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THE HETEROMEROUS INTERTIDAL BEETLES

(Coleoptera: Salpingidae: Aegialitinae)[1]

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Abstract: Characteristics, relationships, and known biologies of the Salpingidae: Aegialitinae are given. The subfamily contains *Aegialites*, with four species found on the Pacific coast from the Kuriles to California, *Antarcticodomus*, with one species found on Campbell and Auckland Islands, and *Elosoma*, a genus incognito with one species from Persia. *Antarcticodomus* is transferred from the Tenebrionidae: Helopinae; the genus forms a connecting link between *Aegialites* and the Salpinginae.

The beetle genus *Aegialites* Mannerheim, 1853, has been somewhat of an enigma to coleopterists. Its placement in beetle hierarchy has been hampered by one thing: *Aegialites* has essentially stood alone in a family, the Aegialitidae (=Eurystethidae), or more recently in a subfamily, the Aegialitinae of the Salpingidae. No other beetle has been placed close to it except for a *genus incognito*, *Elosoma* Motschoulsky, 1845. In such a monobasic taxon, in this case a subfamily, the taxonomic value of a characteristic is not easily determined. In the subfamily Aegialitinae the presence, absence, or shape of a structure might be of generic, tribal, or subfamilial significance; we cannot determine such value for certain. Conversely, in a subfamily with more than one genus, the taxonomic value of a characteristic, whether generic or subfamilial, would be more easily determined. Therefore, we "need" more genera in the Aegialitinae if we are properly to evaluate characteristics. Essentially, the difficulty lies with two morphological characteristics which together are unique in the Heteromera; *Aegialites* has all coxae widely separated (figs. 4, 5) and all tarsi long (fig. 5), with the last tarsal segment especially elon-

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gated and with the claws enlarged. Because of these two morphological characteristics, *Aegialites* has been put in a separate family by most students. But widely separated coxae, long tarsi, and large claws are special adaptations for life on rocks in the intertidal zone, which is the habitat of *Aegialites*. Such specializations can be deceptive to systematists; they can often mask more important and basic differences or similarities.

If we are going to settle the problem of *Aegialites's* placement, we must find its connecting link, that is, a beetle like *Aegialites* except for the specializations. I have hoped to find such a beetle since first I saw a specimen of *Aegialites*. At last one has come before me: *Antarcticodomus fallai* Brookes, 1951, a little beetle that lives under stones on Campbell and Auckland Islands south of New Zealand. Except for narrowly separated coxae (figs. 9, 10), it looks very much like *Aegialites*. Like *Aegialites*, however, *Antarcticodomus* has long tarsi and large claws (fig. 11). Thus part of my desires have been realized; I have seen an *Aegialites*-like beetle without widely separated coxae. And, after all, the widely separated coxae are the most striking feature of *Aegialites*.

Antarcticodomus was placed in the Tenebrionidae, subfamily Helopinae, by Brookes, but the open procoxal cavities (fig. 9) of the genus forbid its placement there. Brookes probably did not have a specimen of *Aegialites* before him for comparison; so, he could not have known of its similarities to his new genus. If I had not known *Aegialites*, I would have placed *Antarcticodomus* in the Salpingidae, subfamily Salpinginae, near *Sphaeriestes* Stephens. In *Sphaeriestes* the last tarsal segment is long, and the wings are full-sized. In other characteristics *Antarcticodomus* and *Sphaeriestes* are quite similar. Eventually *Antarcticodomus* might have to be placed in the Salpinginae, carrying *Aegialites* with it. However, such a transfer is too drastic at present. Our knowledge of higher classification in the Heteromera is too poor, heteromerous larval classification is in the infant stage, and *Aegialites* adults are indeed quite distinctive. I prefer to show the affinities of *Antarcticodomus* by placing it next to *Aegialites*, to show the affinities of the two genera in beetle hierarchy by placing them in the Salpingidae, and to show their uniqueness by placing them in a separate subfamily, the Aegialitinae.

The problem of placement of *Aegialites* and *Antarcticodomus* is most certainly not completely solved herein. We must know much more about their life histories, and their larvae must be studied in detail. Also, we need to know more about various odd genera whose placements in other families are doubtful; there are many such genera in the Heteromera. Of course, a complete reclassification of the Heteromera would solve almost all these problems.

Before continuing, perhaps a word on *Elosoma* is in order. *Elosoma* Motschoulsky, 1845, is unknown to me and seems to have been unknown to all who mentioned it since 1845. It originally contained two new species, *E. persica* from Persia and *E. ? californica* without locality mentioned. According to Article 67(h) of the International Code of Zoological Nomenclature, *E. ? californica* cannot be made the type-species of *Elosoma*; *E. persica* is therefore the type-species by monotypy. Mannerheim in 1853 (p. 178) removed *californica* (=debilis) from *Elosoma* to *Aegialites*. Nevertheless, most authors since that time have kept the two genera separated, either directly or by not mentioning *Elosoma*. My attempts to locate the type of *E. persica* have been fruitless; so I prefer the generic isolation of *Elosoma persica*, using the terms *genus* and *species incognito*. They are not included below in any of my morphological or ecological discussions.

In summary, the subfamily Aegialitinae of the family Salpingidae will now include the following genera: *Aegialites* Mannerheim, *Antarcticodomus* Brookes, and *Elosoma* Motschoulsky, a *genus incognito.*

HISTORICAL ACCOUNT

The following chronological account will show past progress in the classification of what is today known as the Aegialitinae.

1834 Dejean (p. 117) listed *Aegialites debilis* Eschscholtz from boreal North America; placed genus in *Terediles* between *Gibbium*, a ptinid, and *Mastigus*, a scydmaenid; both generic and specific names were *nomina nuda.*

1836 Dejean (p. 131) repeated 1834 listing.

1841 Duponchel (p. 140) discussed but did not describe *Aegialites debilis* and gave citations to previous literature; placed genus in tribe Ptiniores of Latreille; generic and specific name were *nomina nuda.*

1845 Motschoulsky (p. 33) described *Elosoma persica* from Persia and *Elosoma ? californica* without locality; they followed the genus *Parnus*, an elmid.

1848 Gistel (p. XI) proposed the new generic name *Orygmus* for *Aegialatis* [sic] Eschscholtz [Dejean 1834] which he thought was preoccupied by the avian name *Aegialitis* Boie. [*Orygmus* was a *nomen nudum* because it was proposed as a new name for a *nomen nudum.*]

1853 Mannerheim (p. 178) described *Aegialites* and *A. debilis* from California, Sitkha Island, and Kenai Penninsula of Alaska; with *Elosoma ? californica* Motschoulsky listed as a junior synonym of the species; placed in the *Silphalia* following *Colon.*

1859 Lacordaire (p. 738) redescribed *Aegialites,* with *Elosoma* as a junior synonym; reviewed previous history of genus; probably synonymized *debilis* and *californicus*; did not place genus in a family.

1862 LeConte (p. 241) described the family Aegialitidae; included *Aegialites debilis*; placed family between Tenebrionidae and Alleculidae.

1870 Gemminger & Harold (p. 2041) listed in world catalogue *Aegialites,* with *Elosoma* as junior synonym; included two species *californicus* and *persicus*; placed genus in Tenebrionidae between *Talanus* Dejean and *Cylindrothorus* Solier.

