The distribution of phacopid trilobites in space and time

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The richest representation and radiation of phacopid trilobites during their entire development (early Silurian – late Devonian) is within the shallow-water, mostly carbonatic facies in the inferred tropical to subtropical palaeoclimatic zone. The greatest diversity in species and genera is indicated in the geosynclinal regions (e.g. the Bohemian magnafacies of the Palaeotethyan region). Provincialism is manifest, especially in the Lower Devonian. In the Silurian, and Middle and Upper Devonian, there is strong evidence of migration (especially Europe-North Africa and Europe -Central and S.E.-Asia). The influence of environment is markedly expressed in the concentration of phacopids with reduced eyes in pelagic muddy facies and phacopids with well developed eyes in the epicontinental shallow-water facies. The development of phacopids in time is characterized by their sudden appearance at the beginning of the Silurian, a certain crisis in the uppermost Silurian, an acme of development in the early Middle Devonian, and total extinction at the Devonian/Carboniferous boundary. The changes in phacopid evolution, especially during the Late Devonian, reflect the events (possibly climatic, magnetic, or extra-terrestrial) which also affected other animal groups.

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The trilobites of the family Phacopidae Hawle & Corda are an important component of Silurian and Devonian trilobite faunas. Because of their abundant occurrence and world-wide distribution they provide suitable material for palaeobiogeographical studies.

The objective of this paper is to summarize the existing knowledge of the distribution of phacopid trilobites from their appearance at the Ordovician/Silurian boundary, until their extinction at the Devonian/Carboniferous boundary. The impulse to this work was given by the revision of phacopid trilobites from the Silurian and Devonian of Czechoslovakia, and by comparative study of phacopids from other regions.

The submitted report is based on generic and subgeneric levels. The principal taxonomic difficulty is that a large number of species have so far been cited in the literature under the collective generic name *Phacops,* although they represent different genera and subgenera, which often show diverse stratigraphical range of occurrence and distribution. The paper of Campbell (1967) and some more recent works appreciably contributed to the refinement of the phacopid classification. Most genera and subgenera discussed are defined in the Treatise (Harrington et al. 1959); genera and subgenera erected more recently have been described by G. Alberti (1970), Maksimova (1955, 1968), Přibyl & Vaněk (1971), Struve (1972) and the author (1971, 1972). Knowledge about phacopids has been further augmented, especially by the studies of H. Alberti (1965, 1968), Haas (1968), Struve (1970), Eldredge (1972, 1973), Sherwin (1972), etc. The genera and species of questionable validity, and those which the author considers to be invalid, are not discussed (this applies also to the five subgenera of *Phacops* established by Struve, 1972, which are based on features of specific rather than subgeneric value). *Bouleia* Kozłowski and *Dereimsia* Kozłowski are excluded from the family *Phacopidae,* in agreement with Eldredge (1972). The following genera and subgenera are discussed:

Acernaspis Campbell 1967, *Ananaspis* Campbell 1967, *Cryphops* Richter & Richter 1926, *Denckmannites* Wedekind 1914, *Dianops* Richter & Richter 1923, *Dienstina* Richter & Richter 1931, *Ductina* Richter & Richter 1931, *Eocryphops* Richter & Richter 1931, *Eophacops* Delo 1935, *Lochkovella* Chlupáč 1972, *Murphycops* Lespérance 1968, *Nephranops* Richter &

Richter 1926, *Phacopidella* Reed 1905, *Phacops* (*Phacops*) Emmrich 1839, *Phacops* (*Chotecops*) Chlupáč 1971, *Phacops* (*Prokops*) Chlupáč 1971, *Phacops* (*Paciphacops*) Maksimova 1972, *Phacops* (*Boeckops*) Chlupáč 1972, *Plagiolaria* Kegel 1952, *Reedops* Richter & Richter 1925, *Signatops* Přibyl & Vaněk 1971, *Struveaspis* Alberti 1966, *Trimerocephalus* McCoy 1849.

The distribution of seas in the Silurian and Devonian has been reconstructed mainly according to the works published in the Internat. Symposium on Devonian System, Calgary 1967, Atlas of Palaeobiogeography (Hallam, 1973) and some other works, e.g. Boucot, Berry & Johnson (1968), Walter (1972), etc. It should be emphasized that all reconstructions are but approximate and strongly extrapolated. For the sake of objectivity, the occurrences of phacopids are plotted in the maps on continents as they are distributed today, although the author is convinced that the theory of continental drift, postulating a close *approchement* of continents on the southern hemisphere into the incompletely divided Pangaea, is correct.

