Some Ancient and Zoogeographically Significant Carabid Beetles from the South Pacific (Coleoptera: Carabidae), with Descriptions of New Taxa

J. Manson Valentine[1]

ABSTRACT

Bryanites, a new genus of lucifugal agono-sphodrines from Western Samoa, and 2 new species (*B. samoaensis* and *B. barri*) are described herein. *Bryanites* is related to *Prosphodrus*, an archaic, relict genus from New Zealand, and more distantly to *Mexisphodrus* from Mexico. A new tribe, Prosphodrini, is proposed for the reception of these 3 genera. *Neanops pritchardi*, a trechine representing another archaic, relict group, is also described as new; it is an eyeless cavernicole from New Zealand. The origin and affinities of *Bryanites*, n. gen., and *Neanops* are discussed. Zoogeographical problems arising from discontinuous distribution in various taxa of Carabidae are analyzed.

INTRODUCTION

The main objective of this article is to describe 2 enigmatic carabid beetles collected on Savaii I, Western Samoa. I further intend to bring out certain distributional implications involving these beetles, together with their generic relatives, and to unite this complex under a common tribe, Prosphodrini.

The 2 specimens mentioned above show close affinities with 2 large carabid tribes, the Agonini and Sphodrini. These specimens represent separate, yet closely related and apparently sympatric species of a new genus, *Bryanites*. It gives me much pleasure to name this important find after its discoverer, the late Edwin H. Bryan, Jr., whose lucrative explorations of Pacific Islands won him well-deserved fame.

Mr. Bryan reviewed with me his field notes taken in Samoa during an extended South Pacific expedition in 1924. The labels on the 2 type specimens read: "Salailua Samoa, May 23, 1924." However, the entry in his diary for this date mentions only the collecting of a "moderately large, slender carabid under partly rotten bark of the large tree." Actually, these beetles are far from "slender" and there are 2 of them. They are of robust form and their wingless condition and reduced eyes strongly suggest lucifugal habits.

It seems that Bryan had visited caves a few days earlier, since notations for May 20 read: "Visited these lava-tube caves just north of Suitu, one-half mile south of Salailua. They consist of a network of lava-tubes opening by several low entrances from the face of the cliff above the beach. . . . catching 21 bats and a young swift." There was no mention of beetles. In 1979, however, Bryan wrote to me saying: "If, by any chance, the carabid beetles were collected on May 20th and not on May 23rd, up on the Aopa Trail, they may possibly have come from these caves. I was having so much trouble with my injured ankle at this time, it might have interfered with my usual care in labeling."

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1. 1260 Southwest First Street, Miami, Florida 33135, USA.

The ecological habitat of these 2 carabids, whether epigean or spelean, is, therefore, in question. However, their lucifugal facies strongly suggests a spelean habitat.

Another objective of this paper is the systematic evaluation of another primitive, relict stock represented by the genus *Neanops* Britton, a troglobitic group of small trechines inhabiting the North Island of New Zealand. A new species of this genus is described herein. *Neanops* comprises minute, troglobitic forms that exhibit all the characteristics of true spelean modification—anophthalmia, depigmentation, and hypertrophy of sensory setae. A series of 4 specimens of the new species was collected by Eric D. Pritchard and me in an upper gallery of a small, wet cave near Te Kuiti, North I, 26 December 1937. Ours were the first *Neanops* ever taken. On that same expedition we were also fortunate to be the first to collect *Maoripamborus* Britton and to recognize the relationship of this living fossil to Australia's *Pamborus* Latreille.

All holotypes have been deposited in the Bernice P. Bishop Museum, Honolulu, Hawai'i (BPBM). Paratypes will be deposited in the New Zealand Academy of Science, Entomology Division, DSIR, Auckland (NZAC).

TAXONOMY

PROSPHODRINI Valentine, new tribe

This new tribe is proposed to contain 3 primitive genera of ancestral agonosphodrines (*Prosphodrus* Britton, *Mexisphodrus* Barr, and *Bryanites,* n. gen.) that have typically sphodrine, vertically keeled, prosternal intercoxal processes, and have typically agonine aedeagi in which both parameres are conchoidal (the right one always being styloid in the true sphodrines).

Bryanites Valentine, new genus

Type species: *Bryanites samoaensis,* n. sp.

Moderate-sized (11.5–12.5 mm), ferrugineous, apterous carabids. *Body:* elongate-oval, robust, convex, quite generalized in form. *Head:* relatively large; eyes reduced, nearly flush with head's contour; 2 supraorbital setae on either side; antennae moderately long, reaching to about ⅕ elytral length, 4 basal segments glabrous, 3rd segment slightly arcuate, segments 9–11 short and somewhat expanded; mandibles quite long, basally stout and with a strong carina; retinaculum rudimentary, being a single, small tooth; scrobe without a seta; labrum distinctly bilobed-emarginate, bearing 4 setae; maxillae conventional, having elongate palpi that terminate in a capsule-shaped segment; terminal segment of galea falciform; subterminal segment of labial palpi with 2 setae; mentum tooth pronounced with an emarginate (bifid) apex; paraglossae long and arcuate. *Pronotum:* more or less rectangular with evenly arcuate sides showing no sinuation; anterior angles produced, hind angles rounded; margin rather wide with 2 (medial and posterior) setigerous punctures; basal fossae and median sulcus well-impressed. *Elytra:* without discal planation, elliptically rounded, deeply and evenly striate; each bearing 2 anteriorly placed punctures in 3rd stria, plus a series of 3 posteriorly placed in 2nd stria; scutellar punctures well developed; humeri keeled, bordering a transverse channel anterior to abruptly terminating intervals (6, 7 and 8) that coalesce at this point; lateral margins deeply channeled, containing numerous punctures; apices obtusely rounded or truncated, sculptured by irregularly confluent striae; internal carina short, meeting margin in a simple juncture, thus eliminating the more complex condition of an epipleural fold (plica). *Legs:* decidedly elongated, especially mid and hind pairs; testaceous, contrastingly paler than body; forelegs relatively short; protibiae with a rudimentary antennal organ, lacking a well-defined pectinated notch, proximal spur associated with it quite long; protarsi moderately dilated, sparsely furnished with only slightly modified hairs, 4th segment in
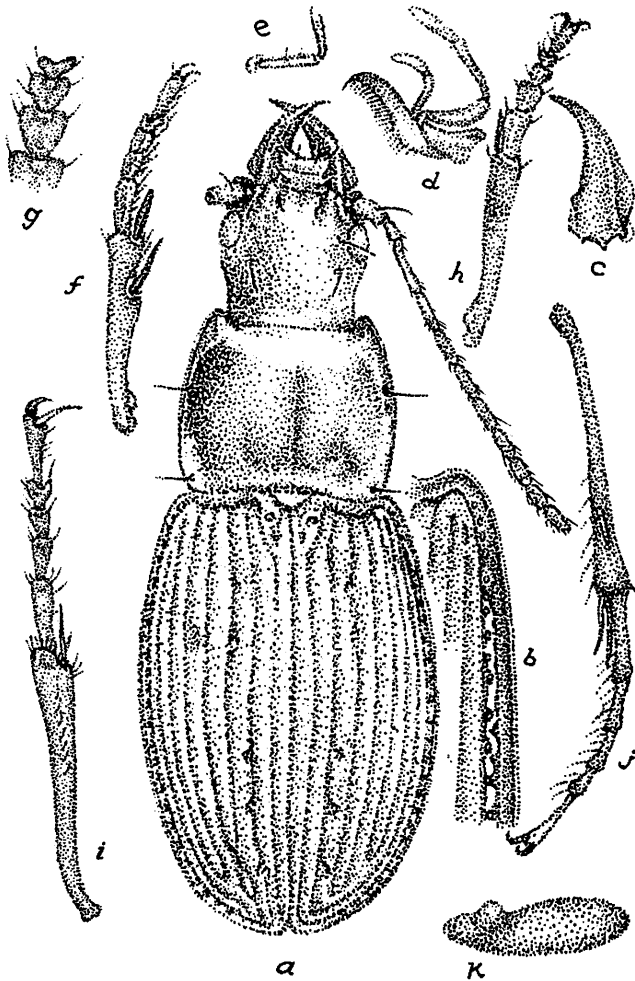
Fig. 1. *Bryanites samoaensis*, holotype ♂, Western Samoa: **a**, dorsal view; **b**, detail of anterior margin of right elytron; **c**, right mandible; **d**, right maxilla; **e**, right labial palpus; **f**, left protibia and protarsus, inner face; **g**, detail of segments 3 and 4 of left protarsus; **h**, right protibia and protarsus, dorsal view; **i**, left mesotibia and mesotarsus; **j**, right metatibia and metatarsus; **k**, right metatrochanter.