1883 LeConte & Horn (p. 388) repeated LeConte's 1862 statements.

1888 Horn (p. 27) described and illustrated mouthparts of *Aegialites debilis.*

1893 Horn (p. 143) discussed generic names; described *Aegialites fuchsii* from Mendocino County, California; synonymized *debilis* to *californicus*; gave key to the two species.

1894 Hamilton (p. 33) in Alaskan catalogue listed *Aegialites californica* from Kenai Peninsula and Sitkha and from California.

1898 Linell (p. 74) described *Aegialites stejnegeri* from Robben Island in the Okhotsk Sea; described sexual dimorphism for the genus.

1899 Sharp (p. 265) gave a short description of Aegialitidae; compared family with Pythidae.

1899 Schwarz (p. 549) recorded *Aegialites californica* from the stomach of a shore bird, *Limosa lapponica*, shot on Walrus Island, 6 miles distant from St. Paul Island of the Pribilof Islands; doubted that Motschoulsky's California record was correct for this species.

1903 Keen (p. 125) described habits of *Aegialites debilis* on Queen Charlotte Island and on mainland of British Columbia.

1903 Ganglbauer (p. 306) included Aegialitidae in Heteromera between Othniidae and Lagriidae.

1904 Fletcher (p. 97) recorded Keen's specimens of *Aegialites debilis* from Metlakatla, Alaska.

1904 Wickham (p. 57) described and illustrated the larva and pupa of *Aegialites californicus* from Metlakatla, British Columbia; said larva was much like larvae of Pyrochroidae.

1904 Wickham (p. 356) described procoxal cavities of *Aegialites*; placed Aegialitidae between Melandryidae and Pythidae, nearer the latter.

1908 Kolbe (pp. 287, 391) included Aegialitidae in Heteromera between Tenebrionidae and Tentyriidae; discussed relationship with other families.

1910 Borchmann (p. 1) listed Aegialitidae, including *Aegialites* with its junior synonym *Elosoma*, and the four species *californicus*, *fuchsi* [sic], *persicus*, and *stejnegeri* in world catalogue.

1912 Sharp & Muir (pp. 551, 619) described and illustrated male aedeagus of *Aegialites debilis*; placed Aegialitidae next to Pythidae.

1912 Fowler (p. 161) redescribed Aegialitidae; placed it in Heteromera between Tenebrionidae and Lagriidae, but believed it closely allied to Pythidae.

1915 Jacobson (pp. 993, 1014, pl. 80, fig. 2) placed Elosomatidae in key to families of Tenebrionoidea between Pythidae and Lagriidae; Aegialitidae and Helosomatidae listed as junior synonymns; included *Elosoma* with *Aegialites* as junior synonym, *E. californicum* from Commander Islands, Pribilof Islands, Alaska, and Canada, with *debile* [sic] as junior synonym, and *E. persicum* from Persia.

1916 Seidlitz (p. 127) proposed *Eurystethes* as a new name for *Aegialites* Mannerheim, 1853, not *Aegialites* Keyserling & Blasius, 1842; changed family name to Eurystethidae; discussed position of family, placed it between Pythidae and Euglenidae, near the latter; said *Elosoma* does not belong to the family.

[*Aegialites* Keyserling & Blasius was a misspelling for the avian name *Aegialitis* Boie, 1822; misspellings do not preoccupy names.]

1918 Van Dyke (p. 307) described *Eurystethes subopacus* from San Mateo and Marin Counties, California; in key to four species, recorded *californicus* from Aleutian Islands, southeastern Alaska, and Queen Charlotte Island; *stejnegeri* from Robben Island; *fuchsii* from Mendocino County and Farallone Islands of California; used family name Eurystethidae; said *Elosoma* belongs to different family.

1920 Lucas (pp. 76, 260) in list of generic names included *Aegialites* with *Elosoma* as junior synonym; listed *A. californicus* as type-species.

1920 Seidlitz (p. 983) repeated 1916 statements.

1920 Leng (pp. 38, 160) catalogued North American species of Eurystethidae, with genus *Eurystethus* [sic] and three species, *californicus*, *fuchsi* [sic], and *subopacus*; placed family between Meloidae and Pythidae or Meloidae and Othniidae.

1922 Winkler (p. 898) listed in world catalogue *Aegialites persicus* from Persia, with *Elosoma* [sic] as a junior generic synonym; placed in Aegialitidae between Othniidae and Petriidae.

1923 Wickham (p. 156) recorded *Aegialites californicus* from St. Paul Island, St. George Island, and Sea Lion Rock, all in the Pribilof Islands.

1923 Stickney (figs. 51, 199, 344, 488) illustrated head capsule of *Eurystethus* [sic] *debilis*; used family name Eurystethidae.

1923 Lefroy (p. 178) gave a short description of Aegialitidae and placed it in Heteromera between Tenebrionidae and Lagriidae.

1925 Handlirsch (pp. 537, 640) redescribed Eurystethidae and placed it in family key in Heteromera between Salpingidae and Petriidae with Aegialitidae as junior synonym; included *Eurystethes.*

1928 Strand (p. 74) in nomenclatural notices said *Aegialites* Mannerheim, 1853, was preoccupied by *Aegialites* Kaup, 1829; said the generic name *Aegialatis* Gistel, 1848, and the family name Aegialatidae should be used. [Actually, Kaup's name was a misspelling of *Aegialitis* Boie, 1822, and a misspelling does not preoccupy a name; Gistel's name *Aegialatis* was a misspelling of *Aegialites,* not a new name.]

1931 Boving & Craighead (pp. 40, 75, pl. 48, figs. A–F) placed Eurystethidae in key to larvae, between Pedilidae and Salpingidae; *Eurystethus* [sic] *californicus* larva illustrated.

1935 Meixner (p. 1317) redescribed Eurystethidae with Aegialitidae as junior synonym; placed in Heteromera between Pythidae and Othniidae; used generic name *Eurystethus* [sic]; described larva.

1936 Kono (p. 141) recorded *Aegialatis* [sic] *californicus* from the Kurile Islands; accepted Strand's 1928 reasons for the use of the generic name *Aegialatis*; gave key to *californicus* and *fuchsii*; gave bibliography.

1938 Hatch (p. 149) recorded *Eurystethus* [sic] *debilis* from Amchitka Island in the Aleutian Islands.

1938 Kono (p. 1) described the subspecies *Aegialatis* [sic] *stejnegeri sugiharai* from four of the Kurile Islands and redescribed *stejnegeri stejnegeri* from Robben Island; gave determination key to two subspecies; described larva of *sugiharai.*

1938 Sugihara (p. 6) described biology of *Aegialatis* [sic] *stejnegeri sugiharai.*

1938 Miwa & Chujo (p. 51) listed in Japanese catalogue under Aegialatidae [sic] the two subspecies *Aegialatis* [sic] *stejnegeri stejnegeri* from Saghalien and *stejnegeri sugiharai* from the Kuriles.

1944 Jeannel & Paulian (p. 81) placed Aegialitidae in the section Tenebrionaria of the division Heteromeroidea, between Pedilidae and Pythidae, on basis of abdomen and male genitalia.

1949 Paulian (p. 915) redescribed Aegialitidae, placed it between Pedilidae and Othniidae in section Tenebrionaria of the division Heteromeroidea; described larva.