SILURIAN

The first unquestionable representatives of the family *Phacopidae* appear near the Ordovician/Silurian boundary. The oldest well known genus is *Acernaspis,* widely distributed in the Llandoverian. The occurrences of *Acernaspis* are concentrated mainly in the shallow-water carbonate facies; they are traceable from eastern North America (Anticosti, Nova Scotia) across the British Isles to the Baltic Region (abundant e.g. in Estonia, see Männil 1970). These phacopids are also widely distributed in similar facies of the Siberian platform and are known from the Arctic region (New Siberian Islands). The occurrences of *Acernaspis* furnish evidence of migration through shallow seas between eastern North America, northern Europe, and Siberia, i.e. in a relatively continuous belt belonging to the warm zone (benthos rich carbonate facies). The absence of *Acernaspis* in southern Europe and northern Africa may be explained by a less favourable living environment in the mudstone facies or by palaeoclimatic conditions (cooler zone of the Silurian southern hemisphere, see the interpretation of mudstone graptolite-

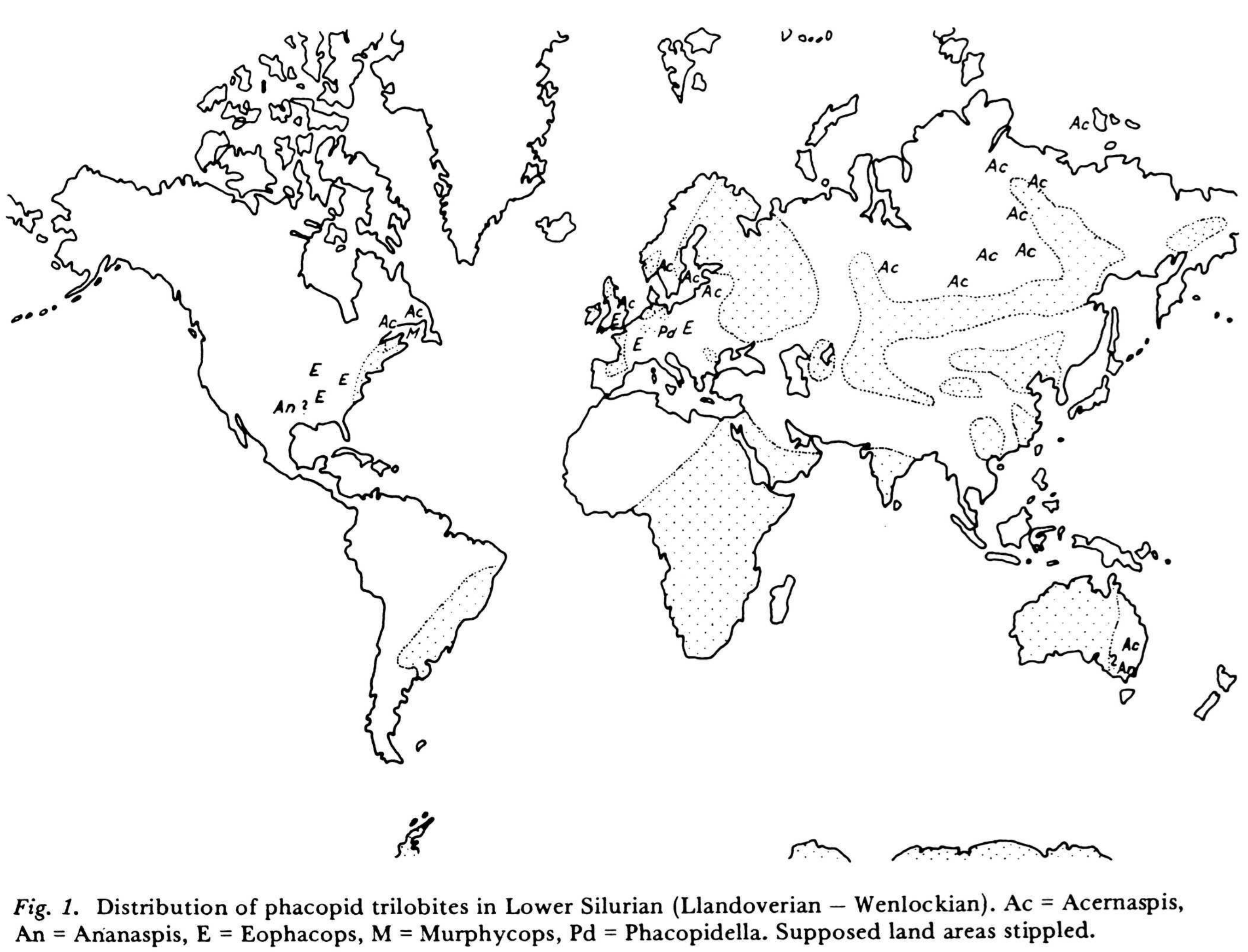

Fig. 1. Distribution of phacopid trilobites in Lower Silurian (Llandoverian – Wenlockian). Ac = Acernaspis, An = Ananaspis, E = Eophacops, M = Murphycops, Pd = Phacopidella. Supposed land areas stippled.

Fig. 2. Distribution of phacopid trilobites in Upper Silurian (Ludlovian – Přídolian). An = Ananaspis, E = Eophacops, D = Denckmannites, L = Lochkovella. Land areas stippled.

bearing facies in Berry & Boucot 1967). The finds of *Acernaspis* in south-eastern Australia suggest that the distribution was greater than is inferable from the occurrences known so far.

In the *late Early Silurian,* in the Wenlockian, and at the beginning of the Late Silurian (early Ludlovian), the genus *Eophacops* shows a conspicuously wide distribution. Its representatives, like those of *Acernaspis,* are confined to shallow-water carbonate facies; they are known to occur chiefly in the U.S.A. (Illinois, Ohio, Indiana, Tennessee), England, Czechoslovakia (Barrandian), Germany, and north-western Africa (Morocco). The occurrences recorded from Asia (Maksimova 1962 et seq.) belong mostly to *Acernaspis.* Compared with the occurrences of *Acernaspis,* those of *Eophacops* are pronouncedly shifted southwards. This very likely reflects the extension of shallow-water carbonate facies at the expense of mudstone facies, consistent with the continental drift tendency during the Silurian (it can also be interpreted by the migration of the greater part of continents into the warm climatic zone).

