipelago or did once occur there.

One entry to New Guinea from the Oriental region is necessary to account for *Eutriacanthus* and at least two for *eucerus* and *associatus* sections of *Plastus*. Detailed study of the closest allies of the species in the last two sections outside New Guinea might suggest more, but as the simplest hypothesis, a single *eucerus* section stock is held to be responsible for subgenera *Syncampsochirus* and *Exochirus* and all New Guinea *Plastus* species except those in the *associatus* section. In subgenus *Syncampsochirus* the wide but fragmented distribution of the *lorquini* section (Fig. 4c) from the Moluccas to Samoa (Fig. 12) agrees with this section's proposed status as the oldest in the subgenus. Figure 12 shows that most faunal movement is from the Oriental region to New Guinea and then eastwards into the Pacific. There is some radial expansion from New Guinea to the Moluccas, Micronesia, Australia and, rarely, to the Philippines but this becomes linear through the Bismarcks and Solomons. The only cases which might indicate movement in an opposite, westerly direction are the *miles* and *conicicollis* sections of subgenera *Syncampsochirus* and *Exochirus* respectively since both have more Solomon Islands than New Guinea species. But the distributions of species in the *miles* section suggest a series of eastwards expansions (Greenslade, 1972) and it is possible that other groups have partly replaced these two sections in New Guinea or have blocked radiation there. Members of the *conicicollis* section are the only very high relief forms in the Solomons where they have proliferated. In New Guinea potential competitors are represented by high relief species in the *eucerus* and *associatus* section of *Plastus* and in the *beccarii* section, *spinosulus* species group of *Exochirus*. In the same way the *miles* section may be limited in New Guinea by the presence of low relief members of the *spinosulus* species group or of the *monilicornis* section of *Plastus*.