1949 Chu (p. 111, fig. 294) placed Eurystethidae in key to larvae; *Eurystethus* [sic] *californicus* larva illustrated.

1951 Brookes (p. 39, fig. 7) described new genus and species *Antarcticodomus fallai* from Campbell and Auckland Islands, with illustration of whole beetle; placed in Helopinae of Tenebrionidae.

1952 Spilman (p. 12) relegated Eurystethidae to subfamily status in the Salpingidae on basis of male genitalia of *Eurystethus* [sic].

1953 Crowson (pp. 39, 51) placed Aegialitidae as synonym of Elacatidae (=Othniidae) with the cryptophagid genus *Trogocryptus* and its allies and with the cucujid genus

Prostominia; Elacatidae placed in key to larvae and adults; generic name *Eurystethus* [sic] used.

1954 Spilman (p. 87) cited type-species of *Aegialites, Eurystethes,* and *Elosoma*; used the name *Aegialites* instead of *Eurystethes*; *Aegialites* and *Elosoma* placed in the Aegialitinae of the Salpingidae.

1955 Crowson (pp. 117, 128) repeated 1953 statements.

1956 Leech & Chandler (pp. 298, 299, 349) included adults and larvae of Eurystethidae in key to families; keyed *Eurystethes fuchsii* and *subopacus* and gave their distribution; gave a short general description with figures of pupa and larva.

1962 Arnett (p. 713) included *Aegialites* in Aegialitinae in generic key to family Salpingidae.

Morphological and ecological considerations

Widely separated coxae, long tarsi, and large claws are undoubtedly special adaptations for life on rocks in the intertidal zone. Many members of the Dryopidae and Elmidae have these same adaptations for clinging to rocks along shore lines of fresh and salt water. Widely separated coxae allow for a wide stance and thus a better purchase on rocks, and long tarsi and large claws allow for a good grip on the rocks' irregular surfaces. Thus two kinds of beetles, well separated in our familial classifications, are adapted to the same habitat in the same way.

Widely separated coxae caused taxonomists to isolate *Aegialites* in a separate family. But a few other characteristics, especially in the mesothorax, caused confusion and error. Perhaps these structures in *Aegialites* can now be understood. If we agree that widely separated coxae can be a special adaptation for clinging to shore rocks, obviously *Aegialites* evolved from a beetle without the special adaptation. Then, if we also agree that *Antarcticodomus* evolved without a change of coxal placement from an ancestor which also gave off *Aegialites,* we can see how changes of coxal placement and other structures are correlated. First, consider the mesothoracic sclerites. In *Antarcticodomus* (fig. 10) the epimeron is slender, long, and almost touches the coxal cavity, while the fused episternum and sternum does not touch the metepisternum; this is the condition in many beetles. In *Aegialites* (fig. 5), however, a lateral displacement of the coxae is correlated with a broad, short epimeron far from the coxal cavities, while the fused episternum and sternum does touch the metepisternum. Second, consider the metathorax. Here the lateral sclerites have not been changed. The coxa extends just as far laterally in *Antarcticodomus* (fig. 10) as in *Aegialites* (fig. 5). Rather the coxa has been medially shortened in *Aegialites* with a wide space between the coxae. This wide space is correlated with the shape of the metendosternite in *Aegialites.* In *Antarcticodomus* the metendosternite (fig. 12) is broadly V-shaped and has a short basal stalk, a ventral flange, weak ventral processes, and long-arms. In *Aegialites* the metendosternite (fig. 7) is very wide, has no basal structures, and has only two long furcal arms arising from the medial limits of the coxae.

Thus, we have what could be considered one morphological characteristic, widely separated coxae, being correlated with changes of shape or position of other structures, namely the lateral mesothoracic sclerites and the metendosternite. Of course, we have no fossil evidence to prove that these two genera have a common ancestor or that displacement of coxal cavities and changes in other sclerites have a "cause and effect" relationship. But, when all other morphological characteristics are considered and found to be similar, we must conclude that the two genera are related and do have a common ancestor. The only alternative explanation is that of convergent evolution, two unrelated beetles having many morphological characteristics in common. It is far simpler and more practical to say that these two beetles are related because they have so many structures similar but only one structure dissimilar than to say the reverse.

Of the many structures that the Aegialitinae, especially *Antarcticodomus*, have in common with the Salpinginae, the male genitalia deserve special mention. The tegmen of *Aegialites* (figs. 26–28) and the penis of *Antarcticodomus* (figs. 37–38) could easily be mistaken for the same structures in *Sphaeriestes*. In fact the second mention of the close relationship of the Aegialitidae to Pythidae was by Sharp & Muir (1912: 619); the relationship was based on the genitalia. Many members of the Pythinae and Salpinginae have a peculiar type of genitalia, which I described previously (1952: 11, fig. 1). Briefly, the tegmen consists of a trough-like pars basalis, a single tapered paramere, and–the peculiarity–a pair of elongate, articulated lobes attached to the paramere. These lobes are often reduced and fused with the paramere or completely lost in some Pythinae and Salpinginae. The presence of these lobes can possibly lead us toward other familial relationships; Sharp & Muir (1912: 557) have already pointed out the similarities of the tegmena of *Pytho* and the odd family Trictenotomidae.

These articulated lobes on the paramere need a special term. In my previous article on male salpingid genitalia (1952: 11, fig. 1), I called these structures lateral lobes. That was an incorrect use of the term; Sharp & Muir (1912) used the term lateral lobes for paired or occasionally single parameres. I now propose to call these articulated lobes the digiti laterales (singular, digitus lateralis), meaning lateral digits or fingers.

The larvae of *Aegialites* and *Antarcticodomus* are, like the adults, quite similar but, also like the adults, they differ in what was thought to be a very important characteristic - the spiracles. Boving & Craighead (1930 : 40) eliminated the Aegialitidae, then containing only *Aegialites*, rather quickly in their family key because the spiracle is located in a separate sclerite (fig. 40). The spiracle itself is a simple, thin-walled annular type. *Antarcticodomus*, on the other hand, has a spiracle (fig. 43) that might be considered rather rare in beetle larvae. This kind of spiracle was described and illustrated by Franz (1955: 58, fig. 9) in the salpingine *Rabocerus mutilatus* Beck. This spiracle is composed of two parts: an annular part is thick-walled, circular, and evidently has a functional opening; a uniforous part is thick walled, curved, U-shaped and has what appears to be an opening between the arms of the U. This uniforous part does not seem to be a continuation of the wall of the annular part, though the two parts do abut.

The small comb-like structures on the molar surfaces of the larval mandibles are interesting (figs. 39, 42). They do not appear to be coarse enough to act as grinding structures but could possibly function as strainers. Perhaps they are what has been described in other larvae as the retinaculum or the prostheca. Boving and Craighead show somewhat similar structures on the mandibles of many Heteromera.

Anal sclerites of beetle larvae are often helpful in determining relationships. The long sclerites, one posterior to and one on each side of the anus, are almost identical in *Aegialites* (fig. 41) and *Antarcticodomus* (fig. 44). Also, these same sclerites are present in *Ra-*

bocerus mutilatus Beck, as illustrated by Franz (1955: fig. 8). Franz said they are parts of the 10th abdominal segment.