The *Upper Silurian,* in particular the Ludlovian, is distinguished by a wide distribution of the genus *Ananaspis,* which is known from North America, the British Isles, Central Europe (Barrandian, Carnic Alps), North Africa (Morocco), and Central Asia (Kazakhstan). The probable representatives from south-eastern Australia (New South Wales, see Sherwin 1972) complement the picture of the wide distribution of *Ananaspis* along the Palaeotethys. The relation of *Ananaspis* to shallow-water carbonate facies and its principal distribution areas is analogous to that of *Eophacops.* Additionally, some remarkable genera of a strongly restricted distribution belong to the Silurian – for example, *Phacopidella,* of phylogenic significance and with some primitive dalmanitid features, which is so far known only from the Wenlockian of Czechoslovakia (Barrandian area), and *Denckmannites* from the Ludlovian of the same area, which provides a good example of eye-reduction depending on the living environment in the facies of the cephalopod limestone.

In the Silurian, the *Reedops* branch of phacopids also appears. It is represented by *Lochkovella,* known from the Upper Silurian of Europe (Carnic Alps) and reaching the maximum development in early Lower Devonian within the Palaeotethys (occurrences in Spain, North Africa, Thuringia, Barrandian, USSR, New South Wales).

The distribution of Silurian phacopids does not show any marked provincialism. This agrees with the observations made on other animal groups (cf. Boucot 1970; Holland 1971).

Yet, the relationship with the shallow water environment of the warm climatic zone is clear. Towards the end of the Silurian (in the Přídolian) a conspicuous decrease in phacopid fauna has been established, which can reflect the palaeogeographical changes or other factors, such as palaeoclimatic changes, changes of magnetic field, etc.

LOWER DEVONIAN

The Lower Devonian is characterized by a distinct differentiation of palaeobiogeographical provinces (cf. Boucot, Johnson & Talent 1967, 1969; House 1971) and by spectacular facies differences within marine regions (cf. Erben 1962, etc.). As to the phacopid trilobites, they experienced an extensive development and rich radiation.