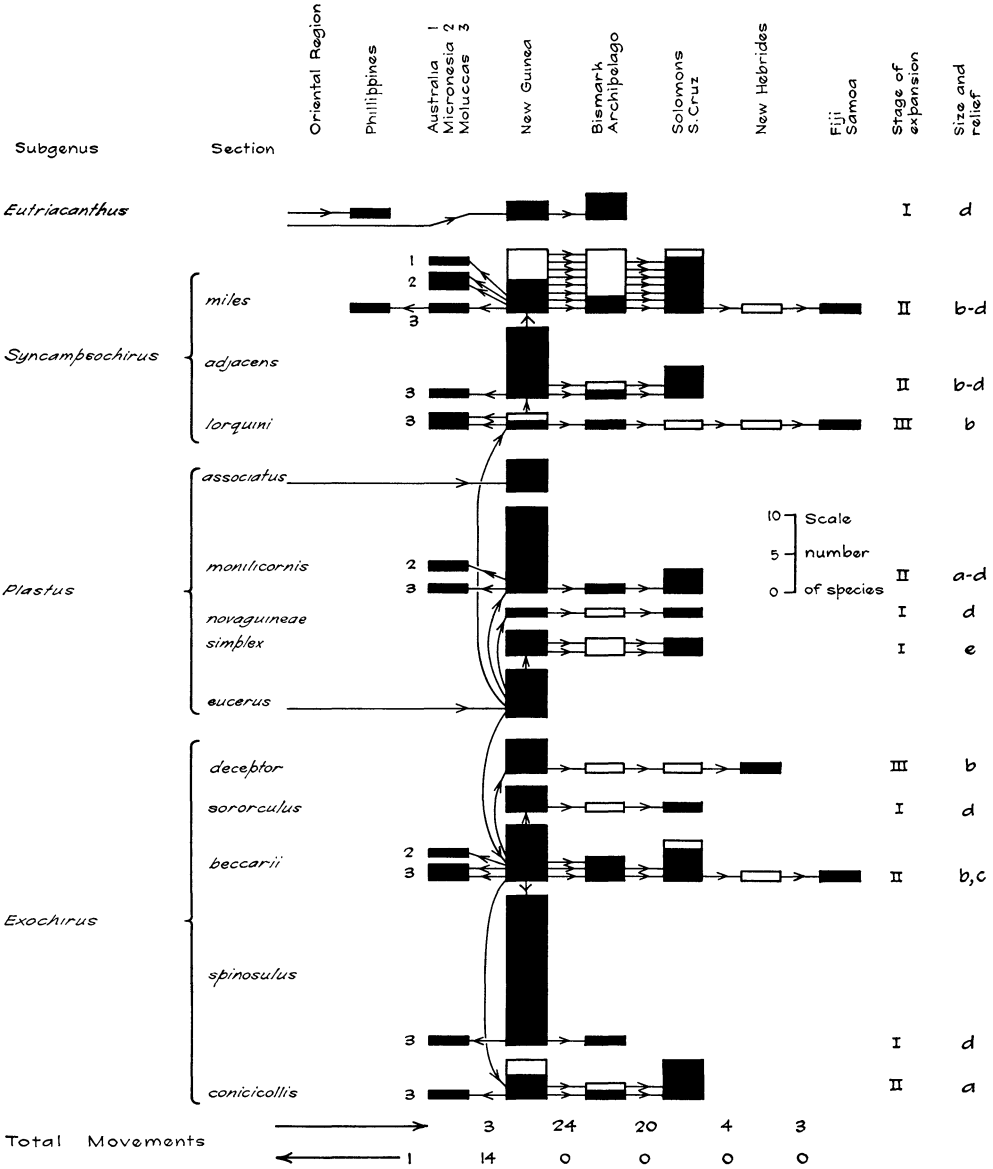

FIG. 12. Expansion and radiation by *Priochirus* in New Guinea and the Pacific. Solid histograms, number of species recorded from islands and archipelagoes, open histograms, species probably present but uncollected or once occurring there. Arrows indicate the minimum number of movements across water gaps necessary to account for distributions. Size and relief of taxa are shown: a, large, high relief; b, large, moderate relief; c, intermediate; d, small low relief; e, very small, moderate relief (litter layer species). I–III, stage of geographical expansion (see text).

Of the *Priochirus* occurring in New Guinea only the *eucerus* and *associatus* sections reach their eastern limit there. The other sections all penetrate into the Pacific and can be divided among three stages of expansion. These are similar but not identical to stages recognized among the ants (Wilson, 1959) and birds (Greenslade, 1968) of this area, precise criteria in each case depending on the animal groups and taxonomic levels involved. Here stage I is represented by sections and species groups concentrated in New Guinea but with one or a few species on nearby archipelagoes. In stage II the total area of distribution is greater and covers more island groups on which there is speciation. In stage III the total number of species declines; some may persist on distant archipelagoes but chances of survival will tend to be proportional to number of species previously occurring so that most should be found in the source, New Guinea, or in areas where radiation has occurred. The stages of expanding groups are shown in Figure 12 and also the ranges of size and relief they represent outside New Guinea. This tends to be low in stage I groups and higher in stage III with stage II covering a wide range. *Syncampsochirus* contains no stage I groups even though it is in an earlier evolutionary grade than the other expanding subgenera. The existence of stage I groups in the latter illustrates the rejuvenating effect of variation in head structure after aquisition of a certain tooth arrangement, and members of the *simplex* section of *Plastus* appear to be penetrating a new habitat for Melanesian *Priochirus*, litter and sticks on the forest floor rather than logs (Greenslade, 1972).

DISCUSSION

The topic of eastwards expansion from New Guinea links this paper and the preceding one which dealt with the process from the point of view of a recipient archipelago, the Solomons. The two accounts show similarities which make it possible to extrapolate from observations on the *Priochirus* fauna of the Solomon Islands and trace the likely course of a subgeneric radiation, emphasising the ecological factors that cause the rise and fall in numbers of species (Fig. 10). Of prime importance is the similarity between the morphological changes accompanying dispersal and speciation in the Solomons (colonisation by low relief forms with simple tooth arrangements, increase in size and relief, eventual persistence of high relief forms) and those shown in Figure 8.

A new subgenus would start, in grade A, from a rather low relief species, near subgenus *Plastus*, but with a distinctive tooth arrangement, appearing as an adaption to early stages of log decay in lowland forest. This requires ability to colonise openings caused by tree-fall, a preadaption to more extensive disturbed sites and the edge of forest. Here, as described for the coastal zone in the Solomons, *r* selection for productivity should prevail. Large populations can develop and range extension is likely. The correlation between wide geographical range, flight, occurrence amongst temporary vegetation, and low relief morphology noted for Solomons *Priochirus* is probably a general one. It is mainly low relief species that expand out of New Guinea (Fig. 12) and many widely distributed Oriental members of *Cephalomerus* and *Eutriacanthus* are small and compressed, implying that range extension usually occurrs between habitats in which low relief is appropriate.