both sexes very small, conspicuously and asymmetrically bilobed; mesotarsi with 4th segment asymmetrically bilobed, mesotibial spurs long; metatibiae and metatarsi elongate, former with very long spurs and lacking a terminal brush; hind trochanters broadly rounded, an anteriorly placed tubercle at their base; tarsal claws simple on all appendages. *Prosternum:* intercoxal process a vertical keel. *Aedeagus:* generalized; median lobe strongly arcuate between well-differentiated basal bulb and completely unmodified apex, which is slightly twisted to right; internal sac containing no clearly discernible sclerotized structures, appearing to lie in an entirely open, troughlike median lobe, enclosed only in basal bulb area; both parameres conchoidal, left one considerably larger than right. *Stylus:* bearing spur on outer face, and with distally disposed setae; terminal stylomere lacking usual spurs on outer face, in place of which are 3 rudimentary denticles; apex bluntly rounded.

Prosphodrus differs from *Bryanites* in having normally developed eyes, reduced humeri, protibiae equipped with an antennal organ, hind trochanters without a basal tubercle, and prosternal carina relatively long (Fig. 4a–f).
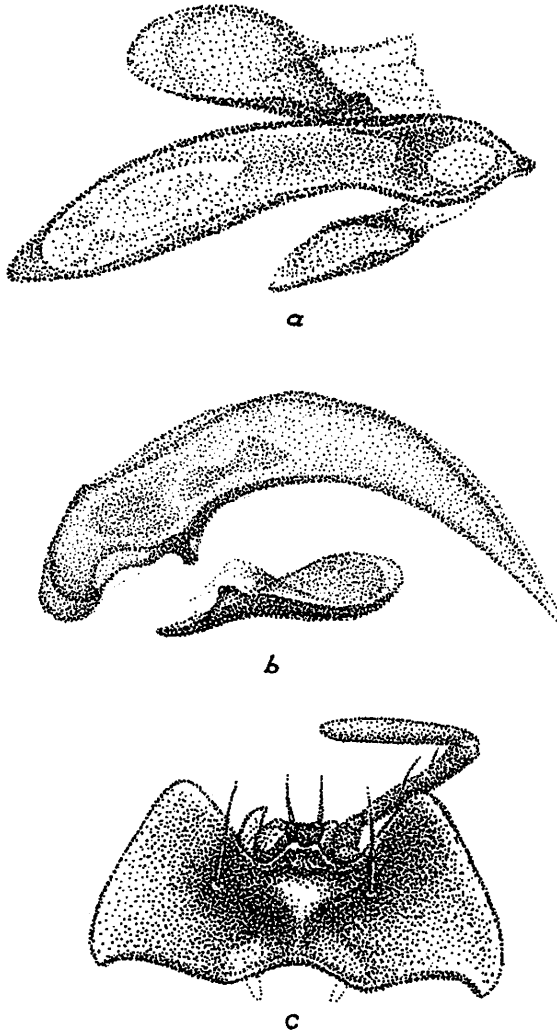
Fig. 2. *Bryanites samoaensis,* holotype ♂, Western Samoa: **a,** aedeagus, ventral view; **b,** aedeagus, left lateral view; **c,** mentum with left palpus.

Bryanites samoaensis Valentine, **new species**   Fig. 1, 2, 4a,b

♂ (holotype). *Measurements* (mm): body length 12.5; width, 4.7; length of head, 3.8; width of head, 2.0; length of pronotum, 3.0; width of pronotum, 3.3; length of elytron, 7.5. *Color:* relatively dark ferrugineous. *Lustre:* glossy with a faintly aeneous elytral sheen. *Head:* large; eyes small, not extending appreciably beyond head's lateral contour; both terminal segments of maxillary palpi relatively long and slender. *Pronotum:* base wider than apex; basal impressions relatively wide. *Elytra:* intervals 6, 7, and 8 merging basally, reaching humerus in combination; apices rounded. *Legs:* basal segment of protarsi shorter than segments 2 and 3 combined; inner claw of mesotarsi longer than outer one; metatrochanters bearing a single tubercle at their base.