The richest development is observable in the *Bohemian magnafacies* of the *Old World Province,* where most of the Lower Devonian genera and subgenera occur. Here are representatives of the genus *Phacops* linked with the Silurian genus *Ananaspis, Phacops (Boeckops), Phacops (Prokops), Lochkovella,* and *Reedops,* which reached its maximum development, and is especially abundant. Apart from the classical Barrandian area, the phacopid faunas of this composition have been found mainly in North Africa (Morocco), in the Bohemian magnafacies of the European Variscan geosyncline (France, southern and eastern parts of the Rheinisches Schiefergebirge, the Harz, Moravia), in Turkey (Bithynia, cf. Haas 1968), Central Asia (Kazakhstan, cf. Maksimova 1968), and probably also in south-eastern Asia and Australia. The migration possibilities within the Old World Province and with the Pacific region (Cordilleran Subprovince) of North America are demonstrated by the presence of *Reedops* in Nevada (Haas 1969), while the find of *Reedops* in Oklahoma (Ormiston 1968) indicates the possibility of migration into the Appalachian Province when a suitable facies is present. These two occurrences are accompanied by other trilobites of Bohemian type.

The typical *Rhenish magnafacies* of the Old World Province with prevailing clastic sedimentation is relatively poor in phacopids. This is most probably caused by unfavourable environment (strong supply of terrigenous sandy material).

