

Early Insect Diversification: Evidence from a Lower Devonian Bristletail from Quebec



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not by itself imply large-scale cooling in a nuclear winter scenario, this example demonstrates that smoke can cause cooling and shows the existence of a feedback mechanism that can enhance and prolong the expected cooling.

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Early Insect Diversification: Evidence from a Lower Devonian Bristletail from Québec

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The earliest insect for which there is significant structural data, a bristletail (Archaeognatha) from the Early Devonian (Emsian Stage) of the Gaspé Peninsula of Québec, Canada, is described. Detailed analysis of the head indicates that this insect had large, bulging, separated, compound eyes, monocondylic mandibles, and numerous sensory setae. This fossil, the oldest record of terrestrial animal life from North America, suggests that early hexapod diversification occurred contemporaneously with the emergence of the first vascular land plants during the Silurian.

THE PALEOZOIC FOSSIL RECORD IS fundamental to understanding the evolutionary history of insects. Currently three Devonian localities have yielded the earliest known hexapods, namely entognathans (those with mouthparts housed in an oral chamber) and insects (those with externally deployed mouthparts) (1). The localities are Rhynie in Scotland (2), and Gilboa (3) and Gaspé in northeastern North America (Table 1). The Lower Devonian (Emsian) Gaspé locality, has produced the earliest record of terrestrial animal life from North America—the single bristletail insect described below. All three localities occur within 10° of the Devonian equator (4) and provide evidence for a panequatorial, marginally marine, terrestrial fauna of trigonotarbids, arachnids, mites, collembolans, bris-

tle tail insects, and other microarthropods. The hexapods from these localities are pivotal for understanding how insects originated in wet, marginal marine habitats during the Middle Paleozoic and then, during the Late Paleozoic, diversified into the dominant group of the planet (5), occupying every major terrestrial and freshwater habitat.

The Gaspé insect was macerated from a sample taken from a 1-cm-thick mudstone horizon occurring in a series of fluvial sediments of the Battery Point Formation, exposed along the north shore of Gaspé Bay, in Québec, Canada. A late early Emsian date is indicated by spore assemblages (6), corresponding to an absolute time between 390 and 392 million years ago (Fig. 1) (7). In the mudstone horizon the specimen was associated with a suite of small plants, some of which are presumably gametophytes of early land plants. The Gaspé insect is composed of unaltered cuticle, but unlike the Gilboa material, the specimen retains three-dimensionality (Fig. 2, A and C).

The Gaspé insect consists of two fragments, a head and a thorax. Each fragment is

about 70% complete. Although not connected, these fragments undoubtedly represent the same individual, as evidenced by (i) the lack of overlapping anatomical regions, (ii) the apparent fit of the head to the thorax, and (iii) the isolation of both fragments from the same mudstone cobble without other arthropod remains. The congruence of external cuticle ornamentation between both fragments strongly indicates a common taxonomic identity (8). The specimen is partially crumpled, but exhibits considerable microstructural detail, including compound eye facets (Fig. 2F), internal bosses for reception of muscle bundles (Fig.

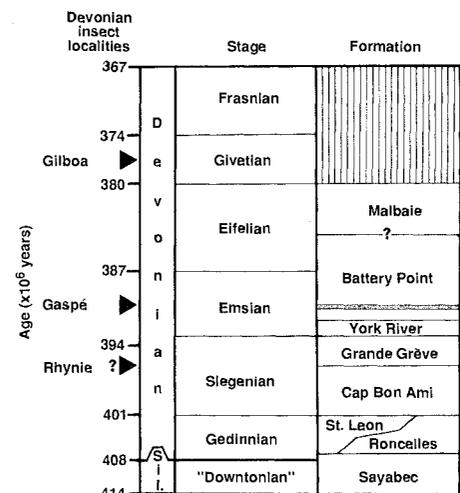


Fig. 1. Stratigraphical and geochronological relationships of the Devonian outcrop containing the Gaspé insect. The stippled interval designates the Gaspé insect horizon, occurring 2.5 m above Geological Survey of Canada locality 5575, in the *Camaronotriteles sexantii* spore assemblage zone (6).

