

## Diversity of Chalcidoidea (Hymenoptera) at El Edén Reserve, Mexico

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Animal diversity is declining worldwide, and our efforts to document this change are hampered by inaccurate estimates of the true number of species. The number of *described* (formally named) species has been estimated to be between 1.2–2.2 million (Stork 1988; Grove & Stork 2000), with insects by far the most dominant group (751,012 species according to Arnett 1985). As groups are revised and types reexamined, many of the names proposed are placed as synonyms of other species. This leads to as much as a 25% decrease in our estimates of the number of described species (May 1999), but not, however, in the tremendous number of species that remain to be discovered.

One of the first accurately quantified estimates of the total number of insect species was 30 million (Erwin 1982). This figure was derived by extrapolation from the number of canopy beetle (Coleoptera) species feeding on *Luhea seemanii* (Tileaceae) in Panama relative to the proportions of described Coleoptera and Insecta. This estimate has been continually revised, but without a real consensus, and we are left with figures that range from 3–80 million species of insects (Erwin 1982; Wilson 1985; May 1988; Stork 1988; Godfray et al. 1999; Grove & Stork 2000). Lower estimates of between 5 and 10 million species are usually considered as a conservative baseline for comparison (Stork 1988; Gaston 1991; Gaston et al. 1996; Grissell 1999; Noyes 2000). Hymenoptera (ants, bees and wasps) is one of the few megadiverse insect orders. Approximately 115,000 species have been described, and anywhere from 300,000–2.5 million species are estimated to be extant (LaSalle & Gauld 1992, 1993; Gauld & Gaston 1995; Stork 1988; Grissell 1999). Parasitic insects, of which most are Hymenoptera, account for approximately 25% of all arthropods in both temperate and tropical ecosystems (Stork 1988).

Among the parasitic Hymenoptera, wasps in the superfamily Chalcidoidea are ecologically and economically the most important insects for the control of other insect populations (Noyes 1978; LaSalle 1993). Chalcidoids are small to minute wasps, ranging from 0.11–45 mm (rarely more than 10 mm), but usually averaging 2–4 mm in body length. Species are distributed in 20 families and 89 subfamilies, and estimates of the number of species have ranged between 60,000 and 100,000 (Noyes 1978; Gordh 1979; Gibson et al. 2000). Most species are parasitoids of other insects, with females depositing their eggs into the eggs, larvae, pupae or rarely adults of almost every group of insect. Relatively few species are phytophagous. Among the most commonly encountered and economically important families are Eulophidae and Pteromalidae, which attack a wide variety of insects, primarily the larval stages of Coleoptera, Lepidoptera and Hymenoptera; Encyrtidae, which parasitize mostly Euhemiptera; Aphelinidae, which are primarily parasitoids of aphids, scales and whiteflies; and Trichogrammatidae, which are egg parasitoids of primarily Lepidoptera (Goulet & Huber 1993; Hanson & Gauld 1995; Gibson et al. 2000).

The importance of Chalcidoidea in sustainable agricultural systems cannot be underestimated. When chalcidoids are removed through the use of pesticides or the introduction of a new pest into a new area without its complement of parasitoids, the results can often be drastic, resulting in the explosion of pest populations (DeBach & Rosen 1991). Chalcidoidea also includes some of the most important species used for the biological control of pest insect populations (Noyes 1978; Noyes & Hayat 1984; Greathead 1986; LaSalle & Gauld 1992; LaSalle 1993). Although Trichogrammatidae are important for augmentative control measures, Aphelinidae, Encyrtidae and Eulophidae are used primarily for the classical biological control of pests such as cassava mealybug, olive scale, citrus blackfly and purple scale (DeBach 1971). Tremendous long-term economic savings have resulted from the introduction of a few beneficial species (Noyes & Hayat 1984; LaSalle & Gauld 1992; LaSalle 1993). In Africa, control of the cassava mealybug alone is estimated to have saved \$250

million and allowed for the continued production of a very important staple food item for a large proportion of the population (Norrgard 1988).

For such an important group, what do we know about Chalcidoidea? Their taxonomy is a nightmare. Original descriptions are poor and often not diagnostic, and identification keys are available for only a few groups. Most descriptions are based on only a single specimen, thus ignoring intra-taxon variation. Indeed, much of the original taxonomic work has been or often must be repeated. Fewer than 5% of the described species can probably be named without comparison to the type specimen (LaSalle & Gauld 1993). Our knowledge of their biology is far less, and based on relatively few representative species.