In the southwest Pacific the direction of expansion is from New Guinea to smaller land masses, mostly to the west (Fig. 12). Over the whole Oriental-Pacific distribution of *Priochirus* there is a west-east gradient of declining land area (relative sizes of main land masses: continental Oriental region > East Indian islands combined > New Guinea > Pacific islands); running parallel with this is an eastwards trend of decreasing evolutionary grade of predominating subgenera, with the most advanced occurring in the west (Fig. 11, Table 2). Succeeding radiations have taken place, therefore, in progressively smaller land areas, as found by Wilson (1961, 1965) for ants of this region.

Depending on the availability of extensive disturbed or open vegetation, the transition from grade A to grade B should be rapid, with range extensions providing opportunities for speciation through geographical isolation. This phase is exemplified by *Syncampsochirus* which has achieved as wide a geograpical range as *Exochirus* or *Eutriacanthus* in grade C but contains fewer species (Table 1, Fig. 11). In the Solomons *Syncampsochirus* was better represented in the coastal zone than *Exochirus* but did not penetrate so far into mountains. In grade B modification of head structure is slight but body-size and, to a lesser extent relief, vary as stocks reenter rain-forest in response to pressures that were discussed in detail for the Solomons. Here, in lowland forest, populations diverge and species accumulate. At the subgeneric level this has its counterpart in the rising number of species in grades B and C (Fig. 10) and the subgenera at this stage (*Eutriacanthus*, *Exochirus*, *Syncampsochirus*) and the equivalent sections in *Plastus* (*eucerus*, *associatus*, *monilicornis*, *philippinus*) are all centred on regions of tropical rain-forest. Over this period *K* selection for efficiency should apply with intensity of species-interactions steering new species to stages of log decay that are least effectively occupied by existing fauna. Increasingly, this entails shifts of habitat towards later stages of log decomposition and to logs in montane forest. In the Solomons this was attributed to variation in the stability of the log habitat and in the size and degree of specialisation of associated faunas.

These events belong to grade C and some of the new head structures that appear, such as the recurring two-tooth, serrate and acuminate types, may initiate further range expansion and radiation. Although the chances of prolonged survival are slight for an individual expanding species, the low relief which places a stock on the right-hand side of the grade C–D dichotomy in Figure 8 can extend its life through secondary cycles. In no case, though, has this been so successful as radiation from the basic *Plastus* stem. It appears that the tooth arrangement in this subgenus has the capacity for developing into efficient new arrangements, and the inability of other subgenera to produce such effective, new structures seems to result from subsidiary teeth becoming irreversibly committed as additional main teeth. Consequently, after the acquisition of three or four main teeth, subgeneric survival entails following the high relief pathway to grade D (Fig. 8) when persistence often requires the accident of reaching cool climates on mountains or in temperate regions where chances of survival are high. Log habitats here resemble those on mountains in the Solomons, for example in the absence or poor representation of the ants, termites and other, large osoriine Staphylinidae that are important in the lowland tropics, and they also support characteristically high relief *Priochirus* species.

In these final stages of radiation a further type of selection, 'beyond *K*', can be distinguished. The small numbers of species in grade D subgenera and their scattered distributions (Tables 1, 2, Fig. 11) indicate lack of ability to disperse widely or to generate new species, although it does not follow that members of these subgenera are inefficient in their habitats. Rather, their status as evolutionary relicts is primarily an effect of habitat that requires high relief morphology so that they become unfitted to recolonise sites and stages of log decay from which major cycles of range expansion and radiation usually start. However there may be selection also against migratory activity and genetic change. It was suggested in the previous paper that montane populations in the Solomons are protected by the mountain climate from adverse affects of dominant lowland groups. A similar observation has been made for insects living in streams and contending with rapidly flowing water and low temperatures. Hynes (1970) describes the habitat as a 'Refuge for many primitive but nonetheless highly adapted types' and refers to the 'Problems faced by more highly evolved forms in replacing (i.e. displacing) well adapted primitives from niches in a severe habitat'. The environments of montane or cool climate *Priochirus* species resemble those of stream insects in being consistently and predictably unfavourable in certain respects. In this they are very different from the temporary, unpredictable habitats of expanding *Priochirus* species. In these mountain or stream refugia selection 'beyond *K*' first requires essential adaptions such as specialised morphology and cold-tolerance, but, since these environments are stable, it will then favour conservation of the adapted type, and may involve selection against migratory activity. Dispersal, leading to entry of previously unrepresented genotypes to small populations may cause permanent changes in their genetic constitution (Haskins and Haskins, 1954). Usually this should have the advantage of preventing inbreeding degeneration and overspecialisation (Lidicker, 1962). This may well apply in the lowland forest phase of continual adjustment to a complex, varying biological environment, but later, under selection 'beyond *K*', any such effects of migratory activity are likely to be disadvantageous.