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2H), external pits with and without centrally raised pegs (Fig. 2F), and various exterior cuticle sculpture, including ridges, sawtooth spinelets, and tubercles (Fig. 2, E to G, I, and J). Notably, sutures between major sclerites are difficult to discern. We emphasize the head fragment here because it is more informative for assessing affinities than the thorax.

The head consists of a near complete capsule, mandible, and labium, some of which have been moved relative to one another by taphonomic processes. Exposed hypognathous mouthparts (Fig. 2, C and D) indicate that this specimen is an ectognath and lacks entognathous mouthparts that are enclosed in an oral chamber (9). The clypeus and labrum are absent. There is a pronounced occipital region that represents fusion of the maxillary and labial segments (10), part of which is folded into the posterior head capsule. The dorsal head region is present, indicating that the eyes, although large, were not situated close to each other dorsally. Although dorsally convergent or approximated eyes are considered diagnostic of modern bristletails (11), this feature is an autapomorphy (derived character) of a clade within the bristletails, since bristletails from the Pennsylvanian also bore separated compound eyes (12).

The prominent, bulging compound eyes have partially collapsed over the optic lobes (Fig. 2, A, C, E, and F) and consist of distinctive truss networks supporting numerous individual hexagonal eye units (ommatidia) (Fig. 2F). The number of ommatidia per eye ranges from 200 to 300, a character diagnostic of modern archaeognathans (10) and winged insects. Lateral ocelli are suggested by darkened, striate sulci

located between the compound eyes and antennal foramina (Fig. 2A).

The right mandible is triangular and prolonged in shape (Fig. 2, C and E; the left mandible is absent). A distal incisor is suggested by a mid-length constriction of the external mandible body. The basal articulation of the mandible with the head capsule is obscured, but the elongate mandibular form and presence of a head side-lobe imply a milling mandible capable of back-and-forth movement and lacking effective adduction (7, 13). Monocondylic, milling mandibles in modern archaeognathans indicate probing for relatively soft food; such mandibles are capable of some picking and cutting, but not the effective tearing and shearing that strongly adducted, dicondylid mandibles would readily permit (10, 13).

The posteriormost part of the head capsule consists of a bilaterally symmetrical structure bearing three long, tapering, lightly sclerotized appendages originating from a common basal plate (Fig. 2, A, C, and E). A faint suture occurs on each appendage, separating a distal region typified by tubercles, small punctae, and a lateral foramen from a proximal region associated with the basal plate. The median appendage retains the fine-grained ridging of the basal plate and may have a bifid tip. We interpret this entire structure as a labium; the basal plate as the mental region (probably a postmentum); the distal portion of the lateral appendages below the suture as paraglossae, with each foramen representing the insertion of a labial palp (not preserved); and the medial appendage as fused glossae. The size and shape of the labium is similar to some modern archaeognathans (14), but fusion of nominally divided glossae into a single, ta-

pering, triangular lobe (Fig. 2C) is unique (10). The robust labium, pronounced lobate paraglossae, and ample endowment of sensory structures suggest that the labium was an important organ for procuring and processing food.

External surface sculpture of the cuticle consists of subparallel to sinuous ridges (Fig. 2, A, C, E, G, I, and J), ovoid tubercles (Fig. 2F), and three types of small to large circular structures (Fig. 2, C, E to G, and J). The sinuous ridges represent sawtooth spinelets of individual epithelial cells, present in extant bristletails (10). Ovoid tubercles are a common sculpture pattern in many insects, including bristletails (15). The smaller circular depressions probably represent the bases of thick tactile hairs, which are a dominant mechanosensory organ in some bristletails (16). The very small circular structures resemble wax-secreting pore canals whereas the largest circular to elliptical depressions are interpreted as campaniform sensillae (cuticle stretch receptors) (17).

The prominent, disk-shaped sagittally symmetrical bosses on the internal dorsal surface of the head capsule (Fig. 2, A, B, and H) are entapodemes for mouthpart-associated muscles. Fifteen bosses occur on each side, extending from a region immediately posterior to the antennal foramina and terminating at the occipital region, posterior of the eye lobes. Each boss bears 10 to 15 pits on an exposed flattened surface and has a girdled base (Fig. 2H). The characteristic pitted microstructure of these bosses is explained as an increase in surface area for resisting tensile forces from the attached muscle tendons (18).