Can such a group be ignored in studies of taxonomy and biodiversity? Most species are very small (May 1988, Stork 1988). In animals in general, the proportion of morphospecies (unnamed species) is inversely proportional to the log of their body length (Lawton et al. 1998, but see Dial & Marzluff 1988). Because of their small size, smaller organisms require more time for proper mounting and curating, and this lag time means they are often not included in the initial estimates of species richness (Lawton et al. 1998). Lawton suggested that current estimates of tropical forest diversity would be 10–100 times higher if inventories of smaller species were ever completed. Earlier studies suggesting that the diversity of Hymenoptera actually decreased from temperate to tropical regions focused almost entirely on larger Ichneumonoidea (Owen & Owen 1974; Gauld 1986). Ultimately, it was pointed out that competition in tropical systems would likely favor species attacking earlier and smaller stages of host insects, and that these forms would likely be more diverse in tropical regions (Hespenheide 1979; Noyes 1989ab). The question of whether smaller parasitic Hymenoptera are more diverse in tropical regions forms a testable hypothesis, that to date has not been thoroughly examined.

Systematists often are interested only in overall species richness (Godfray et al. 1999). Basically, what species are present? This is perhaps a myopic perspective for sampling, and essentially ignores the qualitative aspects of developing species accumulation curves or other such measures that could better estimate the total number of species (Coddington et al. 1991; Collwell & Coddington 1994; Godfray et al. 1999). However, there is only so much time to collect and process the material at hand, and most studies are not comparable because they are biased by sampling time, sampling effort, and collector experience or preference. Even when techniques are very close, such as pesticide fogging of the forest canopy, differences in the apparatus, method of application and type of pesticide means that results are not comparable statistically (Erwin 1995). As well, studies of beta (between places) diversity are often hampered by site differences. Regional comparisons (faunal lists of named species), built up over a long period of time, may ultimately be the most important measures of shared diversity (Bartlett et al. 1999). Quantitative resampling methods can always be reapplied to the data once processed (Kerr 1996; Grove & Stork 2000). For now our questions are simple: given the amount of time and methods used, how many species can be collected and how does this relate to the overall accumulation of data for species richness in Mexico and neighboring countries?

### **How many species of Chalcidoidea?**

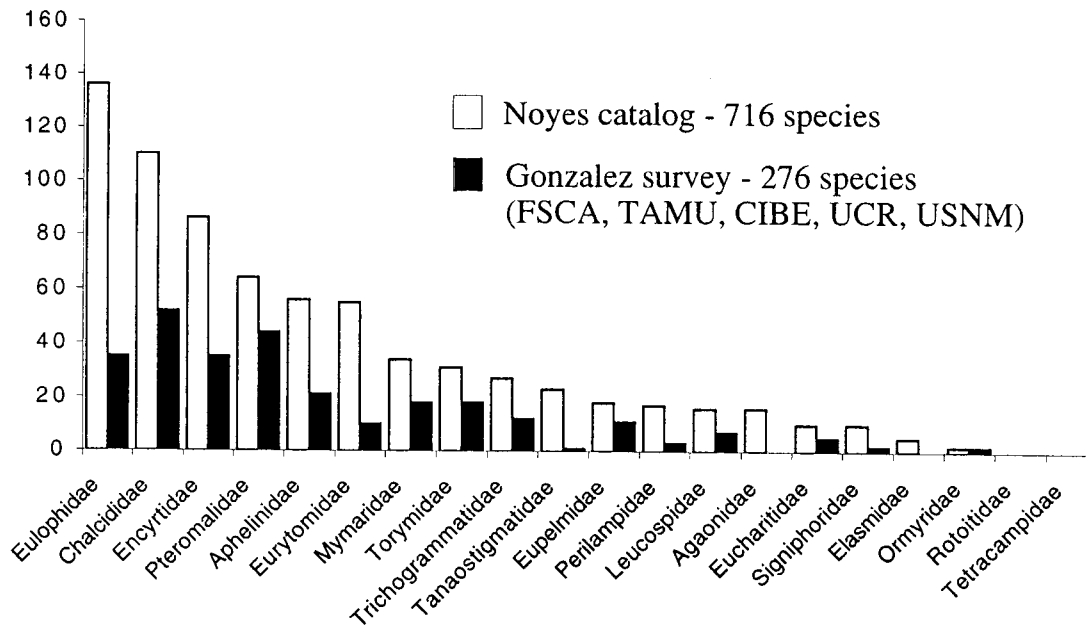
Parasitic Hymenoptera probably account for between 6.5 and 20% of insect species, and a range of between 170,000 and 6 million species of parasitic Hymenoptera has been proposed on the basis of various estimates of the number of insect species (2,650,000–30 million) (LaSalle & Gauld 1992). Approximately 21,000 species of Chalcidoidea have been described (Noyes 1998, 2000). If Chalcidoidea represent about 33% of described parasitic Hymenoptera (LaSalle & Gauld 1992), their estimated number of species could range between 56,000 and 2 million! Using the British fauna as a benchmark, Noyes (2000) estimated that Chalcidoidea represent about 8% of all British insects and proposed that, given a conservative estimate of 5 million insect species, there could be as many as 400,000 chalcidoid species worldwide. Noyes purposefully chose to ignore the ramifications of an increase in diversity at lower latitudes. However, higher proportions of tropical Chalcidoidea are more likely. For example, in canopy fogging samples from Borneo, 26% of about 2800 species of the arthropods collected were chalcidoids (Stork 1988). In Costa Rica, Chalcidoidea represented 28% of 17,065 morphospecies of Hymenoptera collected in Malaise traps (Gaston et al. 1996). Proportions may be even higher for islands. In the Galapagos Islands, Chalcidoidea comprise 44% of the 243

species of Hymenoptera collected (Heraty & Peck unpublished) and on Norfolk Island, 42.3% of 189 morphospecies of Hymenoptera (I. Naumann, pers. comm.).