Type data. Holotype ♂, WESTERN SAMOA: Savaii I: Salailua, 20[23?].V.1924 (E.H. Bryan, Jr.) (BPBM 13093).
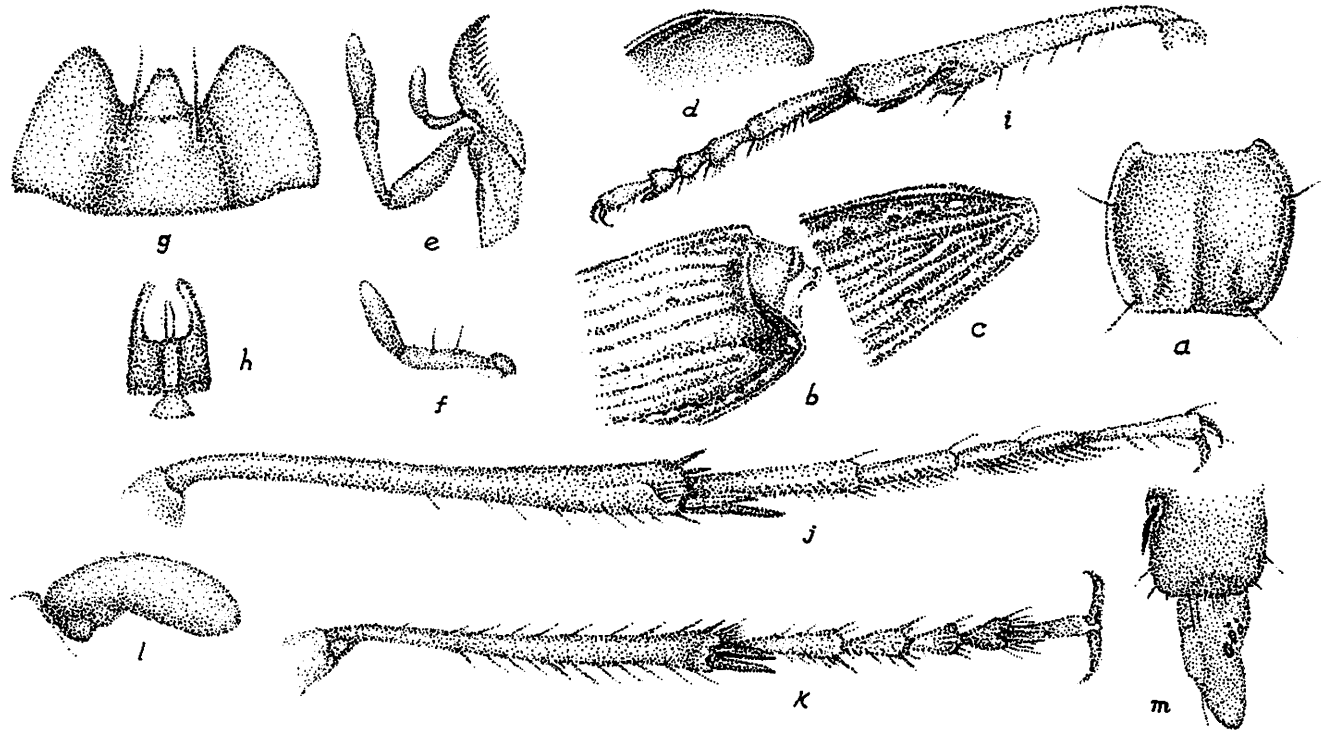
Fig. 3. *Bryanites barri,* holotype ♀, Western Samoa: **a,** pronotum; **b,** basal portion of right elytron; **c,** apical portion of right elytron; **d,** apical portion of left elytron, interior view; **e,** right maxilla; **f,** right labial palpus; **g,** mentum; **h,** ligula; **i,** right protibia and protarsus, lateral view; **j,** right mesotibia and mesotarsus; **k,** right metatibia and metatarsus; **l,** left metatrochanter.
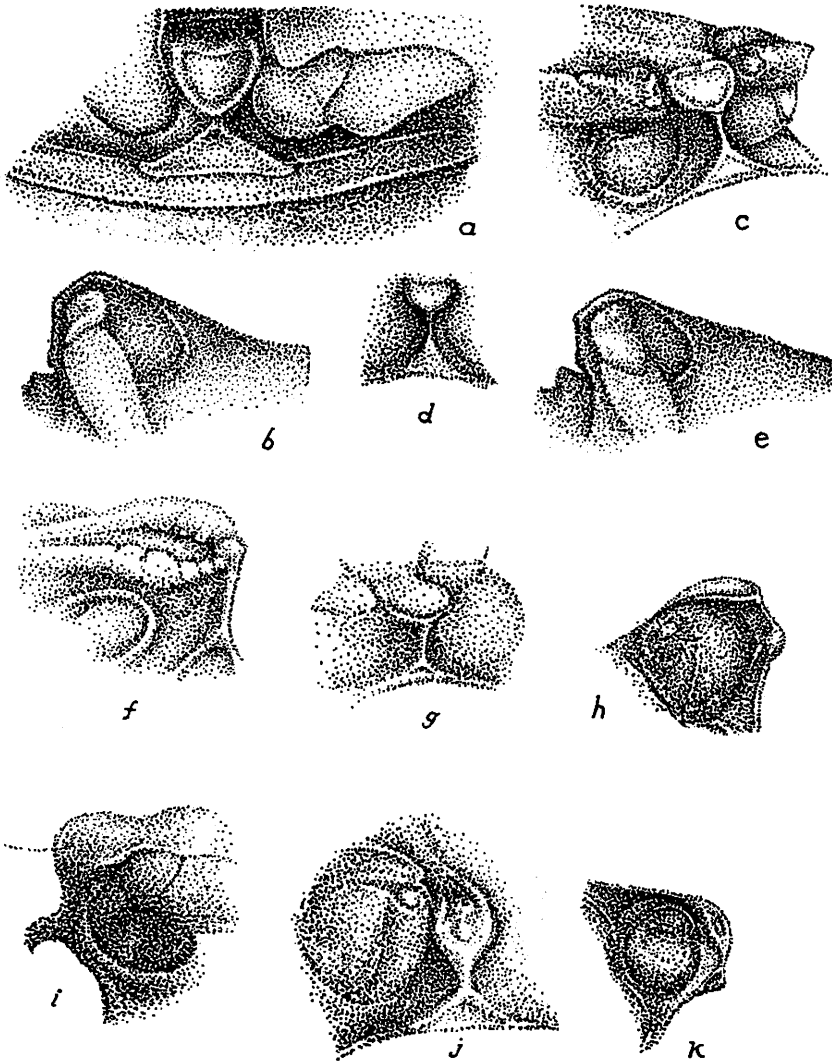
Fig. 4. Prosternal processes in various carabid tribes. **a,b,** *Bryanites samoaensis* (Prosphodrini), holotype ♂, Western Samoa: **a,** ventral aspect showing intercoxal plate; **b,** left lateral aspect showing carina. **c–e,** *Bryanites barri* (Prosphodrini), holotype ♂, Western Samoa: **c,** posterior-lateral view of plate and carina; **d,** posterior aspect; **e,** lateral aspect. **f,** *Prosphodrus waltoni* (Prosphodrini), holotype ♂, New Zealand: right lateral view of carina. **g,** *Sphodrus leucophthalmus* (Sphodrini), France: posterior-lateral aspect. **h,** *Laemostenus complanatus* (Sphodrini), Hawai'i: right lateral aspect. **i,** *Cratoferonia phylarchus* (Pterostichini), Australia: left lateral aspect. **j,k,** *Barypristus* sp. (Agonini), Hawai'i: **j,** posterior aspect; **k,** right lateral aspect.