Boving & Craighead's 1931 larval manual has been a great help in learning the characteristics of families; but their manual is, after all, an illustrated key, not a group of formal descriptions. A key does not necessarily mention all the important characteristics of an animal; it merely mentions characteristics necessary to identify an animal and is thus deficient. We lack a formal description of each family. From what little has been published on heteromerous larvae, I have concluded that the larvae of *Aegialites* and *Antarcticodomus* are most similar to the larvae of *Rhinosimus* as illustrated by Boving & Craighead (1931: pl. 54, figs. A-H) and *Rabocerus mutilatus* Beck as described and illustrated by Franz (1955: 56, figs. 5-9). The larvae of the family Salpingidae may have more uniformity than has been indicated by past larval classifications. The larvae of the Aegialitinae and the pythine genus *Boros* Herbst are rather similar; in fact, I have rather easily modeled my subfamilial description on St. George's (1931: 111) description of what he considered the family Boridae.

Leech & Chandler (1956: 349) said that *Aegialites* is "presumed to feed on mites and other animal organisms." Leech has informed me that this presumption was taken directly from the manuscript of a speech given by Van Dyke on "The Intertidal and Beach Coleopterous Fauna of Western North America," at a meeting of the Pacific Coast Entomological Society on June 18, 1920. Van Dyke presumed correctly; by dissection I found immature oribatid mites in the fore and middle gut of adult *Aegialites stejnegeri stejnegeri* from Robben Island. However, I found only unidentifiable, soft, amorphous material in the gut of *Aegialites* larvae. The gut of *Antarcticodomus fallai* adults yielded the same amorphous material; I did not open the gut of the single larva available to me. On the other hand, Sugihara (1938: 9) studied *Aegialites stejnegeri sugiharai* in the Kurile Islands; although he did not observe feeding, he investigated stomach contents and found that the species is phytophagous. Not very much is known about the food habits of other members of the Salpingidae. Many of the Salpinginae live under bark, at least in the larval stage, and a few are known predators of other insects. Kleine (1907: 79) listed *Rhinosimus planirostris* Fabricius as a predator of four species of Scolytidae and listed *Lissodema quadripustulatum* Marsham as a predator of one species of Scolytidae. Kleine did not say whether the adult or larva or both are predatory. Then, Franz (1955: 56) gave a very good account of *Rabocerus mutilatus* Beck as a predator of the adelgid *Adelges piceae* Ratz. in the ascomycete fungus *Cucurbitaria pithyophila* (Fries) Cesati & deNotaris. Franz said that the beetle larva ate either the adelgid or the fungus and that the adult ate only the fungus. From what little we know of the food habits of the Aegialitinae and Salpinginae, we might infer that there is some basis for putting the two groups in the same family; the predatory habit is present in some stage of the life cycle. However, much more needs to be known before making definite statements on relationships.

Two accounts of the habits of species of *Aegialites* have been published, one by Keen and one by Sugihara. Keen (1903: 125) gave a good account of the actions of *californicus* on rock surfaces and in tides on the coast of British Columbia. The beetles are colonial, move slowly, hide in crevices on the rocks, and they make no effort to escape the incoming tides, allowing water to cover them completely. When Keen covered specimens with water in the laboratory, he noticed an air bubble beneath the elytra. Now, many beetles which can live under water, such as the Dytiscidae, have elytra closely coalesced to the pterothorax and abdomen; such beetles therefore have an airtight chamber under the elytra when the apical abdominal segments are pressed against the elytra. This is not the case in *Aegialites* and *Antarcticodomus*; the elytra are very loosely fitted to the pterothorax and abdomen, and there is thus no airtight chamber. The littoral beetles, such as the Dryopidae and Elmidae, use hydrofuge hairs to provide an underwater layer of air; such hairs are not present in the Aegialitinae. In fact, I could find no morphological specialization for aquatic respiration under water. I do not mean to imply that the respiration of *Aegialites* is extraordinary—almost nothing is known of it. But, the differences between "typical" litoral beetles and the Aegialitinae are interesting.

Sugihara (1938: 6) studied *stejnegeri sugiharai* in the Kurile Islands. The species occurs on the rough surfaces of those shore rocks having some covering sea plants. The rocks, in the intertidal zone, are frequently splashed or submerged and those rocks so remote from the high tide line as to get no splashing seem to be uninhabited by this beetle. The adults hide in crevices of the rocks during low temperatures and misty weather; during sunshine they gather on the sunny sides of the rocks. Many exuvia are found in the crevices of rocks; the larvae are presumed to moult in the crevices.

All specimens of *Aegialites californicus, fuchsi,* and *stejnegeri stejnegeri* that I examined were collected in June or July except for a few specimens of *californicus* collected in late April in the Commander Islands. Keen (1903: 125) collected adults of *californicus* in February and March and found larvae, pupae, and adults in July. Sugihara (1938: 6) collected adults and larvae of *stejnegeri sugiharai* in June and July. *Antarcticodomus fallai* was reported by Brookes (1951: 40) as having been collected in November on Auckland Island; specimens I examined were collected in February, October, and December on Campbell Island.

The most drastic innovation in the taxonomy of the Aegialitidae took place recently when Crowson (1953: 39, 51; 1955: 117, 128) united the family with the Elacatidae (= Othniidae). In the family Elacatidae he also included the cryptophagid *Trogocryptus* Sharp and its allies and the cucujid *Prostominia* Reitter. Unfortunately he did not give reasons for that union, except, of course, that all are keyed out as one family. I cannot imagine why these beetles were put in the same family; they differ in so many ways, in their head and mouthparts especially, in their antennae, their coxal cavities, tarsal formulae, genitalia, and larvae.

Subfamily AEGIALITINAE LeConte

Aegialitidae LeConte, 1862: 241.
Elosomatidae Jacobson, 1915: 993.
Eurystethidae Seidlitz, 1916: 127.
Aegialitinae: Spilman, 1954: 87.

Adult: Salpingid beetles, with the general body form of *Sphaeriestes* spp., and with the following combination of characteristics. Head capsule broad, weakly flattened dorsoventrally, without constricted neck, subparallel-sided posterior to eyes, thence broadly curved to foramen magnum; epistoma with short clypeal area; head capsule anterior to eye either long or short; foramen magnum large; gula broad, lateral borders converging anteriorly, then abruptly broadened to attach to mentum. Antennal insertion lateral, anterior to eyes. Eye small, prominent, laterally placed, coarsely faceted, almost circular but with vertical dimension slightly greater than longitudinal dimension. Antenna of moderate length, weakly clavate, segments weakly triangular to weakly moniliform. Labrum transverse, easily visible. Mandible stout, apically bifid, with distinct molar area. Maxilla of moderate length; galea and lacinia apically rounded; palpus of moderate length, ultimate segment subovoid. Labium short, broad; mentum subquadrate, flat; ligula membranous; palpus short, ultimate segment subovoid. Without cervical sclerites. Prothorax in dorsal view widest before middle; hypomeron with posterior ventral angle acute; coxal cavities circular, open, with well-sclerotized floor internally; sternum moderately long, and with intercoxal process attaining posterior border of coxal cavities, process either slender or broad. Mesepisternum and mesosternum fused. Mesocoxal and metacoxal cavities widely separated or not. Mesocoxal cavities closed laterally. Metasternum short. Metendosternite with slender furcal arms, with either short basal stalk or without stalk. Scutellum broad, triangular, large. Procoxa and mesocoxa globular; metacoxa transverse. Trochanters of heteromerous type. Femora of normal size. Tibiae slender. Tarsi slender, basal segments short, last segment very long, last segment approximately 1.5× length of combined basal segments; ventral setae fine; claws moderately large, simple. Elytron weakly coalesced with abdomen, apically broadly rounded; with striae. Metathoracic wings absent or aborted and spatulate. Abdomen with 5 visible sterna, 1st and 2nd connate or nearly so; intersegmental membrane present between 3rd, 4th, and 5th visible sterna; last visible tergum extending beyond elytral apex. Male genitalia with dorsal trough-like tegmen; pars basalis simple; paramere narrowed apically, with pair of slender, articulated digiti laterales and with basal struts extending to base of pars basalis. Penis either simple and straight or with 180° curvature. 9th tergum small; 9th sternum V-shaped, with apical lobes. 8th tergum and sternum simple, with or without incurved apical borders.