Other examples reinforce our ideas of the large number of chalcidoid species yet to be discovered. In the Galapagos Islands, only 55 species of Hymenoptera were known prior to 1990, and of these 7 were species of Chalcidoidea. From 1985–1990, an additional 101 species of Chalcidoidea were sampled (Heraty & Peck unpublished); a 14 fold increase in the number of species. In one canopy fogging sample in Sulawesi, one family of Chalcidoidea (Aphelinidae) represented 82.8% of the 1,073 species of Hymenoptera collected, and one genus, *Encarsia*, was partitioned into 156 morphospecies, almost as many species as have been described (Noyes 1989ab). Considering Sulawesi is not taxonomically as rich as other tropical countries such as Costa Rica (Noyes 1989a), there is a high potential for a tremendous number of new species. In Costa Rica, only 278 species are currently recognized in published accounts (Table 1), only 6% of the 4705 morphospecies that were sampled (Gaston et al. 1996); a 17 fold increase in the number of species. If we apply this last figure to the total number of described species (21,000), the estimated number of Chalcidoidea is 357,000, a value similar to that proposed by Noyes (2000).

### How many species in Mexico?

Numbers of described species of Chalcidoidea in Mexico were obtained from two sources (Noyes 1998, González-Hernández 2000). Noyes' catalogue is a CD-ROM database of all published records for Chalcidoidea worldwide (~35,000 references and 21,248 species names). From these published records, 716 described species in 18 families are known to occur in Mexico (Fig. 1; numbers adjusted for duplicate species and genus records). Using a different approach, González-Hernández (2000) surveyed specimens in four different museum collections: the Florida State collection of Arthropods (FSCA), Texas A&M University (TAMU), Facultad de Ciencias Biológicas, Universidad Autónoma de Nuevo León (CIBE), University of California, Riverside (UCR) and the National Museum of Natural History (USNM). From the 4,547 specimens entered into his database (of 9,488 examined), González-Hernández found 276 morphospecies in 16 families of Chalcidoidea (Fig. 1). Only Agaonidae and Elasmidae, both reported as being present in Mexico (Noyes 1998), were not encountered in these collections. Of the 276 morphospecies, only 176 (64%) were identified to a described species name. Of these named species, only 49 were not in common with Noyes' list. After combining their results, 765 named species are known from Mexico. With the addition of the 95



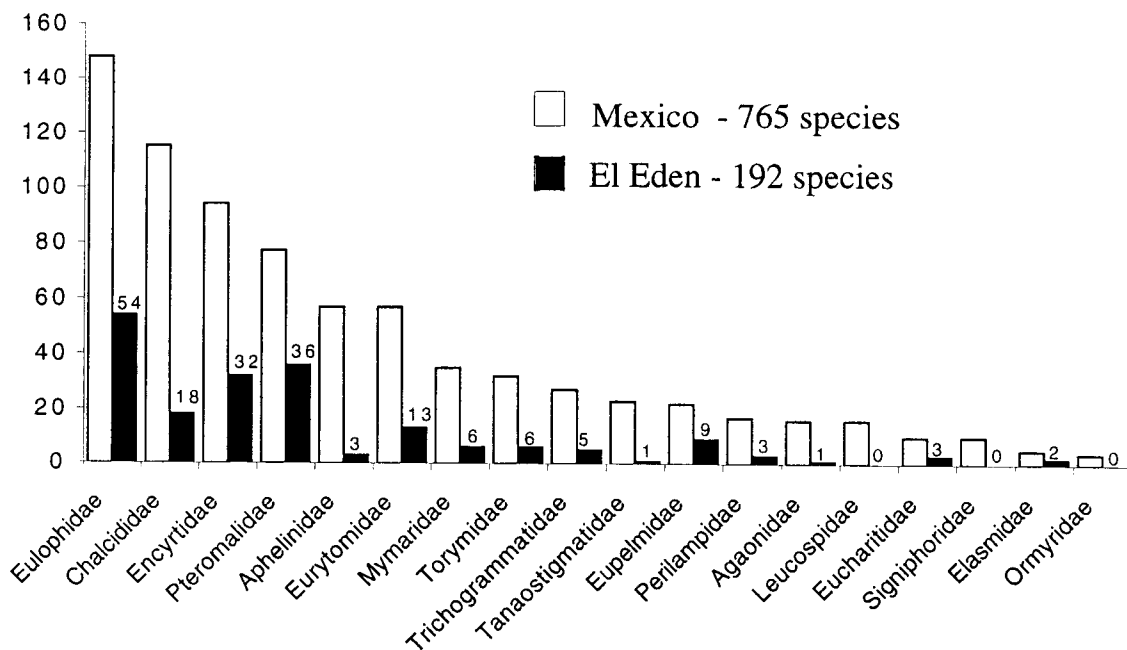
**Figure 1.** Described species of Chalcidoidea in Mexico based on published records (Noyes 1988), and a survey of five museum collections (González-Hernández 2000). Collections acronyms listed in text.