Bryanites barri Valentine, new species   Fig. 3, 4c,d,e

♀ (holotype). *Measurements* (mm): body length, 11.7; width 4.6; length of head, 3.5; width of head, 1.8; length of pronotum, 2.5; width of pronotum, 2.9; length of elytron, 7.0. *Color:* testaceo-ferrugineous. *Lustre:* shining (not glossy); elytra with an extremely faint aeneous sheen. *Head:* slightly larger than normal; eyes relatively small but protruding slightly beyond lateral contour of head; maxillary palpi with both terminal segments relatively short and stout. *Pronotum:* base and apex subequal in width; basal impressions rectilineal.

Elytra: intervals 6, 7, and 8 merging near base but separated from the humeral carina by a wide gap; apices truncated. *Legs:* basal segment of protarsi longer than segments 2 and 3 combined; mesotarsal claws long and subequal; metatrochanters with a double tubercle at their base.

Type data. Holotype ♀, WESTERN SAMOA: Savaii I: Salailua, 20[23?].V.1924 (E.H. Bryan, Jr.) (BPBM 13094).

Remarks. The specific characters listed for the 2 species described above are sufficiently disparate to indicate some distance in their relationship. One of the salient features uniting them, however, is the keeled condition of the intercoxal process of the prosternum. Yet, the length of this carina is considerably shorter in *B. barri* than in *B. samoaensis* (Fig. 4a–e). The more typically sphodrine keel of *Prosphodrus waltoni* Britton is illustrated from the holotype (Fig. 4f).

Genus **Neanops** Britton

Neanops Britton, 1961, Ann. Mag. Nat. Hist., Ser. 13, 4: 672 (type species *Duvaliomimus caecus* Britton).

Very small (3.6–3.75 mm), cavernicolous trechine carabids showing a high degree of spelean adaptation in being depigmented, apterous, and eyeless, and in being equipped with hypertrophied discal and marginal tactile setae. *Habitus:* slender but appendages not elongated. *Head:* frontal grooves complete; ocular area bearing 3 setigerous papillae on either side; genae and antennal groove areas setose; mandibles with a distinct premolar tooth; maxillary palpi elongate-styliform. *Pronotum:* seta present on the hind angles. *Elytra:* discal setae on 3rd stria; recurved apical stria joins 3rd discal stria; marginal internal fold conspicuously visible from above. *Legs:* protibiae glabrous and ungrooved; protarsi of ♂ only slightly enlarged. *Aedeagus:* without differentiation of apical lobe, basal bulb or internal sclerotization; parameres with 3 setae.

Distribution. So far as is known, *Neanops* is restricted to the caves of the southern portion of North I, New Zealand.

Remarks. *Duvaliomimus* Jeannel, being found on both islands, is a more widely ranging genus of cavernicolous trechines in New Zealand than is *Neanops*. The diagnostic characters differentiating *Duvaliomimus* from *Neanops*, with which it had been confused, are these: premolar mandibular tooth absent; rudimentary eyes present; no setae on disc of ocular area, 2 present on its periphery on either side; no setae at posterior angles of pronotum; recurved apical elytral stria enters 5th discal stria; protarsi of ♂ normally dilated; aedeagus with well-defined apical lobe, basal bulb and a complex system of sclerotized elements; parameres bearing 4 setae. It is quite apparent that these 2 genera are only remotely related. Details of the aedeagus of *D. mayae* Britton, hitherto unpublished, are shown in Fig. 5c–e.

Neanops pritchardi Valentine, **new species**   Fig. 5a,b

♂ (holotype). *Measurements* (mm): length, 3.6; width, 1.1. *Color:* pale ferrugino-testaceous; appendages pale testaceous. *Lustre:* glossy. *Habitus:* convex, moderately slender; appendages, except mouthparts, of moderate length. *Head:* frontal grooves long and deep; inner seta of ocular groups of 3 situated opposite outer posterior seta; genae and antennal ridges setose, frons glabrous; antenna with 3 basal segments glabrous, about ⅓ elytral length; mandibles elongated, bearing a scrobal seta and equipped with a small but distinct premolar tooth; maxillary palpi long and slender. *Pronotum:* sides rather strongly arcuate, with acute posterior angles bearing a seta; disc glabrous. *Elytra:* striae rather well impressed, vaguely punctuate; 3 strong discal setae situated on or near 3rd stria; 9 fine, marginal setae arranged in humeral
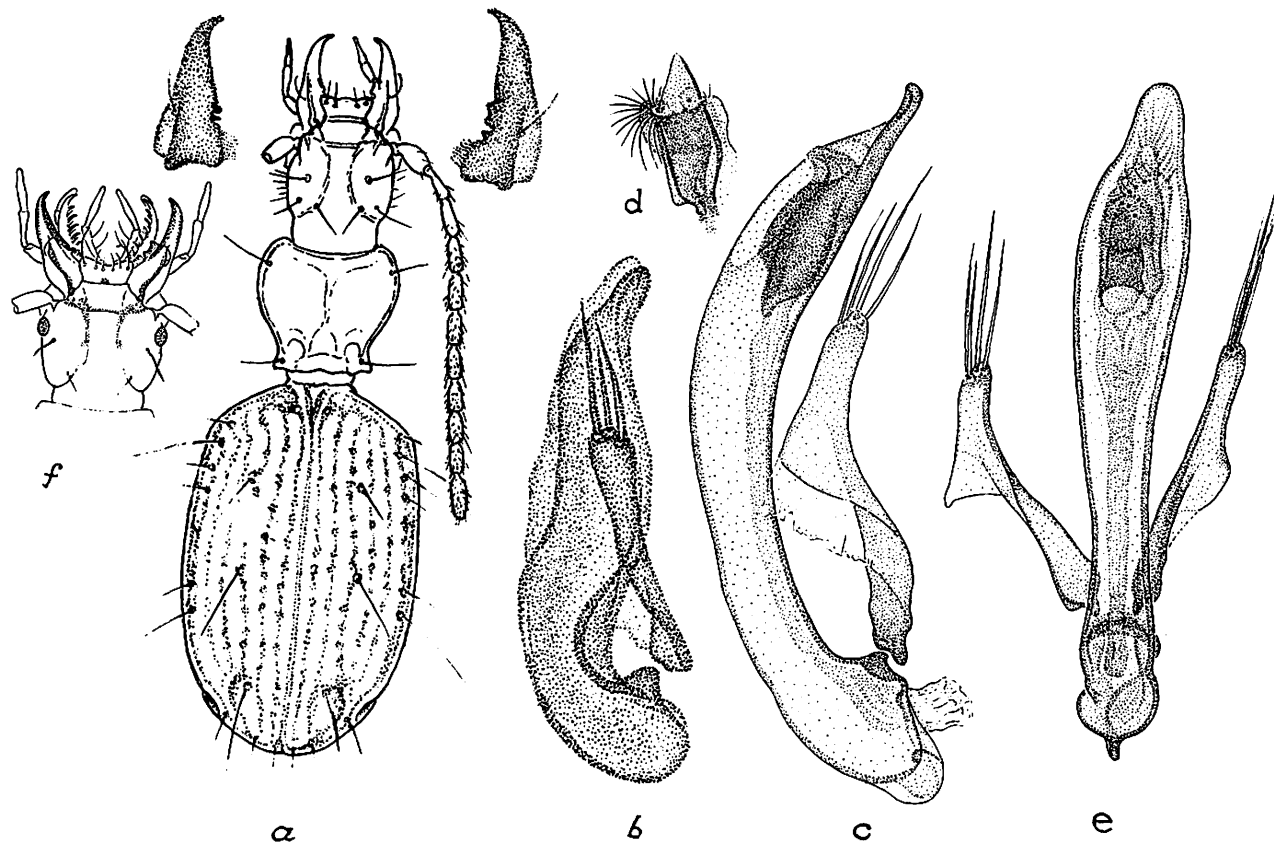
Fig. 5.   Trechini, Te Kuiti, North Island, New Zealand. **a,b,** *Neanops pritchardi,* holotype ♂: **a,** dorsal view with mandibles enlarged; **b,** left lateral view of aedeagus. **c–e,** *Duvaliomimus mayae,* aspects of aedeagus: **c,** left lateral view; **d,** detail of orifice of internal sac; **e,** ventral view. **f,** Dorsal view of head of *Duvaliomimus mayae* to show bidentate dentition.

