A new order of trilobites — the Proetida — is proposed to include the families Aulacopleuridae, Bathyruridae, Brachymetopidae, Celmidae, Dimeropygidae, Glaphuridae, Otarionidae and Proetidae, based on study of a wide range of material of these families. This is believed to be a more natural grouping of these families than that currently adopted. The supposed relationships of these trilobites are based on a comparison of morphological features and ontogenies; new discoveries of early species are consistent with this conclusion. The families are considered to have been derived from various species of the subfamily Hystricurinae, probably during the Tremadoc, from which evolution may have subsequently proceeded along relatively independent lines. Parallelism of morphological features in different groups of the Proetida indicate the repeated adoption of similar life habits.

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During the course of studying early Ordovician faunas from Spitsbergen and Ireland (R.A.F.) and Lower Palaeozoic Proetidae and Otarionidae (R.M.O.), we were led independently to re-examine critically the systematic position used in the Treatise (Part O) of the trilobite families Aulacopleuridae, Bathyruridae, Celmidae, Dimeropygidae, Glaphuridae, Otarionidae and Proetidae, and the subfamily Hystricurinae. We now believe that together these families constitute a major natural group of the Trilobita — the order Proetida. In this paper we summarise the evidence for such a reorganisation, which is based on examination of a wide variety of species of the group, and briefly consider some aspects of its evolution. Various inter-relationships between some of the families named above have been postulated periodically over the last twenty years. Whittington & Evitt (1954: 35-36), for example, noted similarities between dimeropygids, the otarionid-proetid group and hystricurines, and these comments were reiterated by Whittington (1966: 707, 709). Information relevant to classification is derived from three sources:

1. Consideration of comparative morphology
2. Discovery of some new early representatives of particular families
3. Knowledge of ontogenies

Our conclusions are based on as many lines of evidence as possible in a phylogenetic model, and are not consistent with a "single character" classification. The morphology of the Phillipsinellidae seems to us to place that family outside the Proetida as here defined, and we have not studied sufficient material to be able to evaluate the systematic position of the Lecanopygidae and Plethopeltidae. We can find no evidence to suggest close relationships between the Proetida, as defined here, and the illaenid-thysanopeltid group, which are included together in a high-level taxon in the Treatise and in the classification of Bergström (1973: 41).

PROPOSED RELATIONSHIPS OF PROETIDA

It is believed that early representatives of the families included in the Proetida were derived from a plexus of early to Middle Canadian (Tremadoc) Hystricurinae which were widespread across the North American craton, the USSR and China during this period. There are also indications that the geographical range of the subfamily may be greater than the literature indicates at the
moment: for example, "Proetid gen. et sp. indet." from southern France (Dean 1961, Pl. 15: 1–7), *Tasmanaspis* from Tasmania (Kobayashi 1940, Pl. XI: 3, 4) and *Protarchaeogonus* from Bavaria (Sdzuy 1955, Pl. 7: 2–7) may possibly be hystricurines. Various hystricurines are considered to be close enough to early representatives of the families discussed below to be their most likely ancestors.

**DIMEROPTYGIDAE**

Early species of the family Dimeropygidae referable to the genus *Ischyrotooma* Raymond are found in the Arenig of North America (Ross 1951, Pl. 35:18,23–28; Hintze 1953, Pl. 19: 1–10). Characteristic features of these early species are the convex, transversely narrow anterior border, and the slightly converging anterior branches of the facial sutures. In anterior view (Ross 1951, Pl. 35: 23) the cranidium shows a distinctive X-shaped junction between the downward and forward-curving axial furrows and the upward arched anterior border furrow. Large free cheeks lack genal spines, or they are much reduced, but on immature free cheeks (Ross 1953, Pl. 63: 24) they are still prominent. It is believed that *Ischyrotooma* was derived from a hystricurine merely by reduction of the genal spines. The most likely species to be near the origin of the genus are found in *Pseudohystricurus* Ross, a genus which occurs in beds underlying those with *Ischyrotooma* in Utah and may also occur in Kazakhstan (Lisogor 1961, Pl. 1: 15–17). Cranidia of this genus, and particularly *Pseudohystricurus* sp. of Ross (1951, Pl. 16: 26,27,31), show similar structure, with a closely comparable anterior profile. Unfortunately free cheeks and pygidia are not described for *Pseudohystricurus*, but probable hystricurine pygidia with steeply sloping posterior margins not unlike those of *Ischyrotooma* species are present among unassigned pygidia (Ross 1951, Pl. 19: 13) from the same beds as *Pseudohystricurus*. Ross (1953: 638) has also noted the similarity of paired tubercles on small *Ischyrotooma* to those on hystricurines at a similar stage of development. There can be little doubt that species ancestral to *Dimeropyge* are to be found in *Ischyrotooma* (Ross 1951: 123). Other Middle Ordovician dimeropygid genera which are relevant to the problem of the classification of the Glaphuridae are discussed below.