morphospecies from the González-Hernández survey, the number rises to 860 species. These numbers provide a baseline for comparison, but this knowledge must be tempered by the fact that most specimens of Chalcidoidea in these collections are not sorted to species and remain as miscellaneous unsorted material, and some important collections such as the Canadian National Collection (CNC) have not yet been surveyed. On the basis of figures derived from the Galapagos and Costa Rican surveys, we can expect to see about a 15 fold increase in the number of species expected to occur in Mexico, which would translate to about 13,000 species of Chalcidoidea. At the very least, the number of species should exceed the approximately 5,000 species known from Costa Rica.

### Species Richness at El Edén

Sampling of Hymenoptera, with an emphasis on Chalcidoidea, was conducted in the subtropical savanna of the Yucatán Peninsula at the Reserva Ecología El Edén in Quintana Roo, México. The reserve is located 25 km NNE of Leona Vicario and consists of lowland, subtropical savanna, primary and secondary forest, and several lagoons in marshy areas. The area is subject to monsoon rains in the summer and is periodically inundated during the fall and winter.

Numbers of Chalcidoidea from El Edén Reserve are based on a four-month sampling program in 1998. During an initial intensive collecting period in August, active sampling (sweep-netting) and passive insect sampling traps (malaise traps, yellow pan traps and aquatic pan traps) were established in six microhabitats in the Reserve. Sweep-nets were made of a very fine mesh fabric to focus sampling on minute insects. Malaise traps are essentially vertical tents of fine mesh netting with open sides that funnel flying insects into a collecting head filled with 75–80% ethanol (Townes 1972). Pan traps are small (20 cm diameter) yellow plastic bowls filled with water, salt (preservative) and a few drops of detergent (surfactant) to trap flying insects. Pan and Malaise traps were maintained on a casual basis through December 1998 by a resident parataxonomist. All specimens were collected in 70–80% ethanol and point-mounted after being dried with use of hexamethyldisilazane (Heraty & Hawks 1997). Hymenoptera were mounted, labeled and sorted to morphospecies by students at CIBE, UCR and Universidad Autónoma de Querétaro (UQT). Specimens will be housed in collections at UCR and CIBE.



**Figure 2.** Species richness of Chalcidoidea ranked by number of species described from Mexico (Noyes 1988, González-Hernández 2000). Numbers for El Edén based on morphospecies (Heraty & Gates unpublished).

Fifteen of 20 families of Chalcidoidea were sampled, and from only 656 specimens processed to date, we have sorted 192 morphospecies (Fig. 1). Of the 20 families, three were not expected to be collected; Rotoitidae are known only from New Zealand and Chile, Tetracampidae are Holarctic, and Ormyridae are inquilines in oak galls usually encountered at higher elevations (Gibson et al. 1997). Both Agaonidae, fig-pollinating wasps, and Signiphoridae, parasitoids of whiteflies, mealybugs and small Diptera should have been encountered, and their absence probably reflects inadequate sampling procedures. The number of morphospecies is 25.1% of the described species recorded from Mexico. The species richness across families coincides with the most commonly encountered groups elsewhere, with a predominance of Eulophidae (34 spp.), Encyrtidae (32 spp.) and Pteromalidae (36 spp.). Chalcididae (18 spp.) and Aphelinidae (3 spp.) were underrepresented as compared to the number of described species in Mexico (Fig. 1). At least for Aphelinidae and probably Signiphoridae, more species would be represented in the survey if collections were focused on rearing scale and whitefly hosts. The 192 species is a substantial increase in the known fauna, as only five genera and species of Chalcidoidea were known to occur in the State of Quintana Roo on the basis of museum records (González-Hernández 2000).

The next logical step for assessing the collections of Chalcidoidea from El Edén is to provide species names. Only by this means can we compare the distribution to that of the rest of Mexico or to similar habitat types in Central America. Do our studies add to the regional list of species or merely extend the distribution of known species? Unfortunately there are almost no identification keys available for the Chalcidoidea of Mexico (cf. González-Hernández 2000), and few species are described. At best, species can be sorted to genus, but otherwise most will remain as morphospecies and unavailable for beta-level comparisons for the foreseeable future.