group of 4, submedian group of 2, and apical group of 3, 2nd, 6th, and 7th hypertrophied; apical recurved stria well impressed, joining 3rd discal stria. *Legs:* of moderate length, basal segments of ♂ protarsi very slightly enlarged, unmodified. *Aedeagus:* comparatively small; median lobe a sinuate, open trough undifferentiated into apical lobe or basal bulb, containing no discernible sclerotized structures; parameres armed with 3 very stout setae.

Type data. Holotype ♂, NEW ZEALAND: NORTH I, Waitomo Co, Wairere Falls Cave (nr Tekuiti), 26.XII.1937 (J.M. Valentine, E.D. Pritchard) (BPBM 13095). Allotype ♀, same data as holotype (BPBM). 1♀,1♂, paratypes, same data (♀ NZAC, ♂ author's collection).

Remarks. *Neanops pritchardi* is extremely small for a cavernicolous trechine. *Neanops caecus* Britton, the only other known species of the genus, is slightly larger. It can easily be distinguished from *pritchardi* by the following characters: a more attenuate form; elytral sculpture shallower and impunctate; pronotum narrower with obtusely rounded hind angles; inner seta of ocular series situated opposite outer anterior seta; frons and disc of pronotum setose. The primitive aedeagus of *Neanops* is illustrated for the first time (Fig. 5b).

DISCUSSION

Bryanites is one of the most generalized carabid forms I have ever encountered. At first glance, it would not seem difficult to assign this genus to one of the great tribes embraced by the Pterostichitae (Jeannel 1942a: 735), to which major division of the Carabidae it obviously belongs. On superficial examination, it might be classified as a pterostichine, an agonine, or a calathoid sphodrine.

Not long after their capture, the 2 specimens of *Bryanites* were sent for identification to H.E. Andrewes, noted British carabidologist. They were returned with this notation: "pterostichini? gen. nov." Andrewes' comments (1927: 14) concerning their affinities are as follows: "They present some unusual features and certainly belong to a genus unknown to me; indeed they may belong to different genera. . . . Both examples appear to belong to the Pterostichini, but evidently differ somewhat in their characters from the European and Asiatic members of that tribe."

Both the acutely truncated prosternal keel (Fig. 4a–e) and the conchoidal parameres (Fig. 2a,b) of *Bryanites* rule out assignment of this genus to the Pterostichini, since the prosternal process in this rather uniform tribe is bluntly rounded (Fig. 4i) and the right paramere is characteristically a twisted, rodlike element that is often vestigial. The Agonini cannot accommodate *Bryanites* either despite the primitive conchoidal condition surviving in this entire group. The Agonini, however, possesses a prosternal process that is definitely concave (Fig. 4j,k). The 3rd possibility lies with the Sphodrini. *Bryanites* has the facies of a large-headed *Calathus*, a similarity that stops there, since the latter has pectinate claws and a long, styloid right paramere. This type of specialized genital apparatus is common to all sphodrines and is the one character that trenchantly separates *Bryanites* from the more evolved members of the tribe, the so-called "true" sphodrines. In the vertically keeled structure of the prosternal process, however, there is considerable agreement (Fig. 4g,h).

The only forms known to agree with *Bryanites* in both of the primary diagnostic characters discussed above (prosternal and aedeagal) belong to 2 genera separated by the Pacific Ocean: *Prosphodrus* in New Zealand and *Mexisphodrus* in eastern Mexico. It is apparent that we are dealing with exceedingly archaic lines of relict faunas that could have considerable zoogeographic significance if proof of genetic relationship could be established. *Bryanites* and *Prosphodrus* agree totally in basic morphology except for the lack of the antennal organ on the protibiae of the former. *Mexisphodrus* differs from both by having a more typically sphodrine habitus and laterally carinate tarsi. The 1st character denotes a more evolved position in sphodrine evolution, while the 2nd is a distinctive feature that helps to unite

New World sphodrines with those of Palearctic distribution. Consequently, only the shape of the right paramere separates *Mexisphodrus* from the main line of true sphodrines, but this character is so atypical and fundamental, "not at all styloid and elongate as is usual for the tribe" (Barr 1965: 69), that it merits special taxonomic evaluation. For the word "usual" in the above quote, I would substitute "invariable." The retention of this primitive genital condition in the 3 archaic stocks of the Prosphodrini must signify some sort of relationship, either direct or of an atavistic nature. At any rate, to retain *Mexisphodrus* in the Sphodrini would seriously vitiate the basic tribal key.

New genera shown to have affinities with any of these archaic stocks should, of course, be examined for possible inclusion in the Prosphodrini. I refer specifically to *Speocolpodes* Barr, 1973, a Guatemalan cavernicole that awaits the collecting of a male to confirm its taxonomic status.

In distinct contrast to *Mexisphodrus* and other members of the Prosphodrini is the recently described cavernicole from Mexico, *Miquihuana* Barr, 1982. This remarkable beetle is unique not only in its spelean adaptation but also in its claim to being the first "true" (non-*Calathus*) sphodrine ever to be found native to the Western Hemisphere. Salient among other marks of advanced sphodrine evolvement is the right paramere, which is a very long, slender stylus.