**BATHYURIIDAE**

Early species of the family Bathyruridae in the Lower Ordovician of Utah and Nevada belong to the genera *Liciocephala* Ross, 1951 and *Peltabellia* Whittington & Ross, 1953, the appearance of the latter genus preceding that of the former. In contemporaneous deposits over the Siberian Platform the genus *Bioligina* Maksimova, 1955 is widespread, some species of which (e.g. Rozova 1968, Pl. 17: 4–8) are very similar to *Peltabellia* and probably closely related. *Peltabellia* thus probably represents a genus close to the ancestral bathyurid and *Peltabellia* sp. B of Hintze (1953: 175, Pl. 9: 8,11,12) from Canadian, zone G, is the earliest known representative of the family. Cranidia of the hystricurine *Psalictilopsis cuspicaudata* Ross (1953, Pl. 63: 3–5,8,9) are similar to *Peltabellia* sp. B and *P. peltabella* Ross, 1951 in size and position of eyes, in having a convex, steeply downsloping preglabellar field, transversely arched anterior border and in having divergent, anteriorly inward-curving anterior branches of the facial suture. The pygidium of *P. cuspicaudata* differs from that of *Peltabellia* sp. B in having a steeply downturned posterior border which carries a short terminal spine; however it does resemble that of another early bathyurid, *Goniotelina brevis* Hintze (1953, Pl. 26: 8) in these features. Early bathyurids with long terminal spines on the pygidium (Hintze 1953, Pl. 26: 1–6,14; Ross 1951, Pl. 14: 16–22, 25) may be directly compared with hystricurines such as *Pseudohystricurus orbus* Ross (1953, Pl. 63: 10–11, 13–20, 23). This species has a nasute border on the cranidium, characteristic also of early *Goniotelina* species, while the free cheek is closely similar to that of *Goniotelina williamsi* Ross (1951, Pl. 14: 16–22,25) in having a long, gently curved genal spine which does not continue the line of curvature of the lateral border of the cheek, but is kinked abaxially. The border of the free cheek of *P. orbus* carries a sculpture of parallel raised lines which is typical of *Goniotelina* and *Acidiphorus* species, but unusual among hystricurines. The pygidium of *P. orbus* (Ross 1953, Pl. 63: 13,14; Hintze 1953, Pl. 20: 16) tapers posteriorly with the axis continued into a long spine and is closely similar to that of *Goniotelina williamsi* (Ross 1951, Pl. 14: 16–17). The principal difference between *P. orbus* and the early *Acidiphorus* species is in the greater curvature of the palpebral lobes of the latter which restricts the postocular fixed cheek to a narrow (exsag.) strip.

The second major morphological type of bathyurid with a flat, wide pygidium, broad
anterior border to the cranidium and blade-like genal spines, typified by Bathyleurus, is already represented in early bathyurid faunas by species of Licnocephala (Ross 1951, Pl. 28: 12–14; 1953, Pl. 64: 1–29; Hintze 1953, Pl. 10: 1–5). It is conceivable that Licnocephala was derived from a Peltabelia-like ancestor, the pygidium of *P. peltabella* has a wide border onto which the pygidial pleural ribs do not continue, similar in this respect to Licnocephala species, and the free cheek of *P. peltabella* is transversely wide with a tendency towards flattening out of the postero-lateral border (Ross 1951, Pl. 17:7,13). The preglabellar field of *Peltabellia* is relatively wide (sag.), like that of *Licnocephala* and Bathyleurus, but unlike that of *Goniotelina* and Acidiphorus. It seems possible that the Acidiphorus/Goniotelina type of bathyurid may have had an origin in the Hystricurinae independent of that of the Licnocephala/Bathyurellus type, the former arising from a species close to Pseudohystricus orbus Ross, the latter (via *Peltabellia*) possibly from *Psalikilopsis*. If this view is substantiated the separation of the Goniotelina-type bathyurids from *Licnocephala/Bathyurellus*-type bathyurids into two subfamilies (Bathyurininae and Bathyurellinae respectively) as proposed by Hupé (1953: 198) will be justified.

PROETIDAE

Owens (1970, 1973a, 1973b) has redescribed north European Ordovician and Silurian Proetidae, and has recognised two major groups within the family as conceived in the Treatise. These groups, centred on *Proetus* and on *Decoroproetus*, appear to be two natural phyletic units, and on present evidence (Owens 1973b: 79–85) appear to have quite independent origins. The *Proetus* group is here termed 'Proetidae A', and the *Decoroproetus* group 'Proetidae B'.