### **Species Richness in Central America**

The species richness of Chalcidoidea in the United States, Central America and Columbia was compiled using Noyes (1998), with estimates for Mexico adjusted as discussed above (Table 1). For the Nearctic region, which would include parts of Mexico, Gibson et al. (1997) estimated a total of 706 genera and 2,757 described species of Chalcidoidea. This is within 5% of the report of 2,879 described species for the United States taken from Noyes (Table 1). Gaston (1993) estimated that only about 50% of North American species of Hymenoptera are named, which suggests a total of about 5,000 species of Chalcidoidea. Mexican species are probably better known than species of other countries since many would be included in revisionary studies of North American genera. However, even including Mexico, the numbers of chalcidoid species drop precipitously for all of the Central American countries and Colombia (Table 1). Initially these lower values suggest a pattern of decreased tropical diversity or possibly area relationships (smaller countries with fewer species. But these area relationships are not uniform: Colombia, which has access to the entire northern biota of South America, has fewer species than Costa Rica. Admittedly, the large number of North American species represents the extensive land mass and habitat diversity, but it is also a product of a larger number of collectors and systematists and a history of descriptive taxonomy. The lower numbers for Central and South America are more likely representative of the lack of taxonomic focus on collecting in these regions. Two examples support this concept. In El Edén, a relatively uniform lowland habitat, 192 species were collected over four months. This exceeds the number of species in all bordering countries to the south, each of which has more diverse habitat. Secondly, in the example cited above, 4,705 morphospecies of Chalcidoidea have been recognized in Malaise trap samples in Costa Rica (Hanson & Gauld 1995). This means that Costa Rica has at least an equivalent diversity to the United States, which, given the much smaller area of Costa Rica, supports the notion of increased tropical diversity.

### **Where do we go from here?**

The values presented above provide a baseline for examining the diversity of described species for Mexico and surrounding countries. However, especially for Central America, richness values for Chalcidoidea ranging from 50 to 765 species are simply not realistic. If 4,705 morphospecies are found in Costa Rica, then similar numbers should be expected in surrounding countries. We can expect to find 5,000–13,000 species of Chalcidoidea in Mexico alone. These numbers are not exclusive. Tropical species should overlap a great deal between countries throughout Central America, and temperate Nearctic species across much of Mexico. For pimpline ichneumonids in Malaise traps set in lowland tropical forests in Panama and Belize, the overlap in species with the well-

**Table 1.** Number of described species of Chalcidoidea in Central America, the United States and Colombia. Numbers gathered from Noyes (1998) with figures for Mexico modified by additional data (parentheses) from described species records listed by González-Hernández (2000).

Family	USA	Mexico	Guatemala	Honduras	Belize	El Salvador	Nicaragua	Costa Rica	Panama	Colombia
Agaonidae	15	16	0	1	0	1	0	34	10	1
Aphelinidae	211	57 (1)	1	5	0	15	1	10	9	11
Chalcididae	129	115 (5)	18	18	8	6	12	80	38	59
Elasmidae	20	5	0	0	0	1	0	1	0	0
Encyrtidae	449	94 (8)	3	3	0	2	2	43	17	27
Eucharitidae	30	10	2	0	0	0	5	4	6	3
Eulophidae	679	148 (12)	12	12	6	7	7	30	11	35
Eupelmidae	103	22 (4)	12	0	0	2	4	10	25	6
Eurytomidae	271	57 (2)	6	3	1	3	4	8	7	6
Leucospidae	7	16	4	3	0	2	1	4	5	8
Mymaridae	142	35 (1)	1	1	1	1	1	11	7	5
Ormyridae	17	4 (2)	1	0	0	0	0	0	0	0
Perilampidae	35	17	1	0	1	0	4	1	1	0
Pteromalidae	465	77 (13)	12	3	3	8	4	20	15	26
Rotoitidae	0	0	0	0	0	0	0	0	0	0
Signiphoridae	19	10	2	1	0	0	0	1	1	3
Tanaostigmatidae	15	23	0	0	0	0	1	7	2	2
Tetracampidae	2	0	0	0	0	0	0	0	0	0
Torymidae	181	32 (1)	4	2	0	1	5	1	1	9
Trichogrammatidae	89	27	6	3	2	1	2	13	3	13
<b>Total</b>	<b>2,879</b>	<b>765</b>	<b>85</b>	<b>55</b>	<b>22</b>	<b>50</b>	<b>53</b>	<b>278</b>	<b>158</b>	<b>214</b>

known Costa Rican fauna was 96.6% and 84%, respectively (Bartlett et al. 1999). Overlap between all three sites was only 39%, but this lower value was likely because of habitat differences between sites. Tropical lowland species are expected to show lesser degrees of endemism than those at higher altitudes (Gaston et al. 1996). However, without valid names, any beta-level comparisons between sites, habitats or regions are nearly impossible beyond a few representative taxa.

In this paper, we have focused on three aspects of understanding diversity in tropical countries.

1) Use of Published Information. For Chalcidoidea, we now have access to one of the most complete literature databases (Noyes 1998). It is crucial that this time-intensive project be ongoing if we are to keep abreast of changes in new species, new distributions and the synonymy of taxa. Each of these aspects affect our ability to make future estimates of the number of species within and between areas. For examining the diversity of broad groups in this manner, we must be willing to accept errors inherent in the data, since not all literature is trustworthy and not all synonymies are updated. Literature surveys also tend to be broad in their geographical scope and do not take into account state or exact locality differences in distribution. Only by intensely focusing on limited taxa can these problems be addressed, although this places obvious limitations on the scope of the taxa to be included in diversity assessments.