The question now arises: Could *Miquihuana* have been derived from the ancient stock of *Mexisphodrus* independently of its Palearctic counterparts, or does it represent a lone survivor of an extinct colony of "true" sphodrines now restricted to the Old World? The first hypothesis would invoke the principle of parallel evolution; the second would imply the operation of an environment of such selective potential that only surface-dwelling ancestors on the west side of the Atlantic were eliminated. In our present state of knowledge, the former explanation seems inescapable, unless we are ready to consider tectonic block displacement a possibility. In that case, faunal linkages would be made with the East.

Paralleling the considerable deployment of *Mexisphodrus* in the caves of east central Mexico is a rich fauna of the genus *Rhadine* Leconte. This line, however, is typically agonine, lacking the marginally reflexed habitus and the keeled prosternal process of a sphodrine. Although convergence in appearance increases with the degree of spelean adaptation, an almost total effacement of the humeri in *Rhadine* is an important distinguishing character. *Rhadine* also lacks the deeply emarginate 4th mesotarsal segment found in all the Prosphodrini; of course being an agonine, its aedeagus is furnished with 2 conchoidal parameres. The wide range of *Rhadine,* encompassing the entire breadth of North America, is further evidence of its systematic integrity and genetic isolation from *Mexisphodrus.* Also, it provides additional cause to dispute the total demise of a hypothetical and probably contemporaneous fauna of "true" sphodrines in North America that could include an epigean ancestor for *Miquihuana.*

Neanops caecus (Britton, 1960a), the type of the genus, was originally described as a very small species of *Duvaliomimus.* It was, quite properly, removed from *Duvaliomimus* by Britton in a subsequent paper (1960a) and placed in its own genus. The change was made largely on chaetotaxial grounds, without mention of dentition or genital distinctions.

There are drastic differences between the genital systems of the 2 genera, as mentioned above and illustrated (Fig. 5b–e). Of even more significance is the fact, brought out by Uéno (1977), that the mandibles of *Neanops* possess a distinct premolar tooth, a primitive character that decisively removes the genus from the bidentate *Duvaliomimus* and establishes its position among the archaic, tridentate trechines of Antarctic origin and distribution.

Of the 4 "tribes" in this category described by Jeannel (1926: Perileptini p. 397, Aepini p. 440, and Trechodini p. 469; 1927: Homaloderini p. 7), only the last named offers a repository for *Neanops,* whose rudimentary dentition rules out the first 2 and whose closed

basal bulb definitely eliminates the Trechodini. However, there are fundamental departures from the Homaloderini that might necessitate the assignment of *Neanops* to a group of its own. These include the unique condition of 3 setae on the optical areas, unmodified protarsi, terminus of recurved apical stria in the 3rd elytral stria (5th in Homaloderini), and aedeagus of unique form and setae. *Neanops* is not only archaic, it is quite distinctive. Whether or not it deserves tribal distinction depends on the taxonomic value of Jeannel's nomenclatorial system.

To preserve the family concept in taxonomic analyses, we would be well advised, when making sweeping revisions of large groups, to preserve the relative values of established taxonomic categories by adding new ones when necessary, rather than by downgrading the existing system. With this reform in mind, I would reduce Jeannel's family Trechidae (1941: 81) to subfamily Trechinae and his subfamily Trechitae (1941: 299) to its original tribal status, thus causing its component "tribes" to become subtribes. Although no definitions of taxa have been established, it seems essential to maintain some sort of stability in their use based on evolutionary concepts. Heretofore, tribal characteristics that bind groups together, large or small, are diagnostic and have an ancient history of uniformity. The case in point here is *Neanops*. Although *Neanops* does not fit in any of Jeannel's "tribes" of tridentate trechines, there is no justification for giving it tribal or even subtribal rank. At the present state of nomenclatorial confusion, it can only be classified as a highly aberrant homaloderine.

ZOOGEOGRAPHY AND EVOLUTION

It has been convincingly pointed out by Jeannel (1942b) and others that the Antarctic realm was the actual evolutionary cradle of many ancient ancestral lines of vertebrates and, especially, invertebrates. In this connection, the islands of New Zealand have performed a conspicuous role in preserving more than their share of these "living fossils," among them various lines of archaic carabid cavernicoles.

Dr. René Jeannel's revolutionary book, *La Genèse des Faunes Terrestres* (1942b), in which Alfred Wegener's theory of continental drift (1937) was enlarged upon and richly illustrated, especially with reference to trechine carabid faunas, caused so much opposition that for nearly a decade serious interest in the subject became a professional liability. That changed when geologists examined the evidence and the "tectonic plate theory" came into vogue. Actually, there is no basic difference between the 2 approaches except that Jeannel dealt with a 3-dimensional action, allowing for subsidence and elevation of land, while the plate theory limits itself to 2 lateral dimensions only. As far as the geologic time element involving continental change is concerned, there seems to be considerable accord. Which view is the more plausible?

The Wegener-Jeannel Paleantarctica became an isolated landmass at the close of the Cretaceous. It embraced the future Antarctica, Australia, New Zealand, and the southern portion of South America, a subcontinent that theoretically remained intact until the Miocene. Paleantarctica, from early Tertiary times, seems to have been the evolutionary scene of a considerable number of original carabid stocks. For example, *Cicindis* Bruch of Patagonia connects the Cicindelidae with the Carabidae, bringing the former into subfamily status with the latter; *Ceroglossus* Solier of the Chilean Andes and the related *Haplothorax* Waterhouse of St. Helena in the South Atlantic stand at the very roots of the Carabini; *Maoripamborus* Britton of New Zealand is the likely progenitor of long lines of Cychrini in Australia and in both Northern Hemispheres; the deployment of an ancient pogonoid stock, *Mecyclothorax* Sharp, across Polynesia, apparently originated in the Australian realm, while another archaic group, the Migadopini, became widespread in, and restricted to, the Antarctic Region. *Prosphodrus* of New Zealand and *Bryanites* of Samoa represent another ancestral

line, this one bridging the gap between the Sphodrini and the Agonini. With the exception of the holotropical Perileptina, the trechine fauna of the Southern Hemisphere, especially its Antarctic elements, is almost totally dominated today by primitive tridentate groups (Aepina, Trechodina, and Homaloderina), strongly suggesting a Paleantarctic origin for the more evolved bidentate trechines (Trechina) virtually restricted to the Northern Hemispheres.

The temperate carabid faunas of both the Northern and the Southern Hemispheres contain many multispeciated genera, yet a certain qualitative difference seems to separate the 2 biotas. Generally speaking, many genera of the northern latitudes show a relatively higher degree, and therefore possibly a later period, of evolution. The rich tropical and subtropical biotas, intervening between temperate elements, on the other hand, are composed largely of more specialized genera lacking in expansive, evolutionary potential, a probable sign of an even more recent emergence.