PROETIDAE A. — The earliest species belonging to this group is *Cyphoproetus facetus* Tripp, 1954 (Owens 1973b, Pl. 5: 10–12; Pl. 6: 1) from the Caradoc of the Girvan district. *Proetus* has its earliest representatives in the Ashgill (Owens 1973b: 84) and might be derived from *Cyphoproetus* simply by effacement of the deep 1P glabellar furrows. It has been suggested (Owens 1973b: 85) that the proetids belonging to Proetidae A possibly have their origins in the Otarionidae in the earlier Ordovician. A cranidium which is almost intermediate between *Otarion* and *Cyphoproetus* has been figured by Whittington (1965, Pl. 19: 13,14,18) from the Table Head Formation (Llanvirn) of western Newfoundland. This specimen resembles both *Cyphoproetus* and *Otarion* in glabellar characters, and has a short (sag.) convex preglabellar field. *Otarion* has a rather longer (sag.) convex preglabellar field than this specimen, while *Cyphoproetus* typically has a short (sag.) preglabellar field, which is commonly straight in profile. Unfortunately this cranidium is too incomplete for detailed comparison, and the position of the palpebral lobe is unknown, but suggests that Proetidae A might have become separated from the Otarionidae early in the Ordovician. Bergström (1973:41–42) placed the Proetidae and Otarionidae in different orders — the Illaenida and Ptychopariida respectively. A major reason for this classification was because he claimed that Proetidae and Otarionidae exhibited different kinds of enrollment — sphaeroidal and spiral respectively. (For definitions of these, see Bergström 1973: 15). However, on examination of hundreds of enrolled specimens of *Otarion elegantulum* (Lovén, 1845) at the Naturhistoriska Riksmuseet, Stockholm in July 1973 we discovered that both types of enrollment were to be found in the sample, so in *Otarion*, the spiral enrollment would appear to be only a degree of sphaeroidal enrollment rather than a separate and distinct type. This character does not, therefore, preclude a close relationship between the Proetidae and Otarionidae, as Bergström would claim.

PROETIDAE B. — There is now evidence to suggest that Proetidae B were already well established by the late Arenig. Fortey has found cranidia and pygidia of a *Decoroproetus*-like species in the Arenig Tournmakeady Limestone of western Ireland (Fig. 1, D, E, F) and Mr. L. Karis (S.G.U. Stockholm) [verbal communication, July 1973] has found similar cranidia in the Kunda Formation (Arenig-Llanvirn) of Jämtland, Sweden, while Ross (1972, Pl. 16: 16) has figured a *Decoroproetus* pygidium (as 'proetid pygidium') from beds of Llanvirn age in Nevada. *Parapiithopolis* genereactus Hintze (1953, Pl. 7: 6–9) (which we consider to be a hystricurine), from the Lower Canadian of Utah, is strikingly similar to these early Proetidae B in many ways. The moderately inflated, unfurrowed glabella, the weakly convex, declined preglabellar field and the smooth dorsal surface are all features in common with the Tournmakeady cranidia, the principal difference being the larger palpebral lobe of the latter. The type of free cheek and the small, triangular rostral plate are also like those of *Decoroproetus* species. The length-breadth proportions and number and type of axial rings and pleural ribs are all similar to *Decoroproetus*,...
although the characteristic 'imbricate' pygidial pleural rib profile (Owens 1973b: 5, Fig. 2) is not fully developed.

The similarities between Decoroproetus, early Ordovician Decoroproetus-like species and Paraplethopeltis? gener erectus suggest a close link between Proetidae B and hystricurines. Other early species evidently belonging to Proetidae B are not easy to connect directly with the possible hystricurine-Decoroproetus line. Phaseolops sepositus Whittington (1963, Pl. 4: 11–13; Pl. 5: 1–6) from the White Rock (Llanvirn) of Newfoundland may represent a specialised reef-dwelling offshoot. One of the cranidia figured by Ogienko (in Abdullaev, Ogienko, & Semenova 1972, Pl. 55: 10) as Hystericurus secundus Ogienko does not belong to Hystericurus, but the globella shape and deep IP and 2P furrows are reminiscent of Xenocybe micrommata Owens (1973a, Fig. 14: G,H,J) from the Ashgill of Norway, which is a probable member of Proetidae B, but it differs from this species in its granulose surface sculpture (that of X. micrommata is striated). 'Phaseolops? sp. ind.' Whittington (1965, Pl. 19: 1–5) from the Table Head Formation (Llanvirn) of Newfoundland also bears a general resemblance to the cranidium figured by Ogienko, but has a smooth dorsal exoskeleton, and the occipital ring is narrowed laterally. Much more information on these early species is required in order to assess their affinities in more detail.

OTARIONIDAE AND AULACOPLEURIDAE

We agree with Bergström (1973: 42) that these two families are synonymous; the overall cephalic and pygidial morphology of Aulacopleura and Otarion is very similar, and the only major differences between the two genera are the greater number of thoracic segments, lack of the thoracic axial spine, and the presence of well developed eye ridges in the former. The obvious close relationship between the two genera makes a separation at familial level quite artificial.