2) Survey of Collections. The survey of species in collections across North America by González-Hernández (2000) (through the Comisión Nacional de Biodiversidad [CONABIO]), and placement of these records into a progressive database is commendable. On the basis of 639,867 specimens input into CONABIO's all species database, about 80% of all specimens collected in Mexico are currently located in museums in developed countries (Soberón et al. 1996). For birds, 86% of all specimens are held in collections in the United States (Soberón et al. 1996). Information mined from these collections is an important resource for any developing nation. Measures of diversity and other information can be gathered and monitored effectively, but ultimately with the costs of curation and maintaining collections placed on the countries that can best afford these long-term investments. The resources needed to continue updating and expanding these databases are critical and beneficial at an international level.

On the positive side, information from databased collections can be recorded more exactly to include explicit information on date of collection, locality (latitude, longitude), elevation and other

relevant data. Use of this basic data (3,991 museum records of 421 species) were used in a Geographic Information System (GIS) analysis of Amazonian species to conceptualize regions of highest diversity and endemism (Kress et al. 1998). Similar analyses were applied to tracking the diversity and distribution of pierid and papilionid butterflies in Mexico extracted from specimens housed in 15 museums in Canada, Mexico, the United States and Europe (Soberón *et al.* 1996). Increasingly, exact specimen data is being excluded from publications (Snow & Keating 1999), and a return to searching for information found only in the primary collections may be necessary.

Significant problems associated with data mining are the accuracy of current identifications and whether collections have been updated to reflect nomenclatorial changes. Twenty-two (12.5%) of the named species reported by González-Hernández did not include updates in generic or species level synonymies, which makes it difficult to compare names in other lists, such as Noyes' database, which are developed for different collections or from different databases. To address these problems, databases should be integrated with electronic taxonomic catalogues and information on the authority (identifier) and year of identification included for verification purposes. Also, databases are expensive to maintain as museums must be revisited to survey for updated collections or identifications.

3) Sampling and Curation of New Material. The survey of Chalcidoidea at El Edén illustrates the importance of new collections. More than 192 species were discovered in a state that previously had only five species records. This collection forms a groundplan for future surveys and comparisons within El Edén, but on its own does not say much about the diversity in lowland tropical forests in Mexico or Central America. After all, we only have numbers for morphospecies, which cannot be compared with other areas until names are made available. Identification keys are generally not available. Specimens can be distributed to specialists for accurate identification, but with most species undescribed, names may not be available. The absence of names hampers our efforts to make meaningful conclusions surrounding comparisons between sites or regions. For these minute, mostly unnamed specimens, the lag time before they can become incorporated into current studies of biodiversity becomes enormous (Stork 1988). Yet as parasitoids, Chalcidoidea occupy the tertiary trophic levels, both controlling outbreaks of primary herbivores and acting as indicators of the health (diversity) of the primary trophic levels (LaSalle & Gauld 1992, 1993). The need to include this group in biodiversity studies is great.

Two approaches can be taken to increase the value of site collections. First, expend the effort to identify and describe all of the species. Assuming that most species are undescribed, then primary descriptions need to be developed for most of the 192 species. Estimates from the Costa Rican inventory program suggest that \$1,000 is necessary for every species description to cover investigator time, artist support, scanning electron microscopy, miscellaneous supplies and publication costs (J. LaSalle pers. comm.). For El Edén, this would amount to approximately \$190,000, but the investment would provide quick access to reliable information at all levels. Second, accept the lag time in collating the information but assure that specimen data and progress of curation is available for updating the various databases. This is easily accommodated by the use of unique specimen code numbers (unique numbers or bar-codes) linked to a database (for example BIOTA [Collwell 1997]) that includes all of the detailed collection information. This does not mean that accurate label information on specimens should be abandoned. Unique identifiers are just a means to track a specimen as it is resorted, loaned, named, or described, even if the process takes several years to complete. Database records can and should be made universally accessible over the World Wide Web. Problems of single data models for exchange of information have not been resolved, but locality coordinates, date and species name are basic fields that should be easily exchanged. In this way, specimen databases such as that developed by González-Hernández (2000) could be updated on a regular basis without necessarily revisiting collections or possibly even adding information from previously unvisited collections.

Each of the three categories of information listed above are ultimately based on field-collected material. Well-labeled and curated specimens form the basis of local collections, published accounts and specimen databases. An accurate description or identification key make the information available across all platforms. Developing programs and electronic databases that link taxonomic and specimen catalogues, and curating specimens in a manner that make the information accessible, should be a

priority of all collections (Janzen 1993; Soberón *et al.* 1996; Kress *et al.* 1998). Use of this information to provide better estimates of alpha and beta diversities in tropical species-rich countries will ultimately be useful for making more informed decisions on conservation and habitat management decisions.