Larva: Elongate, depressed, moderately sclerotized, without coarse sculpture except on 9th abdominal segment, with few and short setae, color yellowish or brownish. Head extended, porrect, almost as long as broad, lateral borders parallel or nearly so; epicranial halves touching only medioposteriorly; with 5 ocelli contiguous to basal membrane of antenna. Labrum distinct, transverse. Clypeus fused with frons which is limited laterally by a lyriform sulcus. Mandible with 2 apical teeth and 2 blunt irregular teeth on dorsal cutting edge near apical teeth; malar area with comb-like projection. Maxilla of moderate length; mala entire, apically rounded, with long coarse setae apically and medially; palpus with 3 segments of subequal length. Labium with simple, rounded, membranous ligula; palpi stout, 2-segmented. Gula and submentum fused. Prothorax with very large presternum consisting of a medial spatulate part and 2 lateral subtriangular parts. Tergal plates of thorax and first 8 abdominal segments simple, without grooves or pits, with sparse long setae. Sternal plates of first 8 abdominal segments simple. Segment 9 with tergum apically having 4 urogomphi, lateral pair curved dorsally, medial pair curved medially, the latter pair forming a broad notch medially; ventral to this tergum are 1 transverse sclerite posterior to anal opening and a longitudinal sclerite on each side of opening; sternum rectangular, with a pair of small spines near anterior border. Spiracles annular and situated in small distinct sclerite, or annular and modified uniforous and situated in lateral membrane; on prothorax and abdominal segments 1-8. All 3 pairs of legs equal; with tarsus and claw fused into single unguliform article; with setae, without spines or spurs; each pair of coxae widely separated; legs not specialized for digging, evidently designed for walking.

Key to the genera of Aegialitinae

Adult: coxae widely separated, apices of intercoxal process subequal to width of coxae (figs. 4, 5). Larva: spiracle annular, in separate sclerite (fig. 40)... **Aegialites**

Adult: coxae narrowly separated, apices of intercoxal processes obviously much less than width of coxae (figs. 9, 10). Larva: spiracle annular and modified uniforous, in lateral membrane .... **Antarcticodomus**

Genus **Aegialites** Mannerheim

Aegialites Dejean, 1834: 117. [Nomen nudum.]

Orygmus Gistel, 1848: xi. [New name for *Aegialites* Dejean, 1834; nomen nudum.]

Aegialites Mannerheim, 1853: 178.

Eurystethes Seidlitz, 1916: 127. [New name for *Aegialites* Mannerheim, 1853.]

Type-species: of *Aegialites* Mannerheim, *Aegialites debilis* Mannerheim, 1853, by monotypy; of *Eurystethes* Seidlitz, *Aegialites debilis* Mannerheim, 1853, by assuming the type-species of the replaced generic name.

Adult (fig. 1): Head (fig. 3) anterior to eyes relatively short, ratio of distance between anterior border of epistoma and a transverse line through center of eyes to distance from same line to lateroposterior border of capsule is 1.0–2.3; antennal insertion visible in dorsal view, supra-antennal area without shelf but with fine marginal carina which terminates anterior to eye. Eye slightly larger than in *Antarcticodomus*. Mandible (fig. 14) with 1 blunt tooth on dorsal cutting edge; molar area not distinctly delimited. Maxilla (fig.

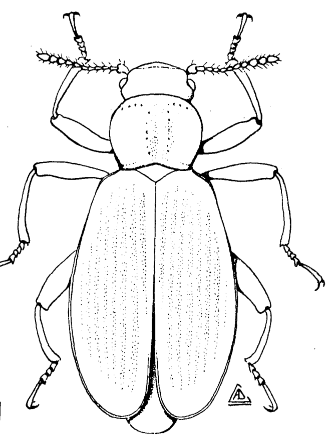

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Fig. 1, *Aegialites californicus*, adult.