Like proetids, aulacopleurids occur only in small numbers in the early Ordovician, but Otarion-like species are already present in the Arenig of the Montagne Noire, southern France (Dean 1966, Pl. 19: 11,13,14) and in the Arenig and early Llanvirn of Spitsbergen, western Ireland and Nevada, and Otarion spinicaudatum Shaw (1968, Pl. 4: 2–6,9–12,16–19) occurs in beds of Llandeilo age in New York State.
Several hystricurines show striking similarities to aulacopleurids. Most similar to *Otarion* is *Hystricurus paragenelatus* Ross (1951, Pl. 8: 14–16; Hintze 1953, Pl. 6: 12–14) from the Lower Canadian, zone B, of Utah. This species has a prelabellar field, weak IP labellar furrows (see Hintze 1953, Pl. 6: 14a–b), incurved lateral margin at the base of the genal spine and a granulose sculpture. Hintze (1953, Pl. 6: 23–26) figures pygidia (which are not assigned to a described species) from the same horizon and locality as cephalon of *H. paragenelatus*, and these, which are transverse with a small number of axial rings and pleural ribs and a weak border, are very similar to the pygidium of *Otarion* (cf. *Otarion* pygidia figured by Whittington & Campbell 1967, Pl. 8: 1–12,16–20,22–26). There can be little doubt that *H. paragenelatus* and the associated pygidia are closely related to *Otarion*. Less closely related hystricurines, but also very similar to *Otarion* in general aspect, include *Hystricurus genalatus* Ross (1951, Pl. 8: 1–13; Hintze 1953, Pl. 6: 1–6) from zones B–C of Utah, which has a small, triangular rostral plate like *Otarion*, but lacks IP furrows and does not have an incurved lateral cephalic margin at the base of the genal spine, and *Parahystricurus pustulosus* Ross (1951, Pl. 12: 17–32) from Middle Canadian, zone F of Utah (which lacks IP furrows). Such species, as well as *H. paragenelatus* are probably members of the hystricurine plexus from which *Otarion* arose. On present evidence, other Ordovician aulacopleurids such as *Panarchaeogonus* appear to be derived from *Otarion* species in Llanvirn/Llandeilo times (*O. spinicaudatum* Shaw, 1968 has moderate cephalic vaulting, a triangulate glabella and a *Panarchaeogonus*-like transitory pygidium, and might belong to the ancestral stock of *Panarchaeogonus*) rather than directly from hystricurines.

**BRACHYMETOPIDAE**

This is the only family within the Proetida to have originated in post-Early Ordovician times. Its earliest members are species of *Cordania* in the early Lower Devonian (Whittington, 1960), and the youngest are known from the late Carboniferous. The general aspect of the cephalon of *Cordania* (e.g. *C. falcata* Whittington 1960, Pl. 51: 8,11,14–18) is *Otarion*-like, but the rostral plate is much wider (trans.) and the thorax has less segments (nine opposed to eleven) and the pygidium is longer with more axial rings and pleuraI ribS. *Cordania* might have arisen from the aulacopleurids by the release of less segments from the pygidium during ontogeny, thus producing the longer pygidium and smaller number of thoracic segments, and by the increase in width of the rostral plate and thickening of the genal spine. In broad morphology, brachymetopids also resemble members of the subfamily Warburgellinae Owens, 1973b (Proetidae B) which became extinct in the early Devonian, so there is also the possibility that they might be related to them. In later brachymetopid genera — e.g. *Australosutura* (Amos, Campbell & Goldring 1960, Pl. 39: 10,11) the rostral plate widens laterally to occupy a major part of the cephalic doublure, thus departing from the typical small triangular rostral plate found in most Proetida. *Brachymetopus* also has a rostral plate like that of *Australosutura*, and the facial sutures become ankylosed, although the eyes are not reduced.

**GENERAs OF PROBLEMATICAL AFFINITIES**

**GLAPHURIDAE, CELMIDAE.** — The systematic position of the family Glaphuridae has presented a persistent problem. Ulrich (1930: 8) placed *Glaphurus* in the Telephinidae, and the glaphurids continued to be classified close to the telephinids in Hupé’s (1953: 200) classification and in the *Treatise*. Janausson (1956: 39) questioned the supposed telephinid-glap hurid relationship, pointing out that the small eyes and broad fixed checks of *Glaphurus* make a relationship to *Telephina* unlikely; this view was supported by Whittington (1963: 53). Whittington disagreed, however, with Janausson’s suggestion that the Glaphuridae might be related to the Upper Cambrian family Catillicephalidae, as this group of trilobites has median or connective sutures on the doublure which are lacking in *Glaphurus*; the large prominent glabella reaching the anterior border of the cranidium of catillicephalids also makes a relationship with *Glaphurus* unlikely. Nor is Henningsmoen’s (1951: 200) suggestion that the Glaphuridae might be related to the Odontopleuridae borne out by present knowledge of these two groups: despite a similar exoskeletal spinosity, the hypostomata and pygidia of the two groups are quite different (Shaw 1968, Pl. 7: 12,15,16), and glaphurids lack the inflated glabellar lobes characteristic of the Odontopleuridae.
We consider that the Glaphuridae belong within the Proetida, although differing in a number of features from other members of the order, and that the family is closely related to certain Dimeropygidae and to Celmus.