In conclusion it is worth repeating two points made in the preceding paper, that evolution in *Priochirus* is a continuing process and one that does not appear to involve any progressive, functional improvement. Interspecific competition may play a part in habitat shifts from coastal areas to forest, and in defining niches and determining the amount of radiation in forest but there is no evidence that later taxa are generally superior competitors able to replace older forms. These points are illustrated by comparing *Priochirus* with *Leptochirus*, its most closely allied genus. *Leptochirus* is morphologically and ecologically very similar to *Priochirus*; it has a few Oriental species and many in tropical America (Scheerpeltz, 1933) the opposite pattern to that shown by *Priochirus* (Fig. 11, Table 2). The eastwards movement of successive radiations in Oriental *Priochirus* has left the few species belonging to advanced subgenera in continental Asia and nearby large islands, where subgenera *Cephalomerus* and *Eutriacanthus* are moving towards grade D or extinction. Although some *Plastus* species in this area should retain potential for renewed radiation provided they have sufficiently uncommitted head structure and occur in, or can enter, disturbed or open vegetation, the genus *Priochirus* does appear to be declining in Asia. The higher density of species in Melanesia (Table 2) lends support to this since diversity and density of ground-layer faunas as a whole are at least as great over much of the Oriental region as in Melanesia; this means that *Priochirus* species were probably more numerous in the former area at one time but have been replaced by other groups. In tropical America, on the other hand, the few *Priochirus* species in the grade A subgenus *Priochirus* may be poised to take advantage of any decline by *Leptochirus* if this genus also undergoes cycles of radiation and this is suggested by its several, distinct subgenera. The world distribution of *Priochirus* could therefore develop into that seen now in *Leptochirus* and so this genus may have had the same early history as that proposed here for *Priochirus*. In this way one genus could replace another over wide areas without any substantial intergeneric differences in functional efficiency.

SUMMARY

1) The classification of the tropical, log-inhabiting genus *Priochirus* into subgenera, sections and species groups depends on characters of the head, especially the form of frontal and lateral teeth (Fig. 1). The morphological relationships of subgenera suggest that all can be derived from a single stem in, or very near the existing subgenus *Plastus*. The subgenera are interpreted as a series of independent radiations all of which pass through four grades: A, simple head condition with two main lateral teeth;

B, acquisition of additional teeth; C, diversification of head structure; D, extreme head structure, typically associated with a large, convex body. Accompanying this sequence, the number of species rises between grades A and B, reaches a maximum in grade C and declines in grade D.

2) Subgenus *Plastus* and the closely related subgenus *Priochirus* sens strict. have a wide, joint distribution from Madagascar, through the Oriental region to Central America. The other subgenera form a geographical series in which those most advanced in the sequence A–D occur in continental Asia and large adjacent islands as far north as Japan, while the least advanced subgenera are centred on New Guinea. In the latter area the direction of faunal movement is from the Oriental region to New Guinea and then into the Pacific. This is part of a larger pattern in which centres of radiation have moved from west to east, from larger to smaller land masses.

3) Conclusions from analysis of the *Priochirus* fauna of the Solomon Islands (Greenslade, 1972) are applied to the history of the genus as a whole. Geographical expansion, radiation and extinction of taxa are related to different selection processes which depend on stability of vegetation types and of the log habitat and on the size and composition of associated faunas in logs. Selection acting on relict taxa existing under predictably and consistently unfavourable conditions on mountains and in cool climates is contrasted with selection affecting earlier stages of radiation.

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