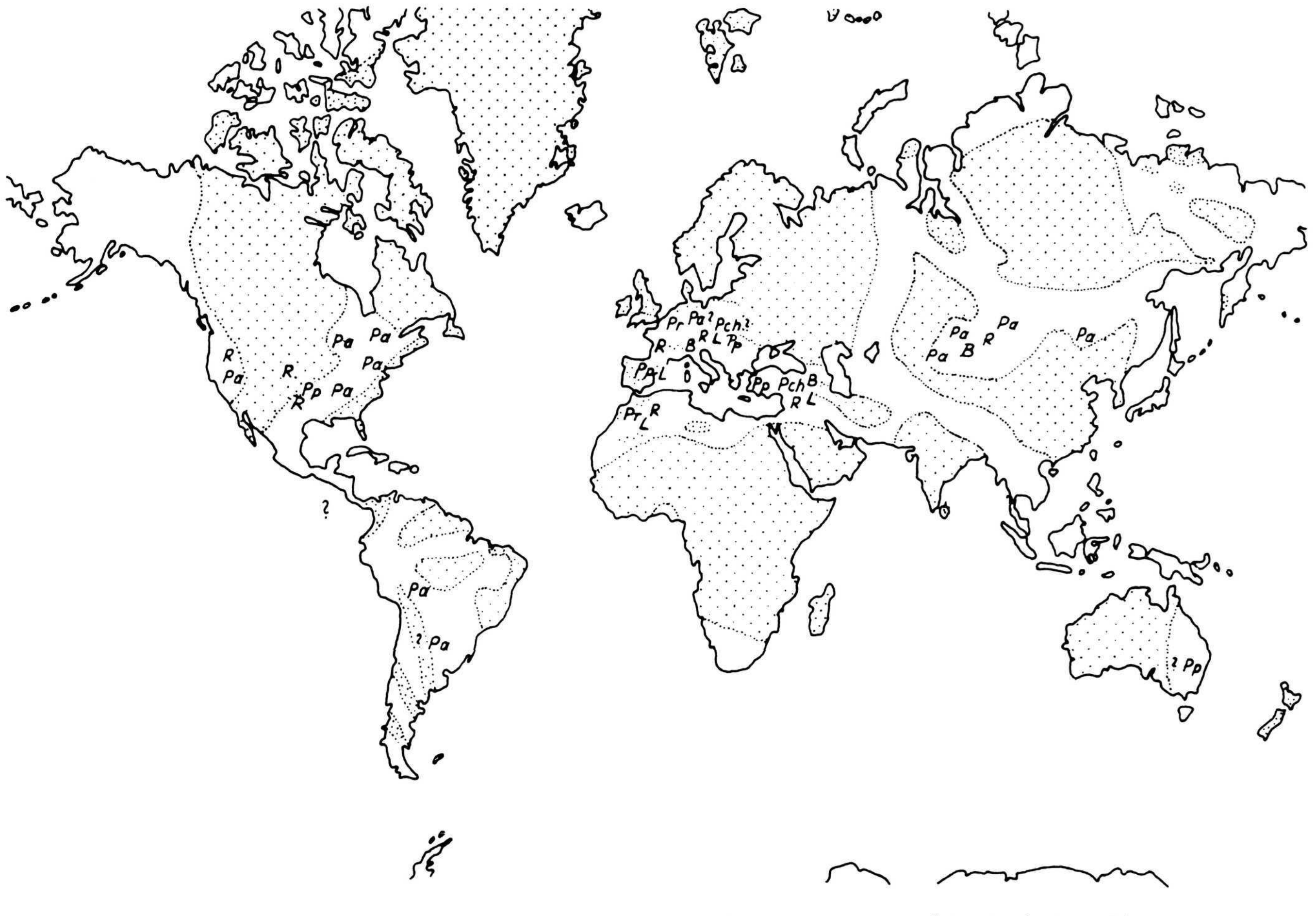

Fig. 3. Distribution of phacopid trilobites in Lower Devonian (Lochkovian – Zlíchovian). Pp = Phacops (Phacops), Pa = Phacops (Paciphacops), Pr = Phacops (Prokops), B = Phacops (Boeckops), L = Lochkovella, R = Reedops. Supposed land areas stippled.

The Appalachian Province of North America is distinguished by a rich development of *Phacops* (*Paciphacops*), which is represented mainly by the *Phacops logani* Group. *Phacops* (*Paciphacops*) is also locally abundant in South America, even in the Malvinokaffric (Austral) Province, characteristic of the cold climatic zone in the Lower Devonian. The occurrences of *Phacops* (*Paciphacops*) in Central Asia and in the Far East (Maksimova 1972) point to the possibility of migration between the Appalachian and Old World Provinces. The phacopids included in *Phacops* (*Paciphacops*) are obviously less environment- and climate-controlled than, for example, *Reedops.*

Comparison of the distribution of Lower Devonian phacopids with the position of continents reconstructed from palaeomagnetic data and with palaeoclimatic conditions (Chlupáč & Krs 1967) shows that the phacopid faunas richest in genera and species were concentrated in the warm palaeoequatorial zone comprising most of the Old World Province and the Appalachian Province. The rather cold water phacopid faunas of South America (Malvinokaffric Province) are poor in genera and species, although the number of specimens is locally large (e.g. in Bolivia, cf. Wolfart 1968).

MIDDLE DEVONIAN

Assessment of phacopid occurrences in the Lower/Middle Devonian boundary interval is difficult because the Lower/Middle Devonian boundary is conceived differently by individual (German, French, Czechoslovak, and Soviet) geological schools. If this boundary were identified with the upper boundary of the Zlíchovian, as the case in the Bohemian magnafacies often is, the beginning of the Middle Devonian would be distinguished by a high differentiation of phacopid genera and subgenera: *Phacops* (*Chotecops*), *Eocryphops, Struveaspis* and *Ductina* would make their first appearance, and *Phacops* (*Phacops*), *Phacops* (*Paciphacops*), *Plagiolaria,* and the last representatives of *Reedops* and *Phacops* (*Boeckops*) would survive from the Lower Devonian. Most of these phacopids occur in the carbonate and pelitic facies of the Bohemian magnafacies of Europe, and North Africa. Remarkable are phacopids with reduced eyes (*Eocryphops,*

Fig. 4. Distribution of phacopid trilobites in Middle Devonian (Eifelian s. lat. – Givetian). Pp = Phacops (Phacops), Pa = Phacops (Paciphacops), Pch = Phacops (Chotecops), B = Phacops (Boeckops), R = Reedops, Ec = Eocryphops, Pl = Plagiolaria, S = Struveaspis, Du = Ductina. Supposed land areas stippled.

Plagiolaria, some species of *Struveaspis*, possibly also *Reedops*) or blind ones (*Ductina*), which occur mainly in the mudstone or cephalopod micritic limestone facies of pelagic environment in Europe and North Africa (Rheinisches Schiefergebirge, Harz, Barrandian, Moravia, Morocco) and south-eastern Asia (north Viet Nam, Thailand, see Maksimova 1965; Kobayashi & Hamada 1968). The relationship between these occurrences and the pelagic, often deeper-water geosynclinal facies provides evidence for the influence of the environment on eye-reduction (cf. Clarkson 1967); the same effect can be postulated even for the Lower Devonian, but phacopids from the shaly pelagic facies of this epoch are little known.