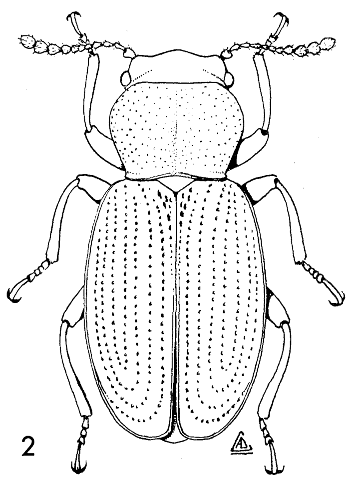

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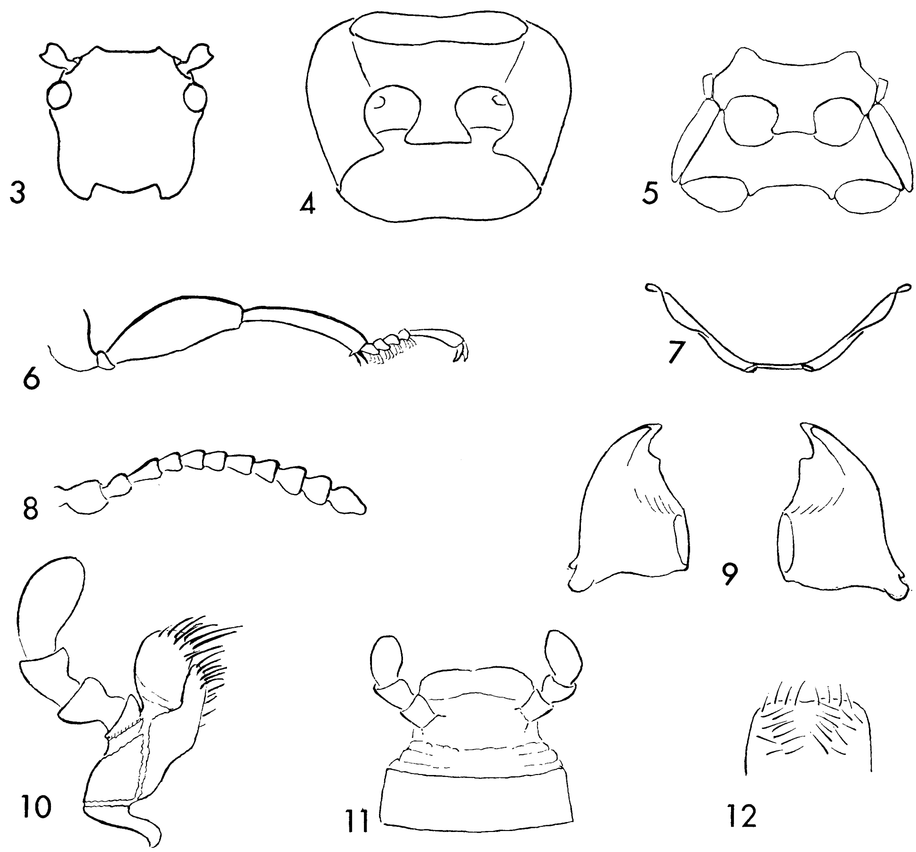
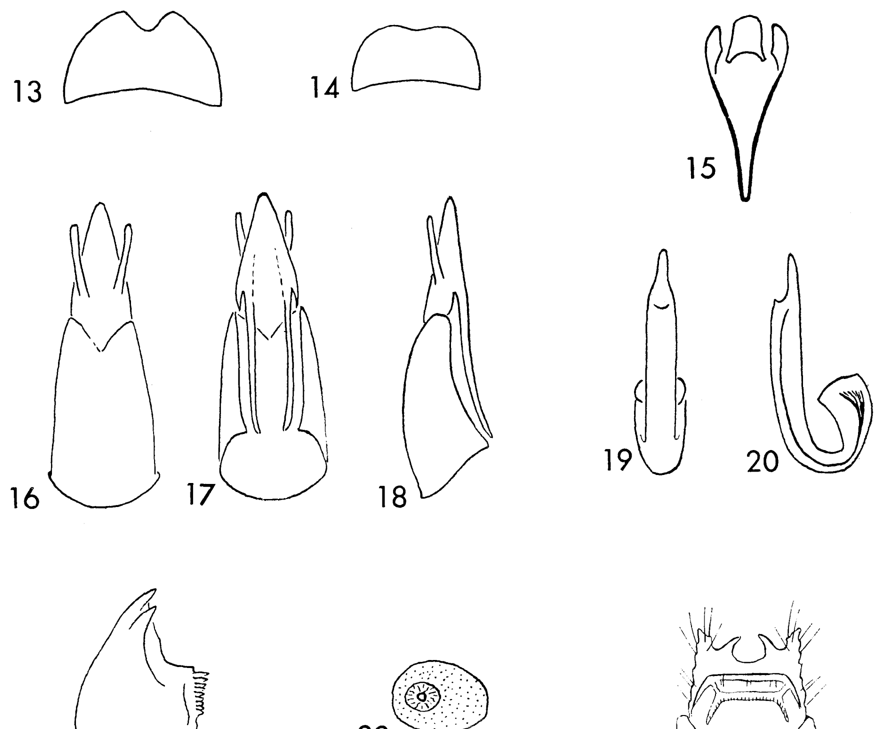
Fig. 2, *Antarcticodomus fallai*, adult.

15) stout; lacinia straight apically, with dense, long, coarse setae medioapically; galea broad apically, with dense, long, coarse setae medioapically; palpus with ultimate segment asymmetrically ovate. Labium (fig. 16) with ligula weakly incised on apical border; adoral surface (fig. 17) with sparse, long setae; palpi with segments stouter than in *Antarcticodomus*. Antenna (fig. 13) with segments 3-10 short, with segment 3 only slightly longer than 4; 11 almost 2× as long as 3; each segment expanded apically with 9-11 very strongly so and forming a moniliform club. Prothorax (fig. 4) with prosternum having intercoxal process very broad, broadest posteriorly and truncate at apex. Mesosternum (fig. 5) relatively broad between coxal cavities and broadly touching mesepimeron, metasternum, and metepisternum laterally; coxal cavities laterally closed; relatively small mesepimeron well displaced from cavities. Metacoxae widely separated, the ratio of intermesocoxal distance to intermetacoxal distance is 1.0-1.7. Metendosternite (fig. 7) without basal stalk; origins of furcal arms widely separated. Scutellum large, broad. Metacoxa short, its length equal to intercoxal distance; ratio of its length to length of metafemur is 1.0



Figs. 3-12, *Aegialites californicus*, adult. 3, head capsule, dorsal view; 4, prothorax, ventral view; 5, meso- and metathorax, ventral view; 6, prothoracic leg, posterior view; 7, metendosternite, ventral view; 8, antenna; 9, mandibles, ventral view; 10, maxilla, aboral view; 11, labium, aboral view; 12, ligula, adoral view.

to 2.8. Tibiae of ♂ weakly arcuate (fig. 6), especially apically; with small apical ventral spine. Tibiae of ♀ straight; without spine. Tarsi (fig. 6) on all legs with ratio of combined lengths of basal segments to length of last segment is 1.0–1.5; ventral setae slightly denser than on *Antarcticodomus*, these setae apically curved. Elytron with humerus very vague; pseudopleuron very vague; epipleura very narrow, disappearing at half length; apex broadly rounded, sutural angle broadly rounded. Metathoracic wings absent. Abdomen with 1st and 2nd visible sterna connate, without intersegmental membrane, with weak indication of intersegmental suture; remaining visible sterna articulated, with intersegmental membranes; intercoxal process very broad; dorsum with ultimate visible tergum heavily sclerotized, penultimate tergum weakly sclerotized, basal terga membranous; spiracles with opening oblong, with coarse filaments, surrounded by sclerotized disc. Genitalia of ♂ with tegmen (figs. 26–28) broad; parameres approximately as long as pars basalis. Paramere in dorsal view with lateral borders strongly converging posteriorly and with moderately sharp apical angle; digiti laterales short, slender; struts long. Pars basalis in dorsal view with posterior border moderately excurved. Penis (figs. 29, 30) large; enlarged basally, in lateral view with 180° curve basally; with strong strengthening rods; with large



Figs. 13–23, *Aegialites californicus*. 13–20, adult male. 13, 8th tergum, dorsal view; 14, 8th sternum, ventral view; 15, 9th segment, dorsal view; 16, tegmen, dorsal view; 17, tegmen, ventral view; 18, tegmen, lateral view; 19, penis, dorsal view; 20, penis, lateral view. 21–23, larva. 21, right mandible, ventral view; 22, spiracle of 1st abdominal segment; 23, apex of abdomen, ventral view.

gonopore; occasionally internal sac everted. 9th tergum (fig. 25) with basal border evenly incurved. 8th tergum (fig. 23) having posterior border evenly excurved; 8th sternum (fig. 24) with narrow emargination.

Larva: Sclerotized areas yellowish. Head with lateral borders weakly arcuate. Mandible (fig. 39) with molar area with comb-like structure large on anterior and dorsal borders, composed of 9 acute teeth, which become gradually shorter posteriorly. Mentum narrower than in *Antarcticodomus*. Abdominal segment 9 (fig. 41) with medial urogomphi long, almost touching on midline; base of notch simple and flat; dorsally with many coarse granules. Spiracles (fig. 40) annular, located on small sclerite lateral to tergal plate in membrane; on prothorax spiracular sclerite protruding from membrane in posterolateral corner. Legs more slender than in *Antarcticodomus*. Length approximately 4.5 mm. (This larval description is based on the larva of *Aegialites californicus*. Larvae of the other 3 species have not been described nor are they known to me.)

Aegialites contains 4 species, one of which has 2 subspecies. Van Dyke (1918: 309) has provided an adequate key to the species. Kono (1938: 3) gave a key to the 2 Asiatic subspecies. The key presented below is a composite of the two. I can add nothing to the recorded geographic distribution of the species. The complete distributions are given in the list of species following the key.