The genus *Ischyrophyma* Whittington, 1963 is a dimeropygid with relatively deep glabellar furrows, the posterior pair strongly backward curving and on some species (e.g. *I. deserta* Billings) — see Dean 1970, Pl. 1: 8) with inner ends isolated within the glabella. Whittington (1963: 49) points out the similarity of cephalic structure of *Ischyrophyma* and *Celmus* and attention may also be drawn to the similarity of the *Celmus* hypostoma (Jaanusson 1956, Fig. 2C) to that of *Ischyrophyma marmorea* Dean (Dean 1970: 8, Pl. 2: 10); examination of material of *Celmus granulatus* shows that these similarities extend as far as closely similar surface sculpture on the borders of the free cheeks of both genera. However, *Celmus* possesses a curious single-segment pygidium unlike that of a early Dimeropygidae such as *Ischyrotoma*, and apparently also that of *Ischyrophyma* (Dean 1970, Pl. 2: 2). Jaanusson (1956) placed *Celmus* in a separate family Celmidae. New silicified material of a species, probably best referred to *Celmus*, from the Tourmakeady Limestone, western Ireland, is shown on Fig. 1, A, B. The cranidial similarity of this species to *Ischyrophyma* is apparent in the sharply backward-deflected and distally deepened IP lateral glabellar furrows, position of the eye lobe, form of the facial suture and surface sculpture. The minute single segment pygidium possesses a pair of flanges similar to those on the pygidium of *C. granulatus* (Jaanusson 1956, Pl. 1: 7; Fig. 2D) and characteristic of *Celmus*. The origin of this unique pygidium may be understood if it is derived from that of a normal dimeropygid by release of anterior pygidial segments into the thorax. The pygidia of *Ischyrotoma* species (Hintze 1953, Pl. 19: 4,7,10) show a pair of prominent tubercles at the tip of the pygidial axis similar to those on the *Celmus* pygidium; release of two pygidial segments into the thorax from such a species as *Ischyrotoma ovata* (Hintze) would leave the terminal piece as a pygidium with a resemblance to that of *Celmus*. Given the other strong similarities between *Celmus* and the Dimeropygidae, it would seem very probable that the peculiar *Celmus* pygidium was connected with a comparable structure on the earliest dimeropygids; no other early Ordovician trilobite known to us has such a pair of nodes at the tip of the axis.

A similar relationship seems to pertain between *Glaphurus* and *Glaphurina* (Shaw 1968, Pl. 7: 18,12,15; Pl. 8: 3,10; Pl. 9: 3). *Glaphurus pustulatus* (Walcott) has ten thoracic segments

![Fig. 2. Possible relationships between some Dimeropygidae, Glaphuridae, and Celmus.](image-url)
and three pygidal segments, whereas *Glaphurina lamottensis* Ulrich has twelve thoracic segments and the pygidium reduced to a single segment. The hypostoma attributed by Shaw (1968, Pl. 7: 16) to *Glaphurus* is similar to that of both *Celmus* and *Ischyrophyma*. Dean (1970: 5) indicates that the posterior lateral glabellar lobes of *Ischyrophyma marmorea* are bicomposite, which Jaanusson (1956: 39) states is also true of *Glaphurina*. The well preserved craniad figured by Tjernvik (1956, Pl. 10: 20–21) as *Glaphurina? insolita*, from the early Arenig of Sweden may be more correctly referred to *Ischyrophyma* (Dean 1970:8) but resembles the craniad of *Glaphurina lamottensis* Ulrich in its general proportions, form of facial suture and size and position of the eye lobe (see also *Celmus? longifrons* Poulsen 1965, Pl. 6: 7–9).

A similar craniad has been described from the Middle Ordovician of Tien-Shan as *Glaphurina quadricornuta* Abdullaev (in Abdullaev, Ogienko & Semenova 1972:238, Pl. 55:1), and another similar species occurs in the Middle Ordovician of Kazakhstan, described as *Glaphurina dulanensis* by Chugaeva (1958, Pl. 8: 13–15).

*Glaphurus* lacks median or connective sutures (Whittington 1963, Pl. 8: 14); i.e. the free cheeks are fused to form a single unit connected by a relatively narrow strip of median doublure. While this is unlike most Proetida, the subfamily Mesotaphraspidinae Jaanusson (1956: 47) of the Dimeropygidae (including the genera *Mesotaphraspis*, *Chomatopyge* and possibly *Toernquistia*) shows exactly the same modification of the sutures. The rostral plate on such dimeropygids as *Ischyrotoma twenhofeli* Raymond (Whittington 1963, Pl. 7: 13) is extremely narrow (trans.) and it may be suggested that in the Mesotaphraspidinae and Glaphuridae, perhaps in response to a need to strengthen the anterior border of the cephalon, this narrow rostral plate was "lost" by ankylosis of the connective sutures. The similarity of early *Glaphurus* growth stages to those of other Proetida is discussed below.