Tracing the various lines of archaic carabids from one hemisphere to another can become quite a problem when, as sometimes happens to ancient stocks, geographic discontinuity reaches the point of remote isolation. The following cases illustrate this phenomenon. Homaloderine trechines, ranging plentifully in several genera eastward across the subantarctic region from southern South America to New Zealand, are represented in the Northern Hemisphere by a single, relict species, *Iberotrechus bolivari* Jeannel, 1920. This beetle is typically homaloderine in all respects, save its habitus and habitat, which are those of a cavernicole. The only other known cave-adapted genera in this entire group are *Neanops* and *Erebotrechus* Britton, 1963, both of New Zealand (Uéno 1977), and some more recently discovered cavernicoles from Tasmania (Moore 1972). *Iberotrechus* inhabits caves in the Cantabrian Mountains of northwestern Spain, where it is a unique relict. The emigration of its ancestral line from its presumed land of origin in the Antarctic to these northern latitudes may have paralleled that of another ancient tridentate stock, the aepines. Subtribe Aepina is composed of 5 genera of highly specialized beetles adapted for life in intertidal pools. Their headquarters is the far southern shores of South America, with offshoots on the Antarctic archipelagos, including New Zealand. Representatives of this archaic lineage somehow reached the shores of western Europe and Morocco, where 2 genera, *Aepus* Samouelle, 1819, and *Aepopsis* Jeannel, 1922, evolved. There is no sign of close relatives over the vast distance separating the 2 centers of distribution.

As in the Homaloderina, so many characters unite the Aepina with their relatives to the south that any explanation based upon convergent evolution seems spurious. One is obliged to accept an environmental cause and to assume that, over the great span of geologic time, suddenly changing climates have taken a selective toll of ancestral faunas and drastically restricted their ranges.

More difficult to explain, perhaps, are the rare cases of relict Southern Hemisphere genera that quite possibly represent the ancestors of large and widespread Holarctic cave faunas. I refer in particular to *Duvaliomimus,* a unique line of bidentate trechines living in a region otherwise inhabited exclusively by archaic tridentate genera. *Duvaliomimus* contains rather large, lucifugal species found in caves on both islands of New Zealand. Their habitus varies from forms with reduced eyes to completely spelean eyeless species. One species with reduced eyes, *D. lamberti* Britton, 1960a, has been determined by Uéno (1977) to have tridentate dentition and therefore could represent an ancestral lineage.

Jeannel described *Trechus maori* (=*Anchomenus walkeri* Broun, 1903) in 1920 and designated it the type species of a new genus, *Duvaliomimus,* in 1928. His inclusion of this genus with the Trechina was based on its bidentate dentition (Fig. 5f), and he referred to it as being "without copulatory pieces in the aedeagus." In recent years, several additional species have been described as belonging to this genus by Britton (1958, 1959, 1960a, 1962, 1963).

On dissecting specimens of *D. mayae* Britton, 1958, which I collected in 1937 at Te Kuiti, North I, New Zealand, I found the internal sac to be provided with a clearly defined copulatory apparatus, including a small basal plate (Fig. 5c–e). Jeannel (1928) had already indicated a probable relationship between *Duvaliomimus* and *Agonotrechus*, 1923, a small group of epigeal isolates from the Himalayas. His opinion was based largely on chaetotaxy, especially in the apical region of the elytra. According to Jeannel, this series of setae "is not evolved" in either genus, indicating a primitive condition and therefore possible genetic connection. Actually, most of the described species of *Duvaliomimus* possess a full complement of apical setae. However, I tend to agree with Jeannel that both groups appear to be extremely archaic.

Duvaliomimus demonstrates its taxonomic variability in a number of ways. Besides its potential for bridging the gap between bidentates and tridentates, it has a wide range of possible relatives in both the Palearctic and Nearctic regions, as evidenced by its recurved apical sulcus joining the 5th elytral stria, the protarsi of the male having 2 basal segments enlarged, and basic chaetotaxial points of agreement. In the Old World many carabid lines would meet these specifications, but in the New World there appears to be only one: the *Paratrechus* series (Jeannel 1928) of spelean and epigean species of several genera, the range of which extends from Mexico to northern South America.

The form and character of the aedeagus of *Duvaliomimus* strongly suggests an affiliation with this series of Nearctic trechines. It seems to bear a particularly close relationship to that aberrant, unique, monotypic genus from Guatemala, *Myaphaenops* Vigna Taglianti, 1977. This strictly spelean relict differs from other genera of the series by having both its discal setae borne on the 3rd elytral stria instead of the 5th as is usual, and in possessing an aedeagus in which the transfer apparatus consists of a single plate in place of the normal pair of elongated sclerites (Barr 1982a). The chaetotaxy of *Duvaliomimus* is identical to that of *Myaphaenops*; and the aedeagus of *D. mayae,* in addition to the usual minute scales that arm its internal sac, contains a small, hyaline basal plate. The elongated aedeagal contour with rounded apex completes the resemblance (Fig. 5c–e).

In distinct contrast to the *Paratrechus* series of the southwest is that very extensive evolvement of cavernicolous trechines of northeastern America, the *Pseudanophthalmus* series (Jeannel 1928); these species inhabit the caves of the Appalachian System, east of the Mississippi, south of the glacial line, and north of the areas invaded by Pliocene seas. The genera of this exclusively bidentate group, featuring *Pseudanophthalmus* Jeannel, 1920, differ from *Paratrechus* and the great preponderance of Palearctic genera in the joining of the recurved apical sulcus with the 3rd elytral stria ["rarely the 4th, never the 5th" (Jeannel 1928)]. This consistency suggests a separate (secondary) ancestry for the eastern North American faunas of cavernicolous trechines. A likely candidate has been cited (Jeannel 1928; Barr 1971) as the genus *Trechoblemus* Ganglbauer, 1892, which is represented today by only 2 species, *T. micros* (Herbst, 1894), a widely ranging Palearctic form, and *T. westcotti* Barr, 1971, apparently confined to the Pacific northwest coast of America. *Trechoblemus* is an archaic, relict member of the Trechina. It is a fully winged and eyed epigeal. Its fused mentum, with multiple submental setae, plus the clear-cut entry of the recurved apical sulcus into the 3rd discal stria, are basic characters that help place this unique genus in the direct line of evolution of North American anophthalmids. The primitive tonguelike sclerite of the internal sac could have produced either the paired sclerites of *Pseudanophthalmus* or the single plate of the aberrant genus *Ameroduvalius* Valentine, 1952.

The phylogenetic homogeneity (close relationship) of these cavernicoles is broken only by the unique relict *Xenotrechus* Barr & Krekeler, 1965, the 1st anophthalmid to be taken west of the Mississippi River, an ancient barrier to the dispersal of cave obligates. *Xenotrechus* is a true cavernicole that Barr has shown to be unrelated to any branch of the *Pseudanoph-*

thalmus series. With its peculiar, serrated posterior pronotal margins, its lack of sclerites in the internal sac, and a recurved apical sulcus that enters the 5th elytral stria (instead of the 3rd), it departs radically from other North American anophthalmids. It does, however, bear a striking resemblance to *Geotrechus* Jeannel, 1919, of the Carpathian Alps, to which series it apparently belongs. Here is another example of the remote isolation of a fragment of an ample genetic line. A possible explanation in this case could be the splitting of a holarctic continent in Paleocene times.