The *Middle Devonian* is characterized by a wide distribution of *Phacops* (*Phacops*), which is represented abundantly in the shallow-water platform and even geosynclinal facies of Europe, North Africa, West, Central and East Asia, and North America. It documents the rather cosmopolitan character of most Middle Devonian faunas, marked e.g. in brachiopods (Boucot, Johnson, & Talent 1967, et seq.). *Phacops* (*Chotecops*) is not so widespread; it is known from Europe (Barrandian, Rheinisches Schiefergebirge, Harz, Moravia, France, South England), Asia Minor (Bithynia) and North Africa. *Phacops* (*Chotecops*) tends to occur in impure limestone, mixed pelitic-carbonate to mudstone facies. Some differences in the distribution of phacopids (see e.g. Burton 1972) can be easily explained by environmental control rather than by geographical barriers, etc.

In North America, mainly in the Appalachian Province, the evolution of *Phacops* (*Paciphacops*), equal here to the *cristata* Group of phacopids, persists to the early Middle Devonian, during which it extends to Central Asia (Kazakhstan) as well. The Upper Eifelian and Givetian of North America are distinguished by an abundant development of *Phacops* (*Phacops*), comprising numerous species of the *Phacops rana* Group and *Phacops* (*P.*) *iowensis* Group (cf. Eldredge 1972).

Remarkable is the lack of phacopids in the Arctic region of Canada, where the facies development is very near the Bohemian magnafacies (elsewhere rich in phacopids). The character of trilobite faunas is also similar to that of the Bohemian type (cf. Ormiston 1967). This feature can be regarded as a manifestation of provincialism and interpreted in terms of geographic isolation or palaeoclimatic conditions.

During the *late Middle Devonian* (*Givetian*) the generic diversity of phacopids generally decreases (cf. Fig. 6). However, imperfect knowledge of the trilobite faunas from the geosynclinal carbonate and mudstone pelagic facies may be partly the cause.

UPPER DEVONIAN

Characteristic of the Upper Devonian Epoch is the extinction of many trilobite families and higher groups; calymenids, calmonids, homalonotids and cheirurids die out near the Middle/Upper Devonian boundary, and scutelluids, harpids, dalmanitids and odontopleurids become extinct during the Frasnian or near the Frasnian/Famennian boundary. This boundary is especially prominent, and represents a sudden break in the evolution of Devonian faunas and their environment on a global scale (extinction of reefs, extension of pelagic facies, etc.). Extra-terrestrial effects are considered as possible causes of this change by some authors (McLaren 1971). However, the evolution of the family Phacopidae was affected, but not interrupted by these events, so that it continued throughout the Upper Devonian until the Devonian Carboniferous boundary.

The evolution of *Phacops* (*Phacops*) and *Phacops* (*Chotecops*) persists during the *Frasnian,* although the number of known species is smaller than in the Middle Devonian (they are known from Europe, North Africa, Central and East Asia and North America). The development of *Cryphops* with reduced eyes decreases in the late Frasnian. *Cryphops* finds are concentrated in the pelagic facies of the Old World Province (England, Rheinisches Schifergebirge, Harz, Thuringia, Carnic Alps, Moravia, Ural Mts., Asia Minor, North Africa, Kweichow in China).

The development of *Phacops* (*Phacops*) and *Phacops (Chotecops)* continues in the *late Upper Devonian (Famennian),* and some species are of a wide geographical distribution – *Phacops (P.) granulatus* (Münster) is recorded from many European regions (south-western England, Rheinisches Schiefergebirge, Harz, Thuringia, Góry Swietokrzyskie in Poland, Silesia, Moravia and Spain), from the South Ural region, Kirgizia, China (Great Chingan) and North-Africa (Morocco, Sahara). One of the youngest phacopids, *Phacops* (subg.?) *accipitrinus* (Phillips) from the *Wocklumeria* Zone, is also widely distributed; it tends to have a greater concentration in shallow-water facies influenced by current activity. Occurrences of this species are known from England, Rhineland, Belgium, northern France, Moravia, North Africa, U.S.S.R. and Afghanistan.