The current focus on biodiversity has unfortunately had a negative impact on sampling efforts (Wheeler, 1995). By extolling the virtues of biodiversity, politicians interpret this in economic terms, which can be good, but the associated protectionism has had a major impact on scientific collecting and even in the loan and exchange of museum specimens. Many countries now impose restrictions on the collection and exportation of insect specimens. In the United States, restrictions are even placed on the importation of preserved, non-endangered insects from other countries (Anonymous, 1981). Ultimately, this leads to further decline in tropical collecting and an understanding of diversity. Shared information, without restrictions to access, is crucial to understanding biodiversity as it is today and how it changes in the future.

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## References Cited

- Anonymous. 1981. Lacey Act Amendments of 1981. Nov. 16, 1981. Public Law 97-79, 16 U. S. Code 3371 nt. 95 Stat. 1073
- Arnett Jr., R.H. 1985. *American Insects: A Handbook of the Insects of America North of Mexico*. Van Nostrand Reinhold: New York.
- Bartlett, R., J. Pickering, I. Gauld and D. Windsor. 1999. Estimating global biodiversity: tropical beetles and wasps send different signals. *Ecological Entomology* 24: 118-121.
- Coddington, J.A., C.E. Griswold, D.S. Dávila, E. Peñaranda and S. Larcher. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems, pp. 44-60. In *The Unity of Evolutionary Biology*, Vol. I, E. Dudley (ed). Proceedings of the fourth International Congress of Systematics and Evolutionary Biology. Disocorides Press: Portland Oregon.
- Coddington, J.A., L.H. Young and F.A. Coyle. 1996. Estimating spider species richness in a southern Appalachian cove hordwood forest. *Journal of Arachnology* 24: 111-128.
- Collwell, R.K. and J.A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* 345: 101-118.
- Collwell, R.K. 1997. *BIOTA*. Sinauer Press: Massachusetts.
- DeBach, P. 1971. *Biological Control by Natural Enemies*. Cambridge University Press, London.
- DeBach, P. and D. Rosen. 1991. *Biological Control by Natural Enemies*, 2nd ed. Cambridge University Press: Cambridge.
- Dial, K.P. and J.M. Marzluff. 1988. Are the smallest organisms the most diverse? *Ecology* 69: 1620-1624.
- Erwin, T. 1982. Tropical forests: their richness in Coleoptera and other Arthropod species. *The Coleopterist's Bulletin* 36: 74-75.
- Erwin, T.L. 1995. Measuring Arthropod biodiversity in the tropical forest canopy, pp. 109-127. In *Forest Canopies*, M.D. Lowman and N.M. Nadkarni. Academic Press: San Diego.
- Gaston, K.J. 1991. The magnitude of global insect species richness. *Conservation Biology* 5: 283-296.
- Gaston, K.J. 1993. Spatial patterns in the description and richness of the Hymenoptera, pp. 277-293. In J. LaSalle & I.D. Gauld (eds), *Hymenoptera and Biodiversity*. C.A.B. International: Wallingford.
- Gaston, K.J., I.D. Gauld and P. Hanson. 1996. Hymenoptera of Costa Rica. *Journal of Biogeography* 23: 105-113.
- Gauld, I.D. 1986. Latitudinal gradients in ichneumonid species-richness in Australia. *Ecological Entomology* 11: 155-161.
- Gibson, G.A.P., J.M. Heraty, and J.B. Woolley. 2000. Phylogenetics and classification of Chalcidoidea and Mymarommatoidea - a review of current concepts (Hymenoptera, Apocrita). *Zoologica Scripta* 28: 87-124.
- Gibson, G.A.P., J.T. Huber, and J.B. Woolley. 1997. *Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera)*. National Research Council Press: Ottawa. 794 pp.
- Godfray, H.C.J., O.T. Lewis and J. Memmott. 1999. Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society of London B* 354: 1811-1824.
- González-Hernández, A. 2000. Chapter 36: Chalcidoidea (Hymenoptera). In *Biodiversidad, Taxonomía y Biogeografía de Artrópodos de México*, v. II. J. Llorente and E. Gonzalez (eds). CONABIO y UNAM.
- Gordh, G. 1979. Encyrtidae. In Krombein, K.V., B. Hurd, D.R. Smith and B.D. Burks (eds), *Catalog of Hymenoptera in America North of Mexico*. Volume 1. Smithsonian Institution Press, Washington. 1198 pp.
- Goulet, H. and J.T. Huber (eds) 1993. *Hymenoptera of the World: An identification guide to families*. Agriculture Canada Research Branch Publication 1894/E.
- Greathead, D.J. 1986. Parasitoids in classical biological control, pp. 287-318. In J.K. Waage & D.J. Greathead (eds), *Insect Parasitoids*. Academic Press, London.
- Grissell, E.E. 1999. Hymenoptera biodiversity: some alien notions. *American Entomologist* 45: 235-244.
- Grove, S.J. and N.E. Stork. 2000. An inordinate fondness for beetles. *Invertebrate Taxonomy* 14: 733-739.
- Hanson, P.E. and I.D. Gauld 1995. *The Hymenoptera of Costa Rica*. Oxford University Press: New York.