The elongate thoracic fragment consists of terga, pleura, and sterna of the prothorac-

Table 1. Devonian localities containing insect or hexapod fossils.

Locale	Formation, stage, and age (million years)	Insects	Plants	Depositional setting and habitat	Reference
Rhynie	Old Red Sandstone; Siegenian (394 to 401)	Neanurid and isotomid collembolans	Algae, zosterophylls, and rhyniopsids	Bog or lake margin; suddenly flooded by hot silicic water, producing chert	(2, 3, 13, 26)
Gaspé	Battery Point Formation; Lower Emsian (390 to 392)	Archaeognath	Trimerophytes, zosterophylls, and lycopsids	Clayey sediments indicating swamp-like environments; later incorporated in coarser fluvial deposits	(7, 26, 27)
Gilboa	Panther Mountain Formation; Givetian (376 to 379)	Probable archaeognath (unnamed)	Progymnospermopsids and lycopsids	Delta deposit of black mudstone; material transported, probably not far; no evidence of tidal deposition	(3)

ic and mesothoracic segments. Three of the four leg bases, where walking legs articulated with the body wall, consist of only a single, triangular, robust sclerite partly surrounding the leg base. This partially encircling arcuate structure is interpreted as a precoxa (= subcoxa) (10, 19). Thoracic cuticular

ridging is more pronounced than the head and distinctive stellate spines are additionally present. There is no evidence of small, paranotal sclerites that would indicate nymphal or adult wings.

Evidence has been marshalled that this insect is a bristletail. Characters that support

this assignment are the mandible, the ommatidial lenses, and the mesothoracic pre-coxae. The nonentognathous, elongate, monocondylic mandible is found only in the Archaeognatha among insects (1, 10, 11, 20). Hexagonal ommatidial lenses occur in bristletails and pterygotes (10) but are absent in other nonpterygote hexapods. In addition, the Gaspé specimen lacks those mesothoracic structures found in insects with dicondylous mandibles—either the three, crescentic, reduced pleurites of thysanurans or the wing-supporting lateral body wall, or pleuron, of pterygotes (10, 11, 20). Although mandibular monocondylic, hexagonal ommatidial lenses, and a triangular precoxa are plesiomorphic within the Insecta, these features partly define the order Archaeognatha (11, 12, 20). Nondiagnostic features consistent with an archaeognathan assignment include the gross morphology of the compound eyes [also occurring in monurans (1)], and presence of lateral ocelli [occurring in smithurinid collembolans, monurans, and fossil and recent thysanurans (1, 10, 12, 21)]. Cumulatively, these features indicate that the Gaspé specimen is the oldest unquestionable representative of the class Insecta. The specimen phenetically resembles modern archaeognathans, although alternatively it also could be a candidate for the stem group (22) of the Insecta.

Most cladistic analyses of the basal hexapod groups show that both entognaths and ectognaths share a common ancestor (11, 20, 23) and that the ectognath (insect) branch is represented by a Diplura + {Archaeognatha + [Monura? + (Thysanura + Pterygota)]} relationship (1, 10, 24). The occurrence of Early Devonian representatives from both of the major hexapodan clades—two families of collembolan entognaths and an archaeognathan ectognath (2, 3, 11, 12, 20, 25)—is noteworthy. These taxa respectively represent two distinctive mouthpart types during the Early Devonian (2, 25), indicating that both piercing and chewing were major functional feeding modes. These two, fundamentally different, approaches of sequestering and processing food represent the earliest major dietary partitioning of food resources in the documented fossil record of insects. These taxonomic and ecological data suggest that the interval of divergence of entognaths and ectognaths, and of pterygotes from primitive ectognath groups may have been the Silurian, contemporaneous with the radiation of primitive vascular land plants (1, 26).