1. Elytra obviously striate.. 2
   Elytra without striae; eyes very prominent; head, pronotum, and elytra alutaceous and subopaque, with punctures hardly evident; longitudinal pronotal line well defined.. **Aegialites subopacus**
2. Head and pronotum not shining and with but few and inconspicuous punctures...... 3
   Head, pronotum, and elytra shining and with numerous well defined punctures; eyes quite prominent; longitudinal pronotal line rarely evident...... **Aegialities fuchsi**
3. Elytra shallowly striate and with small but distinct punctures; head and pronotum coriaceous, elytra rugose; eyes very prominent; longitudinal pronotal line prominent.. 4
   Elytra deeply striate and without distinct punctures; head and pronotum alutaceous, elytra shining; eyes not prominent; longitudinal pronotal line well defined.. **Aegialities californicus**
4. Dorsal surface with greenish lustre; pronotum widest before middle ....**Aegialities stejnegeri**
   Dorsal surface without greenish lustre; pronotum widest behind anterior angles .... **Aegialities stejnegeri sugiharai**

Aegialites californicus (Motschoulsky)

Aegialites debilis Dejean, 1834: 117. *Nomen nudum*.
Elosoma ? californica Motschoulsky, 1845: 33.
Aegialites debilis: Mannerheim, 1853: 180.

Type locality: *E. ? californica*, not recorded. *A. debilis*, not designated; California, Sitkha I., and Kenai peninsula of Alaska recorded in original description.

DISTRIBUTION: Commander Islands, Pribilof Islands, Aleutian Is., SE Alaska, and the Queen Charlotte I. area of British Columbia.

Notes: The species *californicus* does not occur in California. Perhaps Motschoulsky in 1845 did not have before him what is today known as *californicus*; perhaps he had either of the 2 presently known Californian species, *fuchsi* or *subopacus*. This problem can be resolved only by examining Motschoulsky's type.

Aegialites fuchsi Horn

Aegialites Fuchsii Horn, 1893: 143.

Type locality: Mendocino County, California.

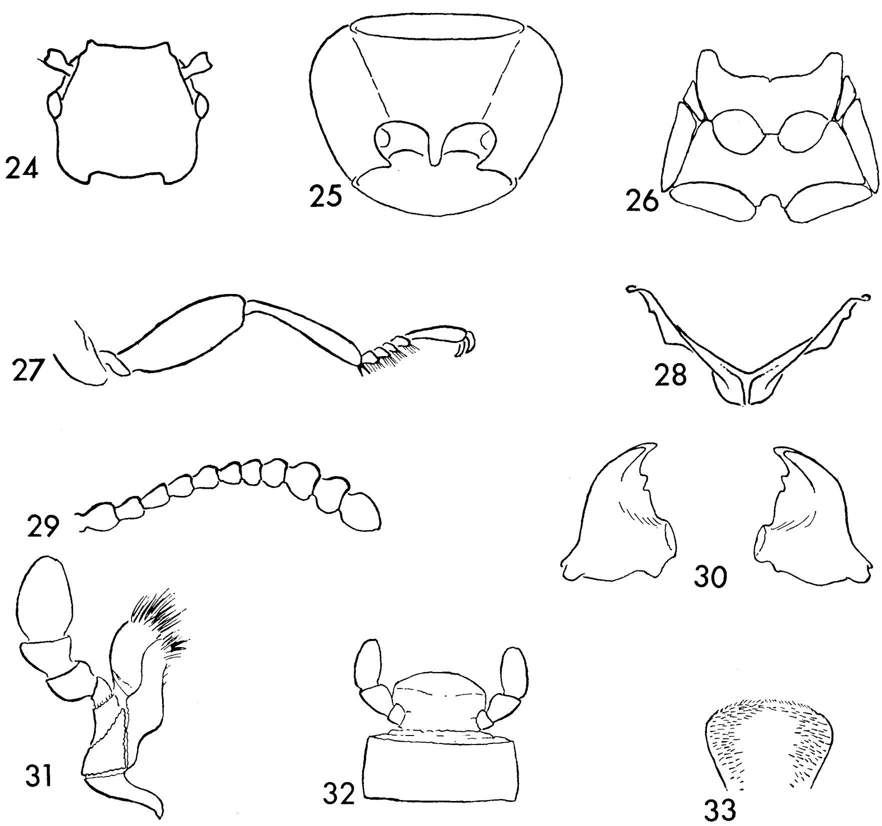
DISTRIBUTION: Mendocino County and the Farallone Is., California.

Aegialites subopacus (Van Dyke)

Eurystethes subopacus Van Dyke, 1918: 308.

Type locality: Moss Beach, San Mateo County, California.

DISTRIBUTION: San Mateo and Marin Counties, California.



Figs. 24–33, *Antarcticodomus fallai*, adult. 24, head capsule, dorsal view; 25, prothorax, ventral view; 26, meso- and metathorax, ventral view; 27, prothoracic leg, posterior view; 28, metendosternite, ventral view; 29, antenna; 30, mandibles, ventral view; 31, maxilla, aboral view; 32, labium, aboral view; 33, ligula, adoral view.

Aegialites stejnegeri stejnegeri Linell

Aegialites Stejnegeri Linell, 1898: 74.

Type locality: Robben I., Okhotsk Sea.

DISTRIBUTION: Robben I., very near E. coast of Sakhalin I. at 48°30′ N, 144°38′ E. Now known as Ostrov Tyuleniy.

Aegialites stejnegeri sugiharai Kono

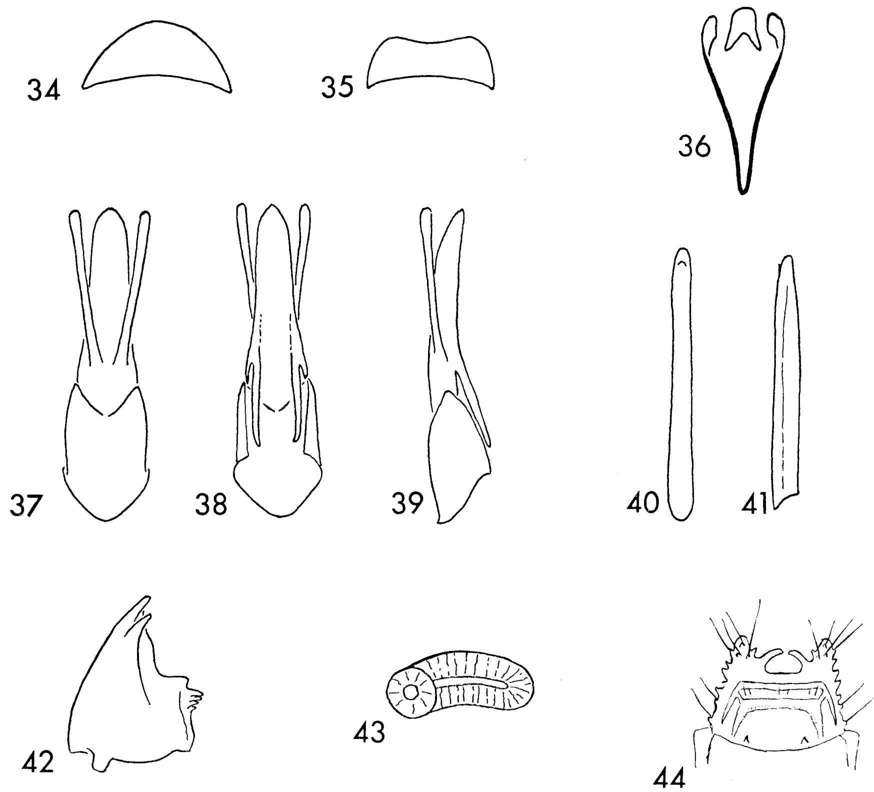
Aegialatis [*sic*] *stejnegeri sugiharai* Kono, 1938: 3, illus.