The Glaphuridae, Dimeropygidae and *Celmus* thus seem to form a closely inter-related group. The differences between *Ischyrophyma* and *Glaphurina* cited by Dean (1970: 8) may be sufficient to justify the retention of the Glaphuridae as a separate family. It is to be anticipated that further discoveries in Tremadoc and Arenig strata will help to provide more definite phyletic links; Fig. 2 is an attempt to show possible connections between known genera. There is evidence to suggest that glaphurids were a distinct group as early as the Tremadoc (e.g. *Glaphurus alimbeaticus* Balashova, 1961), and the possibility of a separate origin for the glaphurid-*Ischyrophyma-Celmus* group from the hystricurines cannot be eliminated.

**PROBLEMATICAL PROETIDS.** — Besides those genera of uncertain affinities mentioned above (under Proetidae B), there is a small number of genera which are apparently proetids, which are difficult to relate to any established subfamilies. These include *Rorrintonia* Whittard (see Owens 1973b, Pl. 15:7–10) and *Analoaspis* Owens (1970: Fig. 8A–H) from the Caradoc, *Parvigena* Owens (1973a: Fig. 14: K–N) from the Ashgill, and *Pseudoproetus* Poulsen (1934, Pl. 3: 1–4) from the Llandovery. Of these, *Parvigena* might be a specialised "smoothed out" (morphological type (3), see below) proetid, but its pygidium is unknown, while the others all share certain characters in common — a forward-tapering, furrowed glabella, small eyes and pygidial pleural ribs with parallel, narrow pleural and interpleural furrows of similar depth — which suggest that they may all be related. *Protarchaeogonus* Sdzuy (1955, Pl. 7: 2–7) from the Tremadoc of Bavaria, Germany, which may be a hystricurine, shows glabellar and pygidial characters which are quite similar to *Analoaspis*, but there are no known similar trilobites in the intervening Arenig to Llandoilo.

Owens (1974) considers that the aberrant genus *Scharyia* (range Ashgill to high Middle Devonian) is probably related to *Panarchaeogonus* (see above, under Otarionidae and Aulacopleriidae).

**HYISTRICURINAES.** — Hystricurines can be accommodated within the concept of the Proetida. If the phyletic links described here are substantiated, separation of the Hystricurinae from the Proetida would seem to be excessively arbitrary, and there would seem to be no reason for excluding them from the order.

**ONTOGENY**

Similarities between early growth stages of the families under discussion have been noted by several authors. Whittington & Campbell (1967: 450,460) discussed the close similarity of
meraspide Otarion and Dimeropyge and considered Otarionidae and Dimeropygidae to be related. Chatterton (1971: 72), in a discussion of the ontogeny of Otarion (Otarion) dabrowi from the Devonian of New South Wales, further extended these comparisons to include Hystricurinae species figured by Ross (1951, Pl. 9: 17–19) and Hintze (1953, Pl. 6: 23–26). Chatterton postulated a common origin in the Hystricurinae for the Dimeropygidae, Otarionidae and Proetidae. Immature cranidia of the Middle Ordovician species "Phaseolops" conus Hu (1971, Pl. 23: 10–12), which is an aulacopleurid, are similar to those of the Devonian Otarionidae figured by Chatterton. Chatterton also (1971: 64) noted a resemblance between early Proetus growth stages and those of the bathyurid Linocephala cavigladius Hintze (Ross 1953, Pl. 64: 8,14). A comparison may also be drawn between small cranidia of Proetus platetus Whittington & Campbell (1967, Pl. 1: 21) and those of Bathyurellus nitidus Billings (Whittington 1963, Pl. 11: 8-10). A meraspis cranidium of Glaphurus sp. from the Tourmakeady Limestone ( Arenig), western Ireland, figured on Fig. 1,C shows marked similarities to early growth stages of Dimeropyge virginiensis (Whittington & Evitt 1954, Pl. 3: 24,28) in the trapezoidal outline of the cranidium, size and position of the palpebral lobes, fusiform glabella and distinct preglabellar field. IP glabellar furrows are developed on this small Glaphurus as on Proetus talenti Chatterton (1971, Pl. 14: 1a–b,2a–b) and Otarion spinicaudatum Shaw (1968, Pl. 4: 3). The immature Dimeropyge and Glaphurus cranidia are themselves closely comparable to small specimens of Parahystricurus fraudator Ross (1951, Pl. 12: 4).