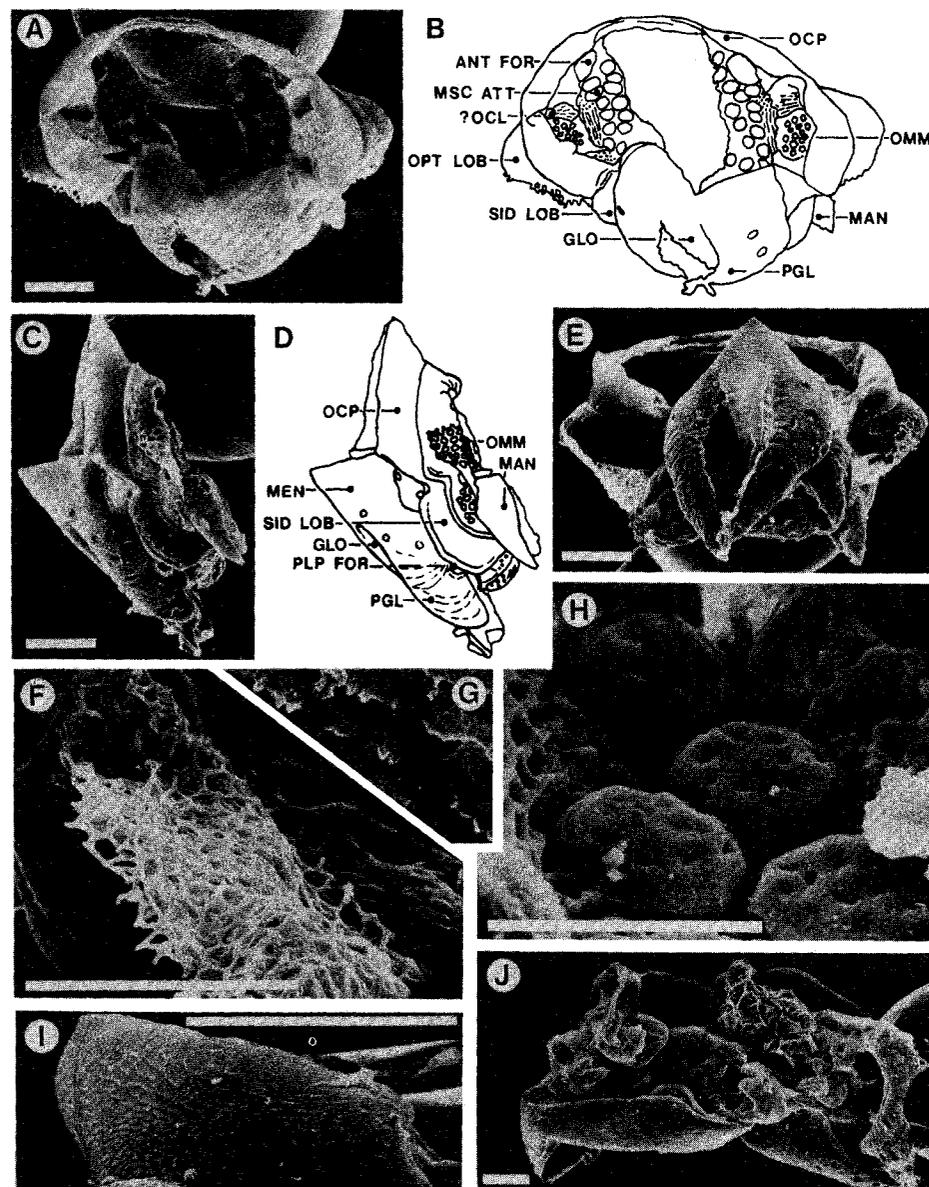


Fig. 2. A new archaeognathan (bristletail) of Devonian age from the Bartery Point Formation of the Gaspé Peninsula, Québec. (A) Posterior (occipital) view of head capsule and mouthparts with pin stub above. Scale bar, 0.13 mm. (B) Interpretation of (A). Abbreviations: ANT FOR, antennal foramina; GLO, glossa of labium; MAN, right mandible; MSC ATT, muscle attachment bosses for mouthpart muscles; ?OCL, possible ocelli; OCP, occipital region; OMM, internal view of compound eye ommatidia; OPT LOB, optic lobe; PGL, paraglossa of labium; and SID LOB, head side-lobe. (C) Right dorsal view of head capsule and mouthparts. Scale bar, 0.13 mm. (D) Interpretation of (C). Abbreviations as in (B), with also MEN, mentum of labium; OMM, external ommatidia of the eye lobe; and PLP FOR, foramen of labial palp. (E) Oblique posteroventral view of head capsule and mouthparts. The labium is in the center, with mentum, glossa, and paraglossae. The compound eye lobes are laterally positioned and the occipital region is shown above as a dark elliptical area partly obscured by the base of the labium. The right mandible is projecting toward the lower right corner. Scale bar, 0.13 mm. (F) Detail of ommatidial truss network of the left compound eye. Scale bar, 0.13 mm. (G) Detail of cuticular sculpture. Magnification approximately $\times 2400$. (H) Detail of attachment bosses for mouthpart musculature. Scale bar, 0.03 mm. (I) Detail of surface sculpture of left occipital region. Scale bar, 0.13 mm. (J) Ventral view of thoracic fragment, with coxae, sternites, and pleurites. The upper left coxa exhibits a catapleurite base and platelike basicoxa. Scale bar, 0.13 mm.