A comparable basic nonconformity in major genetic lines exists in the Palearctic Region, where a small group of anophthalmid trechines, *Duvaliopsis* Jeannel, 1928, from the Transylvanian Alps, shows a direct ancestral linkage to *Trechoblemus* and, hence, an affiliation with Nearctic genera, *Pseudanophthalmus* in particular. In fact, Barr (1964) tentatively assigned 6 species of *Duvaliopsis* (*bielzi* group) to *Pseudanophthalmus* based on the 3rd strial entry of the apical sulcus and other considerations, including aedeagal similarities.

There are many characters, especially in chaetotaxy, mouthparts, and aedeagi, separating and allying the various genetic groupings of the trechines throughout the world. These have been most adequately appraised by specialists in the field, Jeannel and Barr in particular. Rather than review these here, I would like to focus on one of the fundamental features that has aroused some controversy—dentition. In response to Moore's critique (1972) of Jeannel's primary classification of world Trechini using dentition as the basic criterion (1926) and in defense of the latter, I must point out that the exceptions to the norm, on which Moore relies to disqualify the primitive premolar tooth as a valid taxonomic criterion, are rare and indecisive.

The only case supporting Moore's critique within the 4 tridentate subtribes occurs in the South American genus *Plocamotrechus* Jeannel, 1926, where the left premolar tooth is apparently missing. However, the unusually large and emarginate retinaculum on the left side of the mandible may well have originated from a fusion of 2 simple teeth, a secondary condition occurring in some homaloderines.

A few bidentate trechines, notably *Epaphius* Stens, 1830, and *Epaphiopsis* Uéno, 1977, have been reclassified by Moore as tridentates because of the appearance of an extra tooth in the right mandible. This can be explained on the grounds of a not-infrequent double emargination of the retinaculum on the right side. Bilateral increase in teeth in this fashion is also possible, but very rare. *Pseudanophthalmus pubescens* (Horn, 1868) illustrates this aberration nicely, and Moore has given the species tridentate status in spite of its nearest relatives being definitely bidentate. Actually, the retinaculum, especially the right one when hypertrophied, can produce 3, 4, or even 5 cusps, and the left terebrum can produce 2. At least 1 of these can separate from the parent structure, as can be clearly traced in the 3 aberrant genera of cave beetles from northeastern Kentucky, *Nelsonites* Valentine, *Darlingtonea* Valentine, and *Ameroduvalius* Valentine (Valentine 1952). Similar multiple cusp formation can be seen in *Pseudanophthalmus* (*Aphanotrechus*) *virginicus* Barr, 1960. Such evolutionary specialization in no way detracts from the importance of recognizing the truly primitive tridentate condition characterizing all 4 subtribes (Perileptina, Aepina, Trechodina, and Homaloderina) of Jeannel's Trechinae Tridentatae (1926).

Returning to *Neanops*, we find the pattern of dentition primitive, with the right retinaculum short and moderately emarginate, the left a simple tooth. Both are preceded by a small premolar denticle (Fig. 5a). This tooth is so vestigial that it could represent an initial stage in bidentate evolution. In this case, archaic *Neanops*, with its 3rd strial apical groove entry and its simplified aedeagus, could occupy a unique position of extreme antiquity, along with the archaic *Trechoblemus*.

Relict, ancestral faunas are not necessarily those that have adapted to a subterranean existence, a point that is adequately exemplified by the lucifugal (not spelean obligate)

habits of such progenitors as *Prosphodrus* and *Bryanites*, linking the true sphodrines with the agonines. But it is quite apparent that survival from antiquity and cave life are often close correlatives. Anomalous cavernicolous relicts are of surprisingly frequent occurrence. About all we can learn from them is that environmental vicissitudes, taking their toll above ground, did not affect the much more stable milieu of the great caverns into which many lucifugal species took refuge, especially during times of geologic or climatic changes. The more extensive the cave system, the more equable becomes its climate, so it is not surprising to find that our vast limestone galleries have become repositories for "living fossils" sometimes so archaic they leave few clues to their origin. Presumably, only catastrophic flooding or glaciation could terminate their long tenure underground.

It is interesting to speculate on a rough classification of the products of spelean isolation, based on geologic time, distribution, and evolutionary history. A number of categories are in evidence. For instance, there are those troglobitic faunas, such as *Mexisphodrus*, that occupy a unique phylogenetic position (Barr 1982a) and are remote taxonomically from their closest allies (*Prosphodrus, Bryanites*). *Duvaliomimus* also fits this category, since its kinship seems to lie with the *Paratrechus* fauna of Mexico.

Next, we have the category of monotypic (or nearly so) genera occupying exceedingly restricted ranges and whose relatives, established with reasonable certainty, live in a totally different part of the world. I refer to such unique relicts as *Iberotrechus, Xenotrechus,* and the recently described cavernicole from eastern Mexico, *Miquihuana* Barr, 1982a, the 1st true sphodrine (Sphodrina) found beyond the Palearctic realm.

The 3rd category is reserved for those rare products of isolation of such ancient origin that they cannot be assigned with certainty to any known group. A case in point is the unique *Horologion speokoites* Valentine, 1932, a true bathycole forced by flood waters in the Greenbrier Valley of West Virginia into upper cavernous levels. This little, blind beetle presents a mixture of basic characters that render even tribal identity a most difficult task. It has been variously placed in the Trechini, Bembidiini, and Psydrini. My personal preference is the Trechini, where it can be traced to the very foundation of the tribe, the Antarctic Trechodina. The open basal bulb area of the aedeagus of *Horologion* is a diagnostic character of these primitive trechines; and if the minute cusp at the base of the right retinaculum can be accepted as a rudimentary tooth, *Horologion* would find a legitimate place with the tridentates. Its left mandible is typically trechodine. A decision in favor of this view would establish this archaic relict as the first relative of the Trechodina to be found in the Nearctic Region. Actually, its dental equipment is not unlike *Neanops* of New Zealand, establishing the possibility of distant relationship. Both these most ancient lines need at least subtribal recognition.

Neither continental drift nor parallel evolution can satisfactorily explain these erratic faunistic discontinuities. Without a selective lethal factor, the mere separation of landmasses, breaking up a faunistic element into isolated colonies, could not be expected to produce the phenomenon of pinpoint specific segregation such as occurs among the cavernicoles. On the other hand, to solve the problem by introducing the concept of independent, parallel evolution would entail the limitation of a normally expansive process to the creation of a single species or genus.

The more logical approach, it seems to me, is to treat these isolated relicts as the longtime survivors of ancient stocks that elsewhere failed to find the eternal asylum of that sheltering environment, the subterranean cavern.

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