Available ontogenetic information thus supports a phyletic relationship between hystricurines, aulacopleurids, proetids, bathyurids, dimeropygids and glaphurids. Because of their spinosity and smaller eyes small growth stages of Dimeropygidae and Hystricurinae tend to resemble one another more closely than those of the larger-eyed, smooth Bathyuridae and Proetidae. Proetida appear to bear opisthopharian sutures throughout all stages of ontogeny.
DIAGNOSIS

Members of the order Proetida possess a combination of the following characters:

(1) Medially transversely narrow rostral plate which generally tapers backwards (except cases outlined above). This feature in particular suggests that the Bathyuridae are related to the Proetidae rather than to the Illaenidae, which have broad rostral plates. Examples of rostral plates of Proetida are figured for Bathyuridae (Whittington 1963, Pl. 11: 15; Pl. 14: 8), Hystricurinae (Hintze 1953, Pl. 6: 1c), Dimeropygidae (Whittington 1963, Pl. 7: 13), Aulacopleuridae (Whittington & Campbell 1967, Pl. 6: 9), Proetidae (Owens 1973b, Pl. 3: 9; Pl. 15: 3) and Brachymetopidae (Amos, Campbell & Goldring 1960, Pl. 39: 10,11).

(2) Glabella well defined, commonly with a characteristic vaulted profile in anterior view. The front margin of the glabella is rounded on the mid-line, usually strongly so, coming almost to a point medially on many genera (*Bathyurellus*, *Mesotaphraspis*, some cyrtosymbolines s.l.).
(3) Glabellar furrows or muscle impressions (which are usually visible on well preserved material) with following characteristic form: 1P is invariably most strongly developed (longest and deepest), backward-curving; 2P, 3P and 4P are progressively smaller anteriorly, and may not themselves curve backwards.

(4) The occipital ring is normally well defined (exception: *Benthamaspis* (Bathyuridae)).

(5) Genal spines well developed — commonly blade-like — on most species, but may be reduced on some Silurian and later Proetidae, and a few Dimeropygidae.

(6) Eyes with semicircular outline, holocroal, medially or backwardly positioned, and usually of moderate size, although some species with small and some with large eyes are known, and in the Devonian some blind forms appear.

(7) Posterior sections of facial suture diverge at a moderate to high angle, anterior branches usually divergent, may be subparallel. (Exceptions: species with reduced eyes or blind; *Scharyia* with a cedarian posterior branch).

(8) Doublure of convex species usually recurved steeply beneath the border of the free cheek to form a lateral cephalic "tube".

(9) Thorax usually with 8–10 segments, but may be as few as 6 or as many as 22. Width of pleurae equal to or exceeding that of axis, thoracic segments in contact along their length; pleural furrows diagonal.

(10) Pygidium with strong pleural furrows and margin usually entire. (Exceptions, e.g. *Pseudoolenoides* (Bathyuridae) and *Phaetonellus* (Proetidae) develop spinose pygidial margins). Doublure with strong terrace lines.

(11) Hypostoma longer (sag.) than wide with elongate, oval middle body and one pair of relatively posteriorly situated middle furrows, borders narrow.

(12) Preglabellar field variously developed; species with short preglabellar field tend to have a granulose surface sculpture; those with a long (sag.) preglabellar field tend to have a surface sculpture of fine terrace lines.

**EVOLUTIONARY TRENDS AMONG THE PROETIDA**

The range of morphological diversity among the trilobites here considered to constitute the order Proetida may be summarised in terms of a few "end member" morphotypes which were attained many times in the evolution of the group. Similar morphological types were produced in the early Ordovician by the Bathyuridae that were attained in the later Ordovician to the end of the Palaeozoic by the Proetidae.

(1) *Bathyurus-Proetus* type. More convex trilobites with preglabellar field short or absent, strongly furrowed pygidium with convex pleural fields, "rolled" anterior border to the cranidium close to the glabella. Examples are *Proetus* and other Proetinae; *Bathyurus, Goniotelus* and Bathyuridae of the subfamily Bathyurinae Hupé 1953; *Dimeropyge, Ischyrotoma* from the Dimeropygidae.

(2) *Bathyurellus-Tropidocoryphe* type. Trilobites with a broad, gently downsloping preglabellar field, anterior border developed as a more or less horizontal plane. Pygidium typically of low convexity with sigmoidal pleural furrows and commonly relatively flattened border. Doublure wide and flat. Examples are *Decoroproetus, Tropidocoryphe* from Proetidae B and *Bathyurellus* and *Uromystrum* from the Bathyuridae. This morphological type commonly has surface sculpture of fine terrace lines.

(3) Species with large or relatively large eyes and relative obliteration of glabellar and axial furrows, "smoothed out" species. Relatively rare, but include the bathyurid *Benthamaspis*, the aulacopleurid *Isbergia* and the possible proetid *Parvigena*. 

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(4) *Aulacopleura* type. There is a multiplication of thoracic segments, which become narrow (sag. exsag.). Preglabellar field broad and pleural areas relatively wide compared with morphological types 1–3.