- Hespenheide, H.A. 1979. Are there fewer parasitoids in the tropics?. *American Naturalist* 113: 766-769.
- Janzen, D.H. 1993. What does tropical society want from the taxonomist?, pp. 295-307. *In* J. LaSalle & I.D. Gauld (eds), *Hymenoptera and Biodiversity*. C.A.B. International: Wallingford.
- Kerr, J.T. 1996. Species richness, endemism, and the choice of areas for conservation. *Conservation Biology* 11: 1094-1100.
- Kress, W.J., W.R. Heyer, P. Avecedo, J. Coddington, D. Cole, T.L. Erwin, B.J. Meggers, M. Pogue, R.W. Torington, R.P. Vari, M.J. Weitzman and S.H. Weitzman. 1998. Amazonian biodiversity: Assessing conservation priorities with taxonomic data. *Biodiversity and Conservation* 7: 1577-1587.
- Lacey Act Amendments of 1981. Nov. 16, 1981. Public Law 97-79, 16 U. S. Code 3371 nt. 95 Stat. 1073
- LaSalle, J. 1993. Parasitic Hymenoptera, biological control and the biodiversity crisis, pp. 197-216. *In* J. LaSalle & I.D. Gauld (eds), *Hymenoptera and Biodiversity*. C.A.B. International: Wallingford.
- LaSalle, J. and I.D. Gauld. 1992[1991]. Parasitic Hymenoptera and the biodiversity crisis. *Redia* 74: 315-334.
- LaSalle, J. and I.D. Gauld. 1993. Hymenoptera: their diversity, and their impact on the diversity of other organisms, pp. 1-26. *In* J. LaSalle & I.D. Gauld (eds), *Hymenoptera and Biodiversity*. C.A.B. International: Wallingford.
- Lawton, J.H., B.E. Bignell, B. Bolton, G.F. Bloemers, P. Eggleton, P.M. Hammond, M. Hodda, R.D. Holt, T. B. Larson, N.A. Mawdsley, N.E. Stork, D.S. Srivastava and A.D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature*: 391: 72-76.
- May, R.M. 1988. How many species are there on Earth? *Science* 241:1441-1449.
- May, R.M. 1992. How many species inhabit the Earth? *Scientific American* ???: 42-48.
- May, R.M. 1999. The dimensions of life on Earth. *In* *Nature and Human Society: The quest for a Sustainable World*, P. Raven & T. Williams (eds). National Academy Press, Washington DC.
- Norrgard, R.B. 1988. Economics of the cassava mealybug in Africa. *American Journal of Agricultural Economics* 70: 366-371.
- Noyes, J.N. 1978. On the numbers of genera and species of Chalcidoidea (Hymenoptera) in the world. *Entomologist's Gazette* 29: 163-164.
- Noyes, J.N. 1989a. The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecological Entomology* 14: 197-207.
- Noyes, J.N. 1989b. A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History* 23: 285-298.
- Noyes, J.S. 1998. *Catalogue of the Chalcidoidea of the World* [CD-ROM]. ETI: Amsterdam.
- Noyes, J.S. 2000. Encyrtidae of Costa Rica (Hymenoptera: Chalcidoidea), 1. The subfamily Tetracneminae, parasitoids of mealybugs (Homoptera: Pseudococcidae). *Memoirs of the American Entomological Institute* 62: 355 pp.
- Noyes, J.S. And M. Hayat. 1984. *Oriental Mealybug Parasitoids of the Anagyrini* (Hymenoptera: Encyrtidae). CAB International: London. 554 pp.
- Owen, D.F. and J. Owen. 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature* 249: 583-584.
- Snow, N. and P.L. Keating. 1999. Relevance of specimen citations to Conservation. *Conservation Biology* 13: 943-944.
- Soberón, J., J. Llorfente and H. Benítez. 1996. An international view of National Biological Surveys. *Annals of the Missouri Botanical Gardens* 83: 562-573.
- Stork, N.E. 1988. Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* 35: 321-337.
- Townes, H. 1972. A light-weight Malaise trap. *Entomological News* 83: 239-247.
- Viggiani, G. 1984. Bionomics of Aphelinidae. *Annual Review of Entomology* 29: 257-276.
- Wheeler, Q.D. 1995. Systematics and biodiversity: policies at higher levels. *Science and Biodiversity Policy Supplement*, S21-S28.
- Wilson, E.O. 1985. The biodiversity crisis: A challenge to science. *Issues in Science and Technology* 2: 20-29.
- Yasnosh, V.A. 1979. Host-parasite relations in the family Aphelinidae (Hymenoptera, Chalcidoidea). *Entomologicheskoe Obozrenie* 58: 751-761 [Engl. transl.: *Entomological Review* 58(4): 61-70.]