Fig. 5. Distribution of phacopid trilobites in Upper Devonian (Frasnian – Famennian). Pp = Phacops (Phacops), Pch = Phacops (Chotecops), C = Cryphops, D = Dianops, Di = Dienstina, Du = Ductina, N = Nephranops, T = Trimerocephalus.

Characteristic of the *Famennian* is the rich development of phacopids with reduced eyes *(Nephranops, Dienstina),* or phacopids completely blind *(Trimerocephalus, Dianops, Ductina).* As in the Middle Devonian, the phacopids with reduced eyes are concentrated in the facies, which is of rather pelagic, both shaly and impure, limestone character. They can be distinguished from so-called *Clymenia* Limestones, where they are accompanied occasionally by phacopids with well developed eyes (Maksimova 1955; Chlupáč 1966). The occurrences of these phacopids have been established in the Old World Province, mainly in geosynclinal areas: European Variscan geosyncline (southern England, northern France, Rhineland, Harz, Saxony – Thuringia, Frankenwald, Poland, Silesia, Moravia, Carnic Alps, North Africa, Asia Minor, Ural region, Kazakhstan).

The distribution of phacopids during the Famennian, as that of goniatites (House 1971, 1973), suggests the possibility of migration, especially within the Old World Province between Europe, North Africa and Central and South-East Asia, i.e. within the Palaeozoic Tethys. The dependence of some phacopids (in particular with reduced eyes) on pelagic environment explains their absence from the areas of the former Appalachian Province of North America. It is so far difficult to decide whether the lack of these forms, e.g. in the Cordilleran region, Alaska, and in eastern Australia, is the result of provincialism or of insufficient investigation.

The sudden and complete extinction of phacopids near the *Devonian/Carboniferous boundary* is striking. It is extremely remarkable because during the Famennian a relatively rich radiation of phacopids takes place, and at the Devonian/Carboniferous boundary both phacopids of older branches (*Phacops* and its subgenera) and genera appearing as late as in the Famennian die out. The complete extinction of phacopids is approximately synchronous with the extinction of clymeniid cephalopods. It is one of the most important events that justifies the drawing of the upper boundary of the Devonian at the upper boundary of the *Wocklumeria* Zone. On the other hand, it is remarkable that e.g. the development of small cyrtosymbolid trilobites, which in the Famennian are common associates of phacopids, continues from the Famennian into the Lower Carboniferous without substantial changes, and many genera and subgenera of cyrtosymbolids overreach this boundary (cf. Chlupáč 1966 et al.). The sudden extinction of phacopids and clymenids at the end of the Famennian is difficult to explain; it may be tentatively accounted for by the change of geomagnetic field, which is most important to the evolution in general, as pointed out by Crain (1971).

CONCLUSIONS

The main distribution of the trilobites of the fam. *Phacopidae* falls in the *Silurian* in a shallow-water environment (mainly carbonatic facies), where it does not show any marked provincialism and is probably controlled by palaeoclimatic factors. This is also evidenced by the close affinity of phacopids of the Old World and North America, and by synchronous changes in their evolution. The uppermost Silurian (Přídolian) is distinguished by the decrease in phacopids, and reflects a certain crisis in their evolution.

In the *Lower Devonian,* the family shows an extensive development, and phacopids display a distinct provincialism (e.g. marked differences between the phacopids of the Old World Province and the Appalachian Province). The phacopid associations richest in genera and species occur in the Palaeozoic Tethydian region, mainly in the Bohemian magnafacies, and genera-poor associations extend into the Malvinokaffric Province (cool zone in the Devonian). The Rhenish magnafacies is relatively poor in phacopids (probably unfavourable environment in areas of clastic sedimentation).

In the *Middle* and *Upper Devonian* the rich development of phacopids continues in the Old World Province. The phacopids of these epochs attest to the possibility of migration, in particular between Europe and North Africa and between Europe, Central and Southeast Asia. The associations richest in genera are assembled in geosynclinal facies. In North America, a strikingly lower diversity in generic representation has been observed. Although the distribution of phacopids (esp. those with reduced eyes) is environmentally controlled, the lack of phacopids

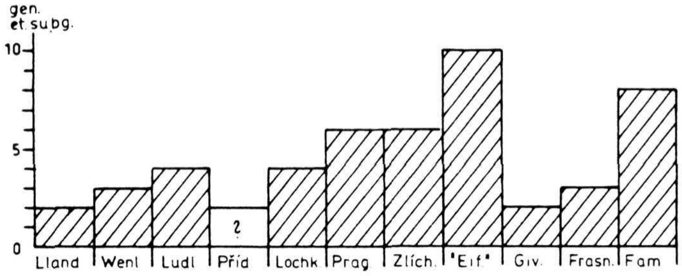

Fig. 6. Representation of genera and subgenera of phacopid trilobites during Silurian and Devonian.

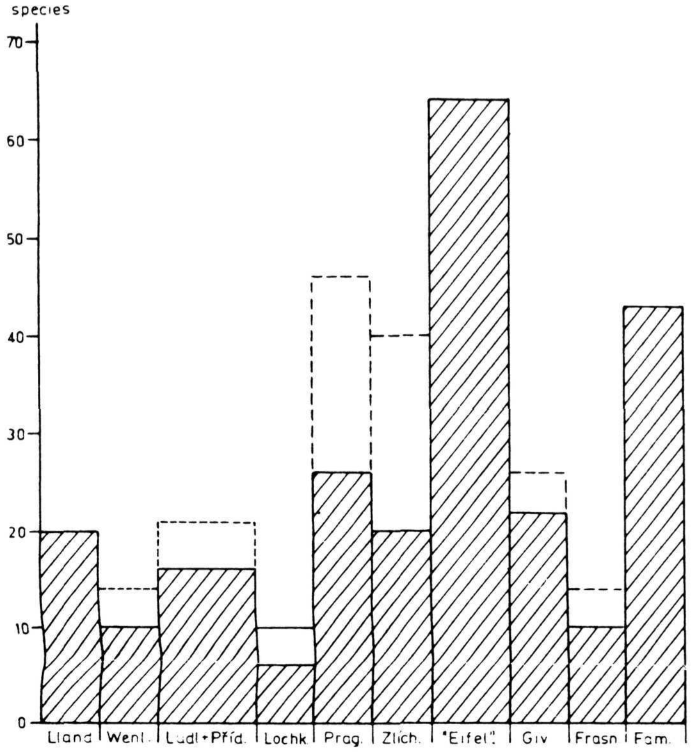

Fig. 7. Representation of species of phacopid trilobites during Silurian and Devonian (as of 1972, empty parts of columns = occurrences of species not precisely dated with regard to stage).

in the Canadian Arctic Islands cannot be explained in these terms, and some other factors causing a certain provincialism should be considered (palaeoclimatic factors, geographic barriers, etc.).

During the *Upper Devonian* (esp. Famennian) there is a striking development of phacopids with reduced eyes, synchronous with the extension of areas of pelagic facies. The changes in the phacopid faunas in the Upper Devonian occur at the same levels as the changes documented in other animal groups (e.g. cephalopods and brachiopods) and mirror the events affecting the character of the marine associations the world over. They can be explained, for example, by climatic changes, changes in the Earth's magnetic field, or in the case of the changes at the Frasnian-Famennian boundary, even by extraterrestrial agents. The extinction of the whole family at the Devonian/Carboniferous boundary is one of the important criteria for drawing this boundary at the upper limit of the *Wocklumeria* Zone.

The diagram of stratigraphic representation of genera and subgenera of phacopids (Fig. 6) reflects a gently progressive development during the Lower and Upper Silurian, a retreat of phacopids in the uppermost Silurian and an increasing diversity during Lower Devonian up to the maximum diversity gradient reached in the early Middle Devonian. The larger diversity in the uppermost Devonian (Famennian) is caused mainly by the development of phacopids with reduced eyes under environmental control. The diagram of species diversity (Fig. 7) shows most features common to Fig. 6. It should be noted, however, that the exact stratigraphical occurrence of many species with regard to the stage division is not sufficiently known, and numbers of species recorded from respective stages are rather approximate.

The areas of wide distribution and radiation of phacopid trilobites during their entire development from the beginning of the Silurian until the end of the Devonian are consistent with the alleged course of the warm periequatorial zone in Silurian-Devonian time, interpreted from the palaeomagnetic, lithologic, and palaeontologic data. Hence, they are in full agreement with the concept and trend of the continental drift during the Silurian and Devonian.

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