Type locality: Kurile Is.

DISTRIBUTION: Kurile Is.

Genus **Antarcticodomus** Brookes

Antarcticodomus Brookes, 1951: 39.



Figs. 34–44, *Antarcticodomus fallai*, 34–41, adult male. 34, 8th tergum, dorsal view; 35, 8th sternum, ventral view; 36, 9th segment, dorsal view; 37, tegmen, dorsal view; 38, tegmen, ventral view; 39, tegmen, lateral view; 40, penis, dorsal view; 41, penis, lateral view. 42–44, larva. 42, right mandible, ventral view; 43, spiracle of 1st abdominal segment; 44, apex of abdomen, ventral view.

Type-species: *Antarcticodomus fallai* Brookes, 1951, by being originally designated and monotypic.

Adult (fig. 2): Head (fig. 8) anterior to eyes relatively long, ratio of distance between anterior border of epistoma and a transverse line through center of eyes to distance from same line to lateroposterior border of capsule is 1.0–1.4; antennal insertion hidden in dorsal view by small supra-antennal shelf which has a fine marginal carina terminating dorsal to eye. Eye slightly smaller than in *Aegialites*. Mandible (fig. 19) with 2 blunt teeth on dorsal cutting edge; molar area distinctly delimited. Maxilla (fig. 20) more slender than in *Aegialites*; lacinia curved apically, with dense, long, fine setae and 2 coarse, short setae medioapically; galea with dense, long, fine setae medioapically; palpus with ultimate segment ovate, narrowed apically. Labium (fig. 21) with ligula broadly rounded apically; adoral surface (fig. 22) with small, very dense setae; palpi with segments more slender than in *Aegialites*. Antenna (fig. 18) with segment 3 long; 4–10 short; 11 long and subequal to 3; each segment gradually expanded apically, 9–11 more strongly so; with very weak 3-segmented club. Prothorax (fig. 9) with prosternum having intercoxal process slender, narrowed posteriorly and acuminate. Mesosternum (fig. 10) relatively narrow between coxal cavities and touching only mesepimeron and metasternum laterally; coxal cavities laterally closed; relatively large mesepimeron almost touching coxal cavities. Metacoxae narrowly separated, the ratio of intermesocoxal distance to intermetacoxal distance is 1.0–1.0. Metendosternite (fig. 12) with short basal stalk which has flange; origins of furcal arms contiguous at apex of stalk. Scutellum large, broad, but smaller than in *Aegialites*. Metacoxa long, ratio of its length to length of metafemur is 1.0–1.5. Tibiae (fig. 11) straight; without apical ventral spine. Tarsi (fig. 11) on all legs with ratio of combined lengths of basal segments to length of last segment being 1.0–1.4; ventral setae slightly sparser than on *Aegialites*; setae straight, ventral setae of male denser than setae of female. Elytron with humerus small; pseudopleuron vague; epipleuron very narrow, disappearing at 3/4 length; apex broadly rounded, sutural angle weakly angulate. Metathoracic wings abnormal, long, spatulate, nonfunctional. Abdomen with all visible sterna articulated, with intersegmental membranes; intercoxal process acute; dorsum of ultimate visible tergum heavily sclerotized disc. Male genitalia with tegmen (figs. 34–36) narrow; paramere approximately 2× as long as pars basalis. Paramere in dorsal view with lateral borders gradually converging posteriorly, then roundly curved and with blunt apical angle; digiti laterales long, slender; struts short. Pars basalis in dorsal view with posterior border strongly excurved. Penis (figs. 37, 38) slender; width subequal throughout its length; in lateral view very weakly curved; with very weak strengthening rods; with small gonopore; everted sac not observed. 9th tergum (fig. 33) with basal border angularly incurved. 8th tergum (fig. 31) having posterior border with narrow, deep emargination. 8th sternum (fig. 32) having posterior border with broad emargination.

Larva: Sclerotized areas smoky brown. Head with lateral borders parallel. Mandible (fig. 42) with molar area having comb small and on medial part of dorsal border only; composed of 4 blunt teeth, which become gradually shorter posteriorly. Mentum broad. Abdominal segment 9 (fig. 44) with medial urogomphi shorter than in *Aegialites*, well separated on midline; base of notch with circular depression and arcuate; with few coarse granules dorsally. Spiracles (fig. 43) annular and modified uniforous, that is, with a heavy, arcuate, U-shaped structure extending from thick annular spiracle; with the U-shaped structure dorsal to annular spiracle on prothorax and posterior to annular spiracle on abdominal segments; located in membrane, not on a sclerite. Legs stouter than in *Aegialites*. Length approximately 3.5 mm.

Only one species of this genus is known.

Antarcticodomus fallai Brookes

Antarcticodomus fallai Brookes, 1951 : 39, fig. 7.

Type locality: Campbell I.

DISTRIBUTION: Campbell I.; Auckland Is.: French I., Port Ross.

Additional distribution and data: Campbell Island: Rocky Bay, on rocks near penguin colony, 18.II.1963, K. Rennell, 1 larva; under stones on beach, 23.X.1961, K. A. J. Wise, 1 adult; Monument Harbor, near beach, 17.XII.1961, J. L. Gressitt, 2 adults; Tucker Cove, under rock, intertidal zone, 6–11.XII.1961, Gressitt, 10 adults.

Notes: The above data were to have been included in the report on the insects of Campbell Island by Gressitt et al. (1964).

Genus incognito, **Elosoma** Motschoulsky

Elosoma Motschoulsky, 1845 : 33

Type-species: *Elosoma persica* Motschoulsky, 1845, by being virtually monotypic.

As explained above this genus has not been discussed in the literature since it was described originally. It is therefore unknown to me. The generic name is carried here in the Aegialitinae merely to give it a place of record. Only one species is included.

Species incognito, **Elosoma persica** Motschoulsky.

Elosoma persica Motschoulsky, 1845 : 33.

Type locality: Persia.

DISTRIBUTION: Persia.

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SPIDERS (Prodidomidae, Zodariidae and Symphytognathidae) IN HAWAII[1]

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Abstract: Two new species, ***Prodidomus singulus*** (Prodidomidae) and ***Zodarium trispinosum*** (Zodariidae), and the ♀ of ***Pseudanapis aloha*** Forster (Symphytognathidae) are described from the Hawaiian Islands.

Examination of leafmold from the island of Oahu by sifting and Berlese funnel techniques has revealed specimens of the families Prodidomidae, Zodariidae and Symphytognathidae. The specimens of Prodidomidae and Zodariidae are new species and represent the first records of these families for the Hawaiian Islands. The female of *Pseudanapis aloha* Forster (Symphytognathidae) is described for the first time and the male palp is illustrated.

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Genus **Prodidomus** Hentz, 1847

Prodidomus singulus Suman, new species Figs. 1-5.

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