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A Larger Spectrum of Severe HIV-1-Related Disease in Intravenous Drug Users in New York City

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Increasing mortality in intravenous (IV) drug users not reported to surveillance as acquired immunodeficiency syndrome (AIDS) has occurred in New York City coincident with the AIDS epidemic. From 1981 to 1986, narcotics-related deaths increased on average 32% per year from 492 in 1981 to 1091 in 1986. This increase included deaths from AIDS increasing from 0 to 905 and deaths from other causes, many of which were infectious diseases, increasing from 492 to 1091. Investigations of these deaths suggest a causal association with human immunodeficiency virus (HIV) infection. These deaths may represent a spectrum of HIV-related disease that has not been identified through AIDS surveillance and has resulted in a large underestimation of the impact of AIDS on IV drug users and blacks and Hispanics.

SURVEILLANCE OF ACQUIRED IMMUNODEFICIENCY SYNDROME (AIDS) in the United States has depended on a surveillance case definition that defined AIDS cases as the most severe manifestations of infection with human immunodeficiency virus (HIV) type 1 (1, 2). This definition was initially based on the unusual occurrence of certain opportunistic infections and rare malignancies that were predictive of defects in cell-mediated immunity. These conditions were first recognized in 1981 to occur largely in homosexual men (3–7). This case definition has been modified as more was learned about the spectrum of severe HIV-related morbidity (8, 9). The AIDS surveillance systems in New York City (NYC) and elsewhere have been highly accurate in identifying diagnosed AIDS cases (10, 11). The information surveillance provides is important in identifying populations at highest risk for AIDS and at greatest need for prevention and health-care services and in

providing data needed for projections of the future impact of AIDS.

Large increases in deaths among intravenous (IV) drug users not reported to have AIDS have occurred in NYC simultaneously with the epidemic of HIV infection. These excess deaths may represent a manifestation of severe HIV-related morbidity and resulting mortality that has not been recognized through AIDS surveillance. We describe the epidemiologic investigation of this increased mortality.

The investigation included a review of vital statistics and AIDS surveillance registry data, a medical record review of deaths among narcotic users in 1985, a histopathologic examination of lung tissue from narcotic users who died of pneumonia, and a determination of mortality in a cohort of IV drug users.

We reviewed the 7884 deaths among NYC residents that occurred between 1978 and 1986 and reported through May 1987

that had been coded as “narcotics-related.” For all deaths occurring in NYC, a death certificate must be filed with the NYC Department of Health (NYCDOH). On the basis of conditions listed on the certificate, an underlying cause of death is assigned in accordance with the International Classification of Diseases, eighth and ninth revision (ICD-8 and ICD-9) (12). If narcotic use is listed on the certificate it is indicated with a specific code (code “9” narcotics-related). Decedents who are suspected of using illicit narcotics (almost all IV) are by law reportable to the Office of the Chief Medical Examiner (OCME), which investigates the cause of death (about half receive autopsies). After confirmation, the OCME will list narcotic use as a cause of death on the certificate. Of the 7884 narcotics-related deaths, 1803 were considered as “AIDS” (primarily ICD codes 279.1, 279.3, and 136.3). The data from the death certificates were then used to classify the 6081 “non-AIDS” deaths into the clinical categories in Table 1.

In order to determine the number of narcotics-related deaths reported as AIDS cases, all narcotics-related deaths occurring from 1982 to 1986 were matched to the NYCDOH AIDS surveillance registry (13)

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