We consider many Proetida to have lived in shallow water, sometimes in "reef" environments. The morphological types 1–3 outlined above are believed to have been adaptations to particular ecological niches in the shallow water environment, niches which were occupied by different groups from the Ordovician to the Permian. Such ecological replacement is not far from the biotische concept of Palmer (1965). Proetida are found in greatest abundance in limestones, but are not confined to that lithology.

We believe that the *Aulacopleura* type, with its multiplication of thoracic segments and hence of thoracic appendages and "gill branches", may have been connected with a mode of life in deeper water, perhaps under relatively deoxygenated conditions giving them a superficial resemblance to olenids which have a comparable mode of life and which occur in similar lithologies. This resemblance has led to the classification of *Aulacopleura* with the olenids (Hupé 1953: 207). *Aulacopleura* is found for example in deeper water facies of the Liten Formation, Prague district, Czechoslovakia (Horný, Prantl & Vaněk, 1958), and is widespread elsewhere in Europe in similar facies—e.g. Holy Cross Mountains, Poland, (Tomczykowa 1957), Dalarne, Sweden (Törnquist, 1884). We consider that this overall flattened morphological type is unlikely to have been a vigorous swimmer.

**GEOLOGICAL HISTORY**

During the early Ordovician (Tremadoc-Arenig) the Bathyuridae rapidly diversified to display a wide range of morphological types (1–3 above) and are abundant as fossils in the shallow water limestones across North America and northeastern USSR. During this period the Proetidae and Aulacopleuridae remained a relatively insignificant part of the fauna. During mid-Ordovician times (Llanvirn-Llandeilo) the Bathyuridae slowly declined and there was a corresponding gradual increase in the diversity of the Proetidae and Aulacopleuridae, some of which have a close overall resemblance in size and in gross morphology to the earlier Bathyuridae (e.g. *Tropidocoryphe* to *Bathyurellus*). In the late Ashgill (e.g. in the Boda Limestone reefs) there was a great increase in diversity of proetids, particularly Proetidae B. Throughout the Ordovician the Dimeropygidae (and Aulacopleuridae from the Caradoc onwards) remained a constant but never dominant element of shallow water faunas. Proetida appear to be almost confined in the Ordovician to areas outside the *Selenopeltis* Province; i.e. if the interpretation of Whittington & Hughes (1972) is correct, they evidently eschewed cold water regions. Throughout the Ordovician, Proetida seem to be found only in shallower water deposits.

In the Silurian, the rate of diversification of Proetidae B gradually increased and that of the Aulacopleuridae remained more or less constant, but *Aulacopleura* (Morphological type 4) was the first representative of the order to colonise a deep water environment, in which it appears to have remained until its extinction in the mid-Devonian. In the later Silurian there was an increase in the rate of diversification of Proetidae A, when many important Devonian lines were established in shallow water environments, particularly in reefs such as those developed in Gotland.

The Devonian marked a further expansion in the importance of the Proetida, and the order became a major constituent of trilobite faunas for the first time since the early Ordovician, and along with the Phacopida dominated Devonian trilobite faunas. Proetida presumably filled niches vacated by other trilobites declining at the end of the Silurian. This is accompanied by major speciation and by the further development of many minor modifications of morphological types 1 and 2 above, and many different lines in both Proetidae A and B achieved similar basic morphology, particularly of type 1, by convergent evolution (e.g. Cornuproetinae and Eremitroetinae among Proetidae B and Proteinae among Proetidae A). In the later Devonian and in the earlier Carboniferous two major groups of Proetida occur (Prentice 1967, p. 209): the deeper water was colonised by thin-shelled small-eyed or blind forms (mostly members of the polyphylectic Cyrtosymbolinae, some of which belong to Proetidae A), while thicker-shelled, commonly granulose, larger-eyed forms (all Proetidae A) occupied the shallow water environment.

The Proetidae are the only trilobites to survive into the Carboniferous and Permian, where they are represented by Proetidae A (in shallow and deep water), Aulacopleuridae and Brachymetopidae (in shallow water only). Proetidae A are represented by the polyphylectic 'phillipsiids', which were probably derived by several lines from the Proteinae and Schizoproetinae, and by cyrtosymbolines. many members of which were probably derived from the Dechenellinae.
deep water genera all became extinct by mid-Carboniferous times, while the shallow water genera, which underwent diversification in the early Carboniferous, and apparently again in the late Carboniferous and early Permian (Hahn & Hahn 1967, Chamberlain 1969) persisted, sometimes in abundance, and particularly in reef environments, until the end of the Permian. Some genera, such as *Paladin*, may have replaced Phacopida in certain niches, as there is some parallel development in expansion and inflation of the frontal lobe of the glabella and in "basisolution" (Richter, Richter & Struve in Moore 1959, p. O383) of the posterior part of the